Assessment of Predictive Habitat Models for Bighorn Sheep in California's Peninsular Ranges

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ABSTRACT We developed predictive habitat models for a bighorn sheep (*Ovis canadensis*) population in the Peninsular Ranges of southern California, USA, using 2 Geographic Information System modeling techniques, Ecological Niche Factor Analysis (ENFA) and Genetic Algorithm for Rule-set Production (GARP). We used >16,000 Global Positioning System locations from 34 animals in 5 subpopulations to develop and test ENFA and GARP models, and we then compared these models to each other and to the expert-based model presented in the United States Fish and Wildlife Service's Recovery Plan for this population. Based on a suite of evaluation methods, we found both ENFA and GARP to provide useful predictions of habitat; however, models developed with GARP appeared to have higher predictive power. Habitat delineations resulting from GARP models were similar to the expert-based model, affirming that the expert-based model provided a useful delineation of bighorn sheep habitat in the Peninsular Ranges. In addition, all 3 models identified continuous bighorn sheep habitat from the northern to southern extent of our study area, indicating that the Recovery Plan's recommendation of maintaining habitat connectivity throughout the range is an appropriate goal. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):859–869; 2009)

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Bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges of California, USA, were listed as an endangered population by the United States Fish and Wildlife Service (USFWS) in 1998, and protection, acquisition, and restoration of habitat were identified as key components of recovery strategies (USFWS 2000). Bighorn sheep in the Peninsular Ranges live in close proximity to some of the fastest growing communities in the United States, making bighorn sheep vulnerable to habitat loss, modification, and fragmentation. Distribution of this population is unique in relation to many bighorn sheep populations in that it tends to be restricted to low elevations, typically <1,400 m (Jorgensen and Turner 1975), resulting in use of a narrow north–south band of habitat vulnerable to fragmentation and urban encroachment. In addition, proximity to large metropolitan areas such as San Diego, Los Angeles, and Palm Springs creates a demand for recreation, mining, and other human activities within areas inhabited by bighorn sheep. Habitat delineation is, therefore, important to many of the strategies outlined by the USFWS Recovery Plan.

Habitat models have been developed to predict or rate suitability of bighorn sheep habitat in other mountain ranges (e.g., Holl 1982, Armentrout and Brigham 1988, Cunningham 1989, Dunn 1996). However, models developed to predict habitat in one mountain range may perform poorly when used to predict habitat suitability in another (Cunningham 1989, Andrew et al. 1999). Turner et al. (2004) developed a habitat model specifically for bighorn sheep in the Peninsular Ranges, but their model was found to have methodological shortcomings that negated its usefulness for predicting bighorn sheep habitat (Ostermann-Kelm et al. 2005). The USFWS Recovery Plan for this population presented a rule-based model specifically designed for this population, guided by expert knowledge of bighorn sheep in the Peninsular Ranges, to delineate essential habitat (USFWS 2000). That model was based primarily on topography (i.e., including areas within 800 m of slopes of $\geq 20\%$) and vegetation (i.e., using chaparral vegetation associations as the basis for upper elevational boundaries; USFWS 2000).

Although expert-based approaches have been effectively used for model building and conservation planning (Clevenger et al. 2002, MacMillan and Marshall 2006), the expert-based model developed for the Peninsular Ranges has not been comprehensively and analytically compared to models based on occurrence data, and it has been criticized for being qualitative and not repeatable (Turner et al. 2004). We used 2 statistical methods and computer-aided habitat modeling techniques to develop and evaluate models of bighorn sheep habitat in the Peninsular Ranges in California. Our objectives were to 1) develop models with 2 quantitative methods, 2) assess and compare predictive power of these models, and 3) compare these results with the existing expert-based model.

