DOCKETED

Docket Number:	09-AFC-07C
Project Title:	Palen Solar Power Project - Compliance
TN #:	200061
Document Title:	CBD's Comments on PSA Final - Attachment 5
Description:	Epps et al. 2004. Effects of CC on pop persistence of desert dwelling mtn. sheep in CA
Filer:	Sabrina Savala
Organization:	Center for Biological Diversity
Submitter Role:	Intervener
Submission Date:	7/29/2013 2:53:52 PM
Docketed Date:	7/29/2013

Contributed Papers

Effects of Climate Change on Population Persistence of Desert-Dwelling Mountain Sheep in California

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Abstract: *Metapopulations may be very sensitive to global climate change, particularly if temperature and precipitation change rapidly. We present an analysis of the role of climate and other factors in determining metapopulation structure based on presence and absence data. We compared existing and historical population distributions of desert bighorn sheep (*Ovis canadensis*) to determine whether regional climate patterns were correlated with local extinction. To examine all mountain ranges known to hold or to have held desert bighorn populations in California and score for variables describing climate, metapopulation dynamics, human impacts, and other environmental factors, we used a geographic information system (GIS) and paper maps. We used logistic regression and hierarchical partitioning to assess the relationship among these variables and the current status of each population (extinct or extant). Parameters related to climate—elevation, precipitation, and presence of dependable springs—were strongly correlated with population persistence in the twentieth century. Populations inhabiting lower, drier mountain ranges were more likely to go extinct. The presence of domestic sheep grazing allotments was negatively correlated with population persistence. We used conditional extinction probabilities generated by the logistic-regression model to rank native, naturally recolonized, and reintroduced populations by vulnerability to extinction under several climate-change scenarios. Thus risk of extinction in metapopulations can be evaluated for global-climate-change scenarios even when few demographic data are available.*

Key Words: climate change, extinction, hierarchical partitioning, metapopulation, *Ovis canadensis*

Efectos del Cambio Climático sobre la Persistencia de la Población de Borrego Cimarrón en California

Resumen: *Las metapoblaciones pueden ser muy sensibles al cambio climático global, especialmente si la temperatura y precipitación cambian rápidamente. Presentamos un análisis del papel del clima y otros factores en la determinación de la estructura de la metapoblación con base en la presencia y ausencia de datos. Comparamos las distribución actual e histórica de la población de borrego cimarrón del desierto (*Ovis canadensis*) para probar si los patrones climáticos regionales estaban correlacionados con la extinción local. Utilizamos un Sistema de Información Geográfica (SIG) y mapas para examinar todas las cordilleras que tienen o tuvieron poblaciones de borregos en California y calificar variables que describen el clima, la dinámica metapoblacional, los impactos humanos y otros factores ambientales. Utilizamos regresión logística y partición jerárquica para evaluar la relación entre estas variables y el estado actual de cada población (extinta o existente). Los parámetros relacionados con el clima (elevación, precipitación y presencia de manantiales confiables) estuvieron poderosamente correlacionados con la persistencia de la población en el siglo veinte. Las poblaciones en cordilleras bajas y más secas tuvieron mayor probabilidad de extinción. El pastoreo de borregos*

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Paper submitted January 17, 2002; revised manuscript accepted April 18, 2003.

domésticos se correlacionó negativamente con la persistencia de la población. Utilizamos las probabilidades de extinción condicionales generadas por el modelo de regresión logística para clasificar a las poblaciones nativas, recolonizadas naturalmente y reintroducidas por su vulnerabilidad a la extinción bajo varios escenarios de cambio climático. Así, el riesgo de extinción en metapoblaciones puede ser evaluado para varios escenarios de cambio climático aun cuando sólo se disponga de pocos datos demográficos.

Palabras Clave: cambio climático, extinción, metapoblacione, *Ovis canadensis,* partición jerárquica

Introduction

Current climate-change scenarios predict an increase in global air temperature of 1.1–3.3° C over the next century (Houghton 1996; Field et al. 1999). Warmer temperatures during the last 30 years have affected the function and composition of ecological communities and the phenology and distribution of many species (Walther et al. 2002). Population declines and local and global species extinctions have also been linked to this warming trend (McCarty 2001).

As climate warms, vegetation communities shift in composition or distribution. High-elevation plant communities decrease in area, fragment, or vanish (Peters & Darling 1985). Species with fragmented distributions and low dispersal capability may be particularly vulnerable because dispersal to new sites may be limited (Walther et al. 2002). Therefore, species distributed in metapopulations (Levins 1969, 1970) may be at high risk. Climate change that decreases habitat quality or area may increase local extinctions and decrease the number of available habitat patches, conditions that can lead to extirpation of a metapopulation before all habitat becomes unsuitable (Hanski 1999). Moreover, environmental stochasticity or environmental change is usually regionally correlated, which reduces metapopulation size and persistence time (Levins 1969; Hanski 1999). We present an analysis of populations of desert mountain sheep (*Ovis canadensis nelsoni*, as defined by Wehausen & Ramey 1993, 2000) that demonstrates a simple and general way to analyze metapopulation response to climate-related environmental variation using relatively sparse data.

Desert mountain sheep, hereafter referred to as desert bighorn sheep, are desert-adapted ungulates with small population sizes, low dispersal rates (Geist 1971), and naturally fragmented distributions often characterized as metapopulations (Schwartz et al. 1986; Bleich et al. 1990; Bleich et al. 1996). Desert bighorn sheep inhabit numerous, but often small and isolated, desert mountain ranges throughout the Sonoran, Mojave, and Great Basin deserts of the southwestern United States. A few populations are also found in the more mesic Transverse and Peninsular mountain ranges of southwestern California. Most populations of desert bighorn sheep are small, with 41 of 56 extant populations in the state of California estimated at fewer than 100 individuals in 1993 (Torres et al. 1994).

Desert sheep are well adapted to xeric conditions (Hansen 1982), persisting as the climate of the southwestern United States has become increasingly arid since the end of the Wisconsonian glacial period (Van Devender & Spaulding 1979; Spaulding 1990). However, recent regional trends in warming and drying have been particularly severe. From 1901 to 1987, mean annual temperature in the deserts of the southwestern United States increased 0.12° C per decade (Lane et al. 1994). Annual precipitation decreased by roughly 20% over the last century in southeastern California, one of the largest such decreases in the United States (Ball et al. 1998). Because drought can cause increased mortality among desert bighorn sheep (Monson 1960), affect recruitment dynamics (Wehausen et al. 1987), and has perhaps led to population extinction in several cases (Weaver & Mensch 1971), the distribution of desert bighorn sheep may already have been affected by these climatic trends.

Biologists have attempted to estimate the presence and size of bighorn sheep populations within California since 1940, and in some cases earlier records exist (Torres et al. 1994; Wehausen 1999). Although imperfect, this data set presented an opportunity to examine the role of spatial and temporal climatic variation and other factors in the population persistence of desert bighorn sheep. Historic and current population sizes have been estimated variously from ground, waterhole, and helicopter surveys (Torres et al. 1994). The nature and quality of these inventories have varied, but partial population inventories were compiled in 1940, 1946–1948, 1957, 1970–1974, 1979–1985, 1994, and 2002 (Wehausen 1999). Significant population turnover was observed: about 30 of 80 populations of desert bighorn sheep have gone extinct in California during the last 60 years, with an estimated 4300 desert bighorn sheep remaining by 1993 (Torres et al. 1994). Desert bighorn sheep have been reestablished in seven mountain ranges by translocation (Torres et al. 1994) (Fig. 1). Three apparent natural recolonizations have been observed in recent years. It is possible that additional extinctions and subsequent recolonizations were undetected between survey periods.

Additional Causes of Population Extinction

Factors other than climate must be considered in any systematic analysis of turnover of bighorn sheep populations.

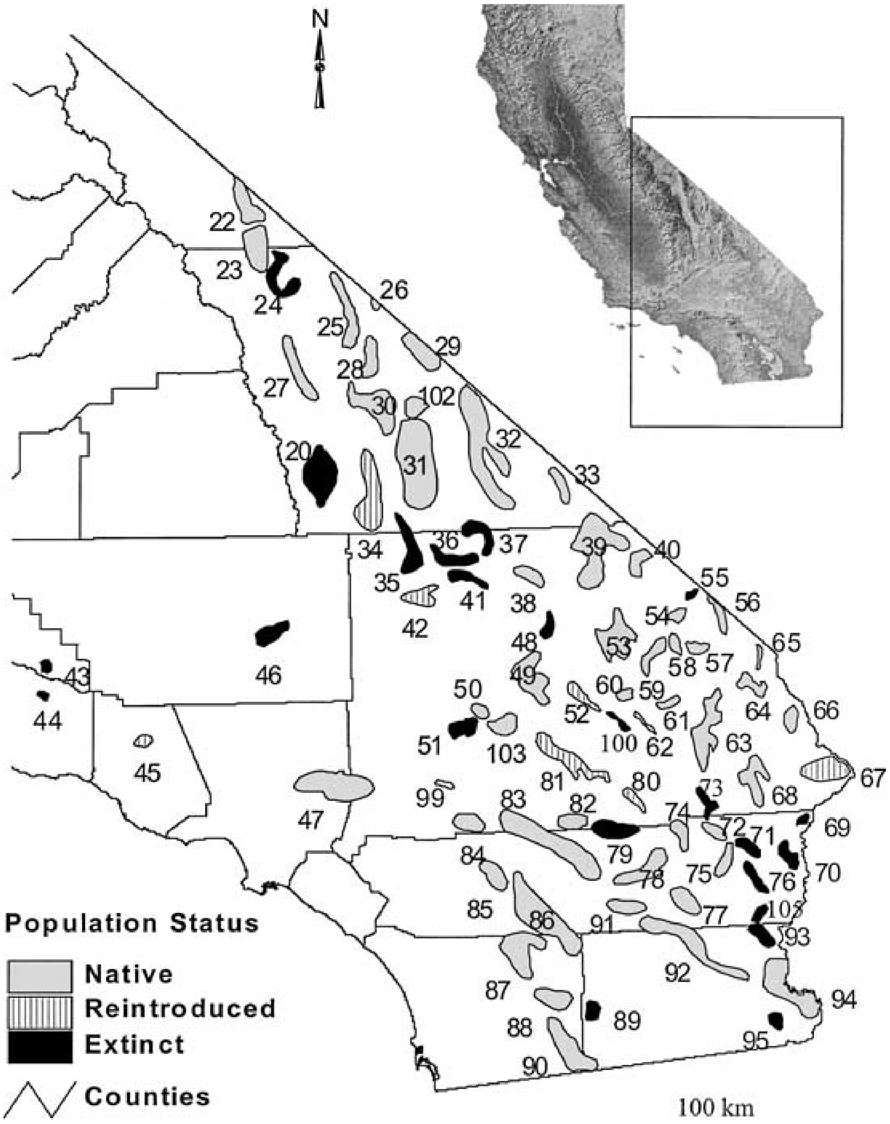

*Figure 1. Native, relocated, and extinct populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in California (from Torres et al. 1994). Numbers are those assigned to the ranges of the populations demarcated by the polygons.*

Many of these factors are related to patterns of historical and current human use. Contact with livestock is detrimental to bighorn sheep because of competition for forage (Hansen 1982) and disease transmission, particularly from domestic sheep (Foreyt & Jessup 1982; Jessup 1985). Feral burros may contribute to the decline of bighorn populations by destroying water holes and competing for forage (Buechner 1960; Hanley & Brady 1977; Dunn & Douglas 1982), but there has been little quantification of subsequent reductions in bighorn numbers (Welles 1962; Jones 1980). Poaching and unregulated hunting have historically reduced populations (Buechner 1960), particularly in areas where mining occurred (Graham 1980), but poaching probably has had little impact in recent times (Weaver 1982). Nonetheless, development and general use of bighorn habitat by humans remains a concern in specific areas (Papouchis et al. 2001; Rubin et al. 2002).