STUDY AREA

The Peninsular Ranges are part of the Colorado Desert division of the Sonoran Desert (Ryan 1968, Dimmitt 2000; Fig. 1). Bighorn sheep were distributed in approximately 8 subpopulations that inhabited, from north to south, the San Jacinto Mountains, the Santa Rosa Mountains northwest of

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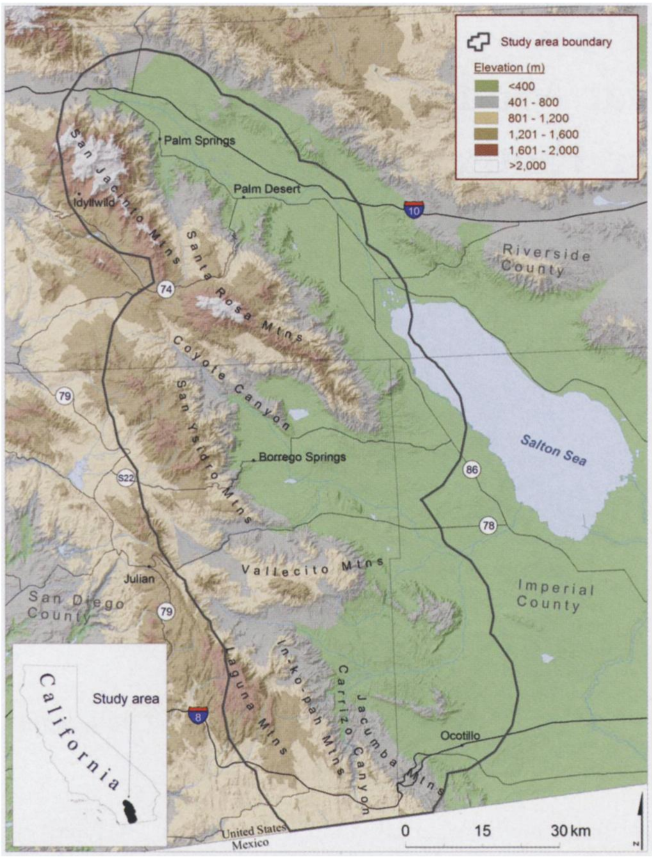

Figure 1. The study area (thick grey line) used to develop predictive habitat models for bighorn sheep in the Peninsular Ranges, California, USA, based on data collected during 2001–2003. Six elevation categories are shown.

State Highway (Hwy) 74, the Santa Rosa Mountains southeast of Hwy 74, Coyote Canyon, the north San Ysidro Mountains (N of County Road S-22), the south San Ysidro Mountains (S of County Road S-22), the Vallecito Mountains, and Carrizo Canyon (Rubin et al. 1998). These subpopulations were connected via male movement and, to a lesser extent, by occasional movement of female bighorn sheep (DeForge et al. 1997, Rubin et al. 1998).

Bighorn sheep are native to the Peninsular Ranges and only the 2 northernmost subpopulations were augmented with animals raised in captivity (Ostermann et al. 2001). In the Peninsular Ranges, bighorn sheep typically inhabited arid canyons, slopes, washes, and alluvial fans, and were most frequently found at elevations <1,400 m (Jorgensen and Turner 1975). Bighorn sheep inhabited a narrow north–south band of habitat bordered on the west by densely vegetated chamise (*Adenostoma fasciculatum*)-dominated chaparral and on the east by the flat Coachella and Imperial Valleys (USFWS 2000). Vegetation associations in the study area are described in Rubin et al. (1998). Temperatures in the study area often reached 46° C in summer, and winters were mild, with temperatures occasionally $\leq 0°$ C. Annual rainfall was variable, with maximums of 4.2–39.9 cm (median = 13.9 cm) during 1962–2004 (National Oceanic and Atmospheric Administration 2006). Land ownership in the northern part of the study area was primarily a mix of private, Tribal, State, and Federal land jurisdictions (USFWS 2000). In the south, Anza-Borrego Desert State Park (ABDSP) provided protection for approximately 243,000 ha (USFWS 2000); however, urban development and other land use activities, including off-road vehicle use and mining, threatened bighorn sheep habitat throughout the range.