Small population size has been considered an important but controversial predictor of population vulnerability of desert bighorn sheep, although the reasons for variation in population sizes have not been considered (Berger 1990; Krausman et al. 1993, 1996; Goodson 1994; Wehausen 1999). There is little argument, however, that population size is a potentially important factor in population persistence (Caughley 1994). Both Berger (1990) and Wehausen (1999) concurred that small populations of these unique ungulates were more vulnerable to extinction than large ones.

Hypotheses

We predicted that the probability of population extinction of desert bighorn sheep in California would be inversely correlated with climatic factors (temperature and precipitation) that increase annual nutrient availability and with the presence of predictable surface water, which helps desert bighorns survive periods of severe drought. Elevation was used as a surrogate for temperature because of the lack of detailed spatial data on temperature, although it is also correlated with precipitation. Furthermore, elevation can be easily measured in other systems where detailed spatial information on climate is not available. Although numerous human-made water sources have been made available to desert bighorn in California (Bleich & Pauli 1990), we limited analyses to natural water sources as a better reflection of water availability during most of the twentieth century.

We evaluated several other hypotheses concerning the distribution of desert bighorn sheep in California. In most metapopulation patch models, extinction probability decreases with increasing patch area (Hanski 1991, 1997). Extinction probability also decreases with increasing immigration, which, in turn, depends largely on interpatch distance (Levins 1969, 1970; Hanski 1991, 1997). Therefore, we tested the following hypotheses: (1) extinct populations inhabit ranges with smaller two-dimensional area than ranges with extant populations, and (2) extinct populations are more isolated from other mountain ranges containing bighorn habitat than are extant populations.

We evaluated additional plausible influences on desert bighorn sheep persistence to control for possible correlation with climate-related variables. These included geological variation, presence of domestic and feral livestock, and measures of human use of bighorn habitat. Finally, after exploring how regional climatic variation affected population extinction, we used the global-climate-change scenario described by Field et al. (1999) to simulate how the risk of extinction for remaining populations might change over the next century.

Methods

Spatial Analysis of Population Extinction

We scored 80 mountain ranges with extinct or extant populations of desert bighorn sheep in California for average annual precipitation, elevation, isolation, area, presence of dependable natural springs, geologic parent material, domestic sheep and cattle allotments, presence of feral horses and burros, deposits of precious metals, cities and towns, and vehicle access (Table 1). We converted all data from the geographic information system (GIS) to raster format in Universal Transverse Mercator (UTM) projection units and overlaid them on the population map (Torres et al. 1994). Data not based on the GIS were recorded only as presence or absence.

To determine which ranges to include, we updated a GIS map of desert bighorn sheep populations (Fig. 1) compiled by Torres et al. (1994) with population lists from Wehausen (1999). The rough population polygons (Torres et al. 1994) generally were based on the basal contours of each range and were usually defined as areas of contiguous mountainous terrain, separated from other populations by areas of flat desert or low relief. Because dispersal between mountain ranges is extremely limited (Ramey 1995), these populations function largely as independent demographic units. The Mule Mountains (Fig. 1, no. 105) were added to the list based on evidence of beds and fairly heavily used trails (R. Weaver, personal communication).

Elevation and precipitation scores were the map-grid cells with the highest value overlapping each population polygon. Bighorn sheep move easily within mountain ranges and thus can select the best conditions within the area; hence, the highest precipitation and elevation values probably best reflect the range of habitat available for use. We determined the presence of dependable springs by interviewing experts on desert water in bighorn sheep habitat in California (Table 1) and consulting reports on wildlife-accessible desert water sources (Weaver et al. 1968, 1969, 1972; Weaver & Mensch 1970*a*, 1970*b*, 1970*c*, 1971; Weaver & Hall 1971*a*, 1971*b*, 1972, Weaver 1972). For each mountain range, we compiled a list of springs that do not dry up even during extended drought.

We estimated isolation for each mountain range by taking the harmonic mean of the distance from the edge of each population polygon to the edge of the nearest three population polygons (Harrison & Ray 2002) (Table 1). Area was calculated directly from the GIS population polygons.

We scored geologic parent material because the geology of bighorn habitat in the Mojave and Sonoran deserts of California is diverse, and the type and quality of vegetation is often influenced by parent material (Barbour et al. 1980). Resulting variation in forage could affect the persistence of bighorn sheep populations. We examined the percent area of volcanic or granite parent material and the presence or absence of limestone in each range.

We used information from the California Desert Conservation Area (CDCA) plan (Bureau of Land Management 1980) to test whether population extinctions were more common when cattle or domestic sheep grazing allotments, feral burros and horses, and mineral deposits suitable for mining were present in bighorn sheep ranges since population inventories began around 1940. The presence of mineral deposits suitable for mining was the best available index of mining activity, thought to conflict with bighorn sheep as a result of poaching by miners in the earlier periods and habitat destruction (Buechner 1960). We interviewed range and wildlife biologists for the U.S. Forest Service, Bureau of Land Management, Deep Canyon Reserve, and San Diego Zoo (S. Loe, B. Brown, M. Frael, A. Muth, & E. Rubin, personal communications) to score mountain ranges not described in the CDCA plan (Fig. 1, nos. 43, 44, 45, 47, 84, 85, 86, 87, 88, 89, 90, 99). We also determined whether degree of road access and

Table 1. Parameters included in logistic-regression analyses of extinction of desert bighorn sheep populations[a] in California.

Parameter	*Descriptive statistic*	*Data type/description[b]*	*Source[b]*
Precipitation	maximum value in each population polygon	GIS/isohyets of average annual precipitation 1900–1960, 400+ ha resolution	UCLA/Teale Data Center[c]
Elevation	maximum	GIS/3-arc-second digital elevation models, 90 m resolution	UCLA/Teale Data Center
Dependable springs	presence/absence	interviews/experts on wildlife water sources in California	G. Sudmeier (SCBS); R. Weaver (CDFG, retired)
Granite	area (%)	GIS/"Geologic Map of the United States"	King & Beikman 1974
Volcanic rock	area (%)	GIS/"Geologic Map of the United States"	King & Beikman 1974
Limestone	presence or absence	paper/1:250,000 scale geologic maps of California	Jenkins 1958
Isolation	harmonic mean of distance to nearest 3 populations	GIS/"Status of Bighorn Sheep in California, 1994"	Torres et al. 1994
Area	polygon area	GIS/"Status of Bighorn Sheep in California, 1994"	Torres et al. 1994
Distance to towns/cities	minimum distance from sheep polygons	GIS/urban areas (1990 census)	UCLA/Teale Data Center
Mining	presence or absence of "economically viable mineral deposits"	paper/map 11, "Economic Mineral Resources"	BLM 1980
Road access (ordinal)	closed (1), approved roads (2), existing roads (3)	paper/map 10, "Motorized-Vehicle Access"	BLM 1980
Feral burros and horses	presence or absence	paper/map 8, "Wild Horse and Burro Management Area"	BLM 1980
Cattle	presence or absence of grazing allotments	paper/map 9, "Livestock Grazing Allotments"	BLM 1980
Domestic sheep	presence or absence of grazing allotments	paper/map 9, "Livestock Grazing Allotments"	BLM 1980

[a] *Population polygons were drawn by Torres et al. (1994) using the basal contour of each mountain range inhabited or formerly inhabited by desert bighorn sheep.*

[b] *Abbreviations: BLM, Bureau of Land Management; CDFG, California Department of Fish and Game; GIS, geographic information system; SCBS, Society for Conservation of Bighorn Sheep; UCLA, University of California, Los Angeles (mirror site of Teale Data Center, Web site: http://gisdb.cluster.ucla.edu:3080/)*

[c] *Stephen P. Teale Data Center, Web site: http://www.gis.ca.gov/*

minimum distance to towns and cities correlated with extinction (Table 1). We assumed that these measures provided an index of general human activity and that current vehicle access (closed or restricted to varying degrees) reflects historical patterns of use.

Logistic Regression and Model Selection

We combined all parameters in logistic-regression models using an approach similar to that of Sjögren-Gulve and Ray (1996). The response parameter categories were "extinct" or "native" population status. We treated all reestablished populations as extinct because reintroductions (translocations through direct human intervention) and natural recolonizations (Fig. 1, nos. 24, 73, 100) took place in ranges where population extinctions occurred previously. We calculated log-likelihood and chi-squared values using JMPstart (Sall & Lehman 1996).

We tested the univariate model for each parameter and determined that Pearson correlations between all parameters were <0.7, as recommended by Hosmer and Lemeshow (2000) (Table 2). Initially, we explored biologically relevant interaction terms between the variables but found little support for further testing.

We used $QAIC_c$, a modified version of Akaike's information criterion (AIC) (Burnham & Anderson 1998), for model selection. This statistic corrects for small sample size relative to the number of estimated parameters and for an overdispersion factor between 1 and 4. Overdispersion was estimated as 3.9 from the likelihood-ratio chi-squared value and degrees of freedom of the global model including all 14 parameters (Burnham & Anderson 1998) and may result from correlated environments among adjacent populations. We grouped parameters by category of hypothesis (climate, geology, metapopulation, domestic or feral livestock, and human use) into models and compared $QAIC_c$ values with univariate and global models. We then combined parameters with strong effects in additional models.

After identifying a series of competing best models, we used hierarchical partitioning to assess the independent and joint effects of each parameter in a single model with all parameters included in the best models (Chevan & Sutherland 1991). Hierarchical partitioning serves as an additional control for multicollinearity and uses a measure of model fit to separate the independent and joint contributions of each parameter by comparing the fit of all models containing a particular parameter to all corresponding

Table 2. Correlation of parameters in global logistic-regression model of desert bighorn sheep population extinction.

Variable	*Elev.*	*Spr.*	*Grn.*	*Volc.*	*Lim.*	*Iso.*	*Area*	*City*	*Mine*	*Road*	*Bro.*	*Ctl.*	*D.Shp.*
Precipitation	0.65*	0.33*	0.03	−0.21	0.20	0.34*	0.16	−0.36*	−0.05	−0.12	−0.18	0.23*	0.43*
Elevation (Elev.)	—	0.47*	0.07	−0.22	0.49*	0.06	0.35*	−0.09	0.18	−0.22	0.16	0.39*	0.21
Springs (Spr.)		—	−0.03	0.08	0.04	0.08	0.27*	−0.04	0.09	−0.26*	0.14	0.23*	0.21
Granite (Grn.)			—	−0.28*	0.01	−0.04	0.04	−0.22	−0.02	0.04	−0.24*	0.21	−0.02
Volcanic (Volc.)				—	−0.16	−0.06	−0.12	0.30*	−0.18	0.08	0.10	0.10	−0.08
Limestone (Lim.)					—	−0.07	0.18	0.03	0.29*	0.10	0.19	0.33*	0.03
Isolation (Iso.)						—	−0.05	−0.18	0.15	−0.13	−0.15	−0.09	0.66*
Area							—	−0.32*	0.21	−0.10	0.05	0.03	0.06
City distance (City)								—	0.23*	−0.01	0.30*	0.16	−0.17
Mining (Mine)									—	0.13	0.21	0.09	0.04
Road access (Road)										—	0.08	0.05	−0.08
Burros/horses (Bro.)											—	0.08	−0.08
Cattle (Ctl.)												—	−0.04
Domestic sheep (D.Shp.)													—

**Significant Pearson correlation,* $p < 0.05$.

models without that parameter. This allows greater confidence that the action of a parameter is not masked in the model by coaction with other parameters (Chevan & Sutherland 1991; Mac Nally 1996, 2000). We used the likelihood-ratio chi-squared statistic for each model as the measure of fit to be hierarchically partitioned (Chevan & Sutherland 1991; Mac Nally 1996). The likelihood chi-squared statistic compares the log-likelihood of the model to that of the reduced model with predictor variables removed (Sall & Lehman 1996). Larger values indicate a better fit.