METHODS

Relocation Data

We used 2 sets of bighorn sheep relocation data for this project. The first, which we call the GPS data, was collected during October 2001–November 2003, when animals were collared with Global Positioning System (GPS) collars (Televilt GPS-Simplex™; TVP Positioning AB, Bandygatan, Sweden) for habitat and behavior studies in 5 of the 8 subpopulations. All field procedures were approved by the Zoological Society of San Diego's Institutional Animal Care and Use Committee and USFWS Section 10(a)(1)(A) permit (no. TE047253-0).

We used 16,064 daytime GPS relocations (Vallecito Mountains: 1,319; San Ysidro Mountains: 7,392; Coyote Canyon: 3,627; Santa Rosa Mountains SE of Hwy 74: 3,726) from 34 animals (Vallecito Mountains: 2 M, 1 F; San Ysidro Mountains: 6 M, 10 F; Coyote Canyon: 3 M, 4 F; Santa Rosa Mountains SE of Hwy 74: 5 M, 3 F). Although our original GPS data set included day and night relocations, we used only daytime relocations for development of our models. An examination of GPS data and previous studies (e.g., Krausman et al. 1985) indicated that bighorn sheep exhibited limited activity at night. Although nocturnal habitat selection likely differs from diurnal habitat selection, it is likely that nocturnal habitat is a subset of diurnal habitat and that inclusion of nighttime locations could possibly have resulted in a model influenced unnecessarily by the more geographically static and restricted nighttime locations. For our analysis, we used 2 randomly selected daylight relocations ≥ 4 hours apart/24-hour period for each animal, because an examination of GPS data indicated that animals were able to traverse their home ranges within this period.

Our second data set, which we call the non-GPS data, included relocations of radiocollared animals tracked on the ground and via aerial telemetry and uncollared animals observed during waterhole counts, foot surveys, and opportunistic sightings. This data set, which spanned multiple years (1940–2000 with most data collected post-1990) and includes 21,632 detections of males and females representing all 8 subpopulations, is depicted in the USFWS Recovery Plan for this population (USFWS 2000). For our analysis, we used only data collected southeast of Hwy 74, represented by 7,503 relocations, because bighorn sheep distribution north of the highway was altered by habitat loss and urban development (Rubin et al. 2002, Ostermann-Kelm et al. 2005). Of this subset, 3,388 relocations were collected via direct observation during studies conducted during 1993–2000, and included relocations of 154 animals collared with very high frequency collars and representing 6 subpopulations (Rubin et al. 1998, 2000, 2002; Boyce et al. 1999; Hayes et al. 2000).

We used non-GPS data from all 8 subpopulations to delineate our study area because GPS data were not available for all 8 subpopulations. Because the number of animal locations varied extensively among areas due to different study objectives and monitoring intensities, we generated a 95% fixed-kernel utilization distribution (UD; Worton 1989) for each of the 8 subpopulations and merged them to form a collective UD. The construction of individual UDs followed by subsequent merging avoided the problem of artificially skewing the UD towards subpopulations with disproportionately large occurrence data sets. We then buffered the resulting single polygon by 15 km to produce our overall range-wide study area. We assumed that a buffer of 15 km would provide the model with the necessary range of habitat types both used and unused by bighorn sheep in the Peninsular Ranges and would, based on observations and a literature review of bighorn sheep movement patterns (e.g., Schwartz et al. 1986), also be within colonization distance of known bighorn sheep locations. Our study area encompassed 7,873 km^2 (787,300 ha) and included areas occupied by bighorn sheep, as well as areas not believed to be occupied (Fig. 1).

Modeling Methods

Bighorn sheep in the Peninsular Ranges of southern California declined to precariously low numbers in recent years (with the population estimated to include 276 animals in 1996; USFWS 2000), and some historically occupied areas have not been inhabited in recent years (Rubin et al. 1998). In addition, desert bighorn sheep are wide-ranging with large home ranges, and only a sample of animals was monitored with GPS collars. It was, therefore, difficult to separate true absences, where bighorn sheep truly did not occur, from false absences, where bighorn sheep did occur but were not recorded or where they occurred only during some periods. False absences can cause considerable bias in models designed to evaluate or predict habitat use (Hirzel et al. 2002*a*, Gu and Swihart 2004, Keating and Cherry 2004). For these reasons, we chose presence-based modeling methods that did not make strict assumptions about absences.