We used parameters included in the competing best-fit models to evaluate extinction probabilities for all native, naturally recolonized, and reintroduced populations for the next 60 years: the mean and modal times of earliest population estimates for all desert bighorn sheep populations in California were 63 and 60 years, respectively. Logistic-regression models give the probability of transition between response variables for each observation (Sall & Lehman 1996) and therefore can be used to calculate the conditional extinction probabilities for each population with regard to factors considered in the model (Sjögren-Gulve & Ray 1996). To assess future risk to native and reintroduced populations, we calculated extinction probabilities (E) as

$$E_i = \frac{e^{(a+bx_i+cy_i+dz_i)}}{1+e^{(a+bx_i+cy_i+dz_i)}}, \tag{1}$$

where a is a constant, b, c, and d are the parameter estimates for the ith population, and x, y, and z are the corresponding predictor variables.

Using the Extinction Model to Evaluate Climate-Change Scenarios

We modeled how population extinction of desert bighorn sheep in California may change with decreasing precipitation (Ball et al. 1998) and increasing temperature (Field et al. 1999) over the next 60 years by using observed relationships with climate-related variables in the final best-fit extinction models. We used the same model chosen for hierarchical partitioning. A warming trend in climate results in a given average temperature occurring at a higher elevation, and organisms with minimum elevation requirements will be found at higher elevations (e.g., Grabherr et al. 1994). To simulate this, we regressed average maximum daily temperature on elevation from 21 weather stations throughout the study area against station elevation (over station history, usually from about 1940 to present) to calculate the adiabatic lapse rate, or rate at which temperature changes with elevation. Bighorn sheep are largely diurnal, and average daily maximum temperature better reflects the extreme temperatures encountered in daytime during foraging and watering. Further, elevation was most correlated with maximum temperature.

We converted 100-year estimates for future temperature change (Field et al. 1999) to 60-year estimates by assuming a linear rate of change. Using the adiabatic lapse rate, we translated the minimum and maximum predicted temperature changes into "losses" in elevation. We subtracted these elevation losses from each population's elevation score. To simulate a further decrease in precipitation, as was observed in the twentieth century in the study area (Ball et al. 1998), we decreased each precipitation score by 12% (60% of the observed 20% change). Finally, using the chosen best-fit extinction model, we used the modified precipitation and elevation scores to recalculate extinction risk for each population.

Results

Causes of Extinction

The AIC testing revealed three competing models within two ΔQAIC units of the best model, which contained

Table 3. Logistic-regression models of bighorn sheep population extinction in California, with log-likelihood values, number of parameters (*k*) including model parameters, intercept, and residual variance (Burnham & Anderson 1998:17), and $QAIC_c$ values.[a]

Rank	*Model*	*Log likelihood*	*k*	$QAIC_c$	$\Delta\ QAIC_c$
1	precipitation, elevation, sheep	−29.67	5	25.87	0.00*
2	precipitation, springs, sheep	−30.56	5	26.33	0.46*
3	precipitation, elevation, springs, sheep[b] (climate + sheep)	−28.48	6	27.61	1.74*
4	elevation, springs, sheep	−33.12	5	27.63	1.75*
5	elevation	−46.79	3	30.08	2.46
6	water	−47.71	3	30.55	2.93
7	sheep	−48.11	3	30.75	3.14
8	area	−49.82	3	31.62	4.01
9	cattle	−49.99	3	31.71	4.09
10	limestone	−50.80	3	32.12	4.50
11	mining	−51.14	3	32.29	4.68
12	precipitation	−51.31	3	32.38	4.76
13	isolation	−51.59	3	32.52	4.90
14	volcanic	−52.44	3	32.95	5.33
15	burro	−52.50	3	32.98	5.37
16	granite	−52.79	3	33.13	5.51
17	city distance	−52.79	3	33.13	5.52
18	limestone, sheep	−45.43	4	31.61	5.73
19	road access	−50.27	4	34.06	6.45
20	isolation, area, sheep (metapopulation + sheep)	−42.74	5	32.52	6.64
21	isolation, area (metapopulation processes)	−48.55	4	33.19	7.31
22	burro, cattle, sheep (domestic, feral livestock)	−44.95	5	33.64	7.76
23	precipitation, elevation, springs (climate)	−45.00	5	33.67	7.79
24	city distance, roads, mining, sheep (human use + sheep)	−39.75	7	32.47	9.88
25	granite, volcanic, limestone, sheep (geology + sheep)	−44.98	6	36.00	10.12
26	granite, volcanic, limestone (geology)	−50.52	5	36.47	10.59
27	city distance, road access, mining (human use)	−47.51	6	37.28	11.40
28	global model (all parameters)	−23.39	17	55.75	29.87

[a] *Models are ranked by $\Delta QAIC_c$ values (a modified version of Akaike's information criterion); competing models with $\Delta QAIC_c$ values of <2 are marked with an asterisk.*

[b] *Model used for hierarchical partitioning and climate simulations. Coefficients are 11.497549 ± 0.55382193 (negative if dependable natural springs are present) ± 7.2903257 (positive if domestic sheep grazing is present) $- 0.0161136 * \text{precipitation} - 0.0015005 * \text{elevation}$ (see Eq. 1 and Results).*

the parameters of maximum average annual precipitation, maximum elevation, and presence of domestic-sheep grazing allotments (Table 3). The three competing models included the presence of dependable springs, the presence of domestic-sheep allotments, and either maximum annual precipitation, maximum elevation, or both (Table 3). Extinction was negatively correlated with precipitation, elevation, and dependable springs but positively correlated with the presence of domestic-sheep grazing allotments. We chose to use model 3 (Table 3) for hierarchical partitioning and climate simulations because it included all the parameters in the three competing models.

Hierarchical Partitioning of Parameters

Hierarchical partitioning of model 3 (Table 3) revealed that all four parameters retained in the four best competing models had reasonably large independent effects (Table 4). The action of elevation was largely independent. The presence of dependable springs had the weakest independent effect on the model and a large, positive joint effect, indicating that its action in the model was due in part to a high correlation with precipitation and elevation (Table 2). The presence of domestic-sheep allotments had a large negative joint effect, as did precipitation (Table 4). A likely interpretation is that the presence of domestic-sheep allotments was strongly correlated with precipitation but acted in opposition to it with regard to extinction (Table 2): domestic sheep are primarily grazed in the wetter ranges that otherwise favor the persistence of bighorn sheep populations.

Modeling Climate Change

Elevation explained 94% of the variation in average maximum daily temperature at 21 weather stations throughout the study area ($p < 0.0001$) but only 58% of the variation in minimum daily temperature ($p < 0.0001$). Using the regression of maximum daily temperature on elevation, maximum daily temperature $= -0.0078 *$ (meters elevation) $+ 31.687$, we calculated the adiabatic lapse rate (rate at which temperature changes with elevation) as 7.8° C/1000 m of elevation. A mean global temperature increase of 0.7° C over the next 60 years (60% of a 1.1° C

Table 4. Hierarchical partitioning* of third-ranked extinction model of desert bighorn sheep populations in southeastern California, containing maximum annual precipitation, maximum elevation, presence of dependable natural springs, and presence of domestic sheep allotments.

	Precipitation	*Maximum elevation*	*Dependable springs*	*Domestic sheep*
Parameter alone	3.23	12.28	10.43	9.61
Independent effects	7.92	9.80	6.76	24.42
Total independent effects (%)	16	20	14	50
Joint effects	−4.69	2.48	3.67	−14.81
Total joint effects (%)	18	10	14	58

**Hierarchical partitioning uses likelihood ratio* χ^2 *statistics from logistic regression models as a measure of model fit, and using all possible combinations of models with any of the above four parameters assesses the independent contribution of each variable to model fit. Negative joint effects indicate that a variable acts in opposition to or "suppresses" other variables. The sum of the independent and joint effects for each parameter equals the* χ^2 *statistic of the univariate model for that parameter.*

increase over the next century) thus translates to a "loss" of 85 m elevation in our climate-change simulations. An increase of 2.0° C over the next 60 years translates to a loss of 254 m. We assumed no change in the availability of surface water and set all domestic-sheep allotment scores to "zero" because domestic-sheep allotments are generally no longer permitted on desert bighorn habitat (K. Allison, personal communication).

In the minimum temperature-change scenario of +0.7° C in the next 60 years (Field et al. 1999), average extinction probabilities of native populations increased only slightly, from 0.21 to 0.22. However, in the maximum temperature-change scenario of +2.0° C in the next 60 years, average risk of extinction increased substantially to 0.26. Extinction risk also increased drastically when precipitation was reduced, such that a 0.7° C increase combined with a 12% decrease in precipitation elevated extinction probabilities to levels observed with a 2.0° C increase with no change in precipitation. Average extinction risk increased from 0.21 (no change) to 0.30 when a 2.0° C increase was combined with a 12% precipitation decrease.

Discussion

Elements in the Final Model

Extinction of desert bighorn populations in California in the twentieth century did not occur randomly. Populations in mountain ranges of lower elevation were much more likely to become extinct, particularly at <1500 m (Fig. 2a). Populations in regions with the lowest annual precipitation, especially <200 mm annual precipitation, were also more likely to become extinct (Fig. 2b), as were populations without dependable springs and populations in which domestic-sheep grazing allotments formerly overlapped or abutted desert bighorn habitat. This suggests not only that desert bighorn sheep are vulnerable to climate warming but that climate warming has already affected their distribution in California.

Hierarchical partitioning established that elevation and precipitation each had relatively strong independent effects in the model, despite their high degree of colinearity (Table 4). We suggest that the correlation between low elevation and higher risk of extinction resulted largely from the highly predictive relationship between elevation and temperature. Lower mountain ranges experience higher temperatures, and, as a result, bighorn sheep could have a greater dependency on water sources or poorer nutrition, resulting in lower survival. Higher-elevation ranges have an extended growing season: spring growth starts first at the lower elevations, and green-up progresses up the elevation gradient. Therefore, taller

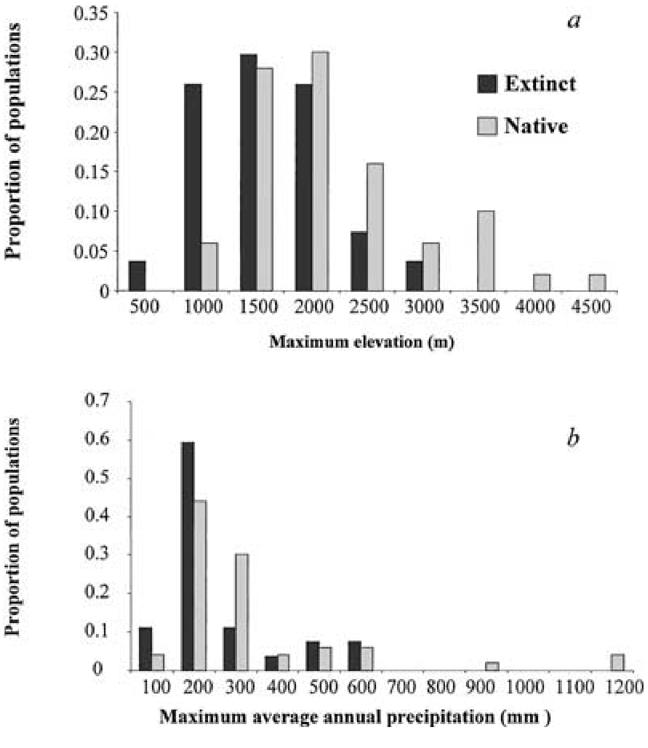

*Figure 2. Distribution of (a) maximum elevation and (b) maximum average precipitation values for ranges of native and extinct bighorn sheep (*Ovis canadensis nelsoni*).*

mountains have some green vegetation and thus better forage for much longer periods than low-elevation ranges (Wehausen 1980, 1992).

The relationship between extinction and precipitation probably results from the dynamics of water availability, soil moisture, and forage quality. Shrub cover in the Mojave Desert strongly correlates with mean annual precipitation (Beatley 1974). In arid regions even a slight decrease in moisture content, whether through increased temperature and increased evapotranspiration or through a decrease in precipitation, could have drastic effects on diet quality and therefore demography. Douglas and Leslie (1986) found that precipitation during gestation accounts for the largest proportion of variability in lamb survival. Wehausen et al. (1987) detected a positive relationship between winter precipitation and recruitment in the Santa Rosa Mountains of California (Fig. 1, no.86). Thus, precipitation apparently plays a large role in reproductive success. More explicit spatial data describing temperature and precipitation may further clarify these relationships.

The absence of dependable natural springs was also correlated with extinction, although this relationship was weaker than that of other model elements (Table 4). Nonetheless, bighorn sheep in many ranges make extensive use of springs and water holes, occur close to water during hot summer months (Andrew et al. 1997, 1999), and physiologically depend on ready access to water during summer (Turner & Weaver 1980).

Extinction of populations of desert bighorn sheep in California was not sensitive to patch size (two-dimensional area of the inhabited mountain ranges). This was surprising because patch size is often considered the most important predictor of population persistence (Hanski 1999; but see Fleishman et al. 2002), and this effect has been detected in Rocky Mountain bighorn sheep (*O. c. canadensis*) (Singer et al. 2001). The strong effect of patch size on persistence is thought to result from the expected correlation with population size if populations are strongly regulated by density dependence. If populations are regulated by environmental factors, however, one can expect a much weaker relationship between patch size and population size (Andrewartha & Birch 1954). Our findings that precipitation and elevation, but not patch size, were correlated with population extinction are consistent with strong environmental regulation of desert bighorn sheep populations.

Population isolation also did not affect extinction in our analysis. We measured isolation as the harmonic mean of the distance to the nearest three mountain ranges used at some time by bighorn sheep, but when adjacent populations were extinct, distances to the nearest inhabited patches may have been much greater. We could not use these distances as a measure because the timing of extinctions are poorly known. However, populations of desert bighorn sheep are generally demographically independent because of low female dispersal rates (Ramey 1995; Boyce et al. 1999). Although extinctions may appear regionally clustered (Fig. 1), this is probably a result of autocorrelated environmental factors such as precipitation.

Higher risk of extinction in lower, drier ranges was detected despite significant correlation of higher precipitation and higher elevation with sheep and cattle grazing and proximity to cities (Table 2). However, elements not retained in final models may still be important to consider during management on a case-by-case basis. Our conditional "extinction probabilities" (Fig. 3) are related solely to variables included in the final best-fit models. Thus, our models provide potentially biased estimates of extinction probabilities that are not all-inclusive.

Evaluating How Climate Change May Influence Population Extinction

Although crude, these climate-change simulations demonstrate that global warming could have serious consequences for desert bighorn sheep, particularly if coupled with decreases in precipitation. Other scenarios can be evaluated with these models as climate projections change. Absolute extinction probabilities should always be viewed with caution (Beissinger & Westphal 1998), but they provide a way to compare the vulnerability of populations to specific threats.

Changes in precipitation patterns, which are more difficult to predict than changes in temperature (Field et al. 1999), could balance or amplify the effects of changes in temperature because precipitation may be more limiting than temperature in these ecosystems (e.g., Wehausen et al. 1987). Careful analyses of how precipitation and temperature affect the growing season of forage plants, and thus diet quality among sheep, may improve future models of the population persistence of wild sheep. Climate warming may have more complicated or more detrimental effects when competition, predation, and disease affect desert bighorn sheep.

Our results have important implications for management actions. For future reintroductions of desert bighorn sheep, managers should consider expected precipitation and elevation within the mountain range of consideration. We do not advocate abandoning all efforts in mountain ranges that are at high risk: some may serve as valuable "stepping stones" for gene flow or demographic "rescue" (Bleich et al. 1990), and the extinction model may not be correct for all locations at all times. However, knowledge of climate-based risk of extinction may allow managers to focus further efforts on locations with the highest probability of success. Understanding which populations are under the most climate-related stress could also be critically important in coming decades (Fig. 3). Because of regionally correlated environmental conditions, whole regions of populations and subsequent opportunities for gene flow or recolonization may be lost (Fig. 3).

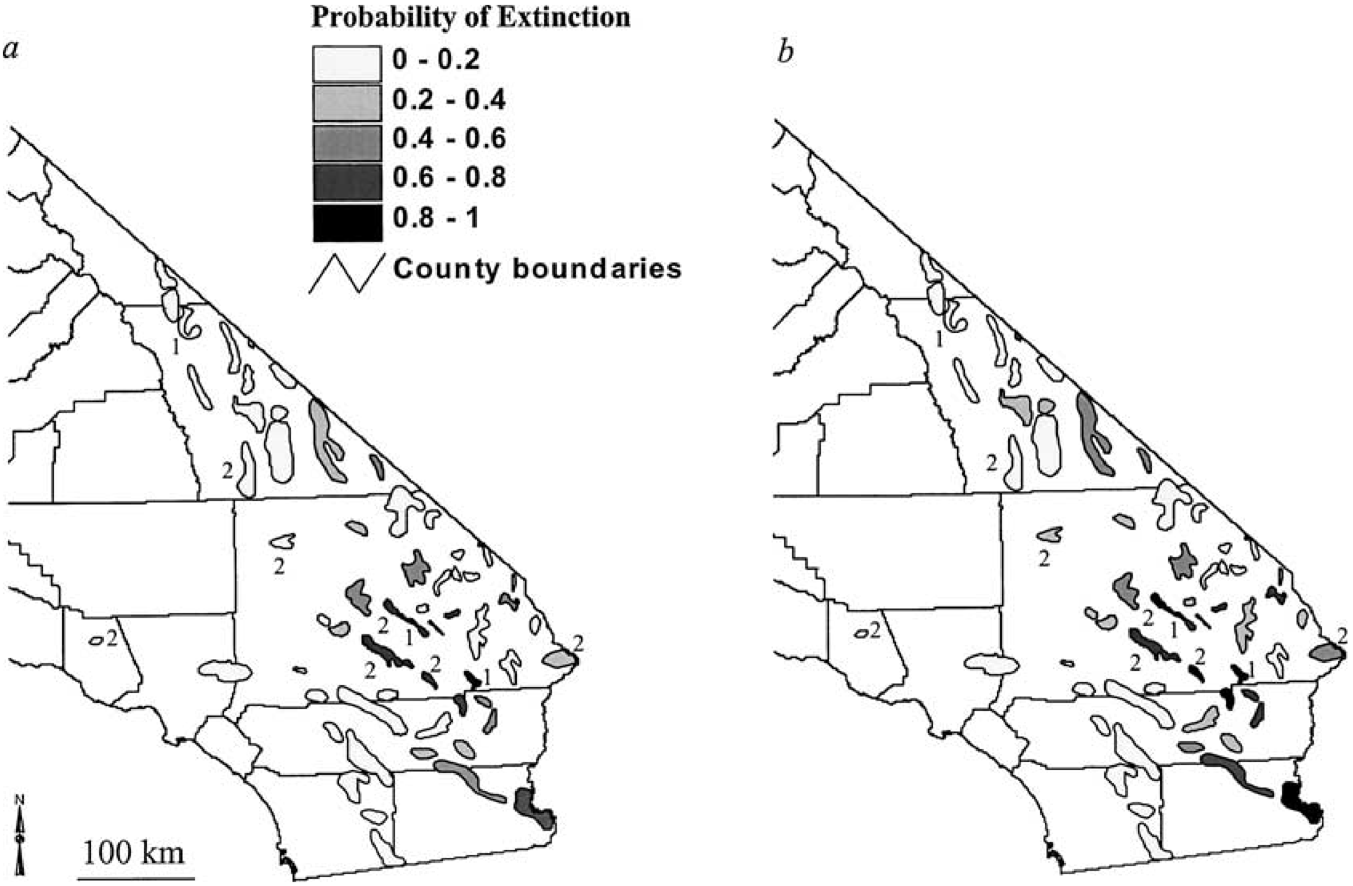

*Figure 3. Conditional extinction probabilities for unnumbered, native desert bighorn sheep (*Ovis canadensis nelsoni*); 1, desert bighorn sheep naturally recolonized since 1994; and 2, reintroduced populations of desert bighorn sheep for the next 60 years; assuming (a) no further climate change and no interactions with domestic sheep or (b) the maximum predicted increase in global temperature (+2.0° C), a 12% decrease in precipitation, no change in surface-water availability, and no interactions with domestic sheep.*

Heightened monitoring of population size, condition, and water availability, with appropriate action, may be necessary to conserve populations of desert bighorn sheep in the future.

The changes in the distribution of desert bighorn sheep observed in the twentieth century are consistent with directional climate change, but we cannot rule out the action of climatic stochasticity. It may be that the distribution of the desert bighorn in California has fluctuated for centuries, with expansion into areas of poorer habitat during cooler and wetter periods and retreat during times of increased drought frequency and intensity. Although the relationships between local climate and extinction are clear, whether current trends are the result of long-term climate change is not.

Using presence and absence data, we demonstrated that population extinctions of desert bighorn sheep in the twentieth century are consistent with a range contraction to areas of higher elevation and greater precipitation. Updated and more detailed climate scenarios can be explored through the relationships with extinction risk, elevation, and precipitation described here. This approach demonstrates that simple population viability analysis can sometimes be conducted even when detailed demographic data are absent. A similar approach might be used in systems where no prior population surveys existed, if suitable criteria for identifying empty habitat patches existed, in a variation of the incidence-function approach used by Hanski (1999) to parameterize metapopulation models.

Many species, particularly those in arid or montane regions, may have already suffered some effects of global climate warming. Elevational shifts in distribution consistent with climate change have been detected in Edith's checkerspot butterfly in the Sierra Nevada of California (Parmesan 1996), montane trees (Fisher 1997), and species in the cloud forests of Costa Rica (Pounds et al. 1999). Sparse data on population size and distribution may have hampered our ability to detect these changes elsewhere. Desert bighorn sheep may serve as a model to help us understand how similar systems may react to the coming changes.

Acknowledgments

We thank R. Weaver and G. Sudmeier for sharing their encyclopedic knowledge of desert waterholes, and S. Loe, B. Brown, M. Frael, A. Muth, E. Rubin, K. Allison, and S. Ostermann for their assistance in determining mining and livestock use on bighorn range. R. Mac Nally and T. Epps provided help with hierarchical partitioning. We would also like to thank S. Beissinger and several anonymous reviewers for thorough and insightful suggestions that greatly improved this paper.

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