We used Ecological Niche Factor Analysis (ENFA) implemented in the Program BioMapper (Hirzel et al. 2002*a*, *b*), and Genetic Algorithm for Rule-set Production (GARP) implemented in the Program Desktop GARP (Stockwell and Noble 1992, Stockwell and Peters 1999). Both approaches, previously used to predict distribution of a wide range of species in diverse environments (e.g., Illoldi-Rangel et al. 2004, Santos et al. 2006, Kostelnick et al. 2007, Jaquiéry et al. 2008, Skov et al. 2008), are based on ecological niche theory (Hutchison 1957) and recognize that a certain multidimensional set of environmental conditions must exist to allow for a species' presence. Although using different methods, both programs evaluate species occurrences (presence data) in relation to characteristics of the background matrix of environmental characteristics, which can be characterized by numerous habitat parameters called eco-geographical variables (Hirzel et al. 2002*a*). The methods use these relationships to predict the set of conditions under which the species is expected to occur.

The ENFA evaluates the distribution of each eco-geographical variable (e.g., slope or elevation) in cells used by the species in relation to the distribution of each variable within the study area to generate 2 statistics. For each variable, it compares the mean value in cells used by the species and the global mean across the study area to identify the marginality of the species. In addition, ENFA compares the variance of each variable in cells used by the species with the variable's variance across the study area to generate an index of specialization (Hirzel et al. 2002*a*). Factor analysis is used to extract combinations of variables that are most important in determining a species' marginality and specialization. The ENFA generates scores for each cell by weighting each cell by corresponding marginality and specialization values (Hirzel et al. 2002*a*, *b*). The combination of scores for all variables is used to generate an overall suitability index for each focal cell, with ratings ranging from zero to one (Hirzel et al. 2002*a*). Although Hirzel et al. (2002*a*) call these suitability ratings, we call them frequency-of-use ratings because the ratings also indicate a relative frequency of use (of a particular habitat type).

The GARP is a machine-learning approach that uses presence data to find the best set of rules to explain how a species is distributed on the background matrix of eco-geographical variables. Through an iterative process, GARP evaluates a series of decision rules and algorithms (e.g., logistic regression, bioclimatic rules) to generate the best set of variable criteria that explain how species locations are distributed on the landscape. Rules are tested using available presence data, modified, incorporated, or rejected through thousands of iterations until the best set of variable conditions most accurately predicting the species' distribution is determined. These rules define the parameters that are then collectively mapped using Geographic Information Systems (GIS) to predict the geographic distribution of the species of interest (Peterson and Vieglais 2001). More detailed descriptions of GARP methods are available in Stockwell and Peters (1999) and Payne and Stockwell (no date).

We generated GIS data-layers for 17 eco-geographical variables believed to possibly influence distribution of bighorn sheep (Table 1). We used ArcGIS 9.0 to determine slope, elevation, and aspect for each cell of the study area, using a 30-m cell resolution. Because Biomapper does not accept categorical variables and aspect measurements are problematic due to the circular nature of the degree measurement, we used incident radiation as a surrogate for aspect. Incident radiation is similar to a heat load index, which rescales aspect to a scale of zero to one, and is symmetrical around a northeast–southwest axis, with a value of zero representing the coolest aspect (NE) and a value of one representing the warmest aspect (SW; McCune and Keon 2002). Measures of incident radiation additionally incorporate latitude and slope information, with steeper

Table 1. Eco-geographic variables included in development of predictive habitat models for bighorn sheep in the Peninsular Ranges, California, USA, based on data collected during 2001–2003.

Eco-geographic variable	Description
Slope	Slope (%) of individual 30-m^2 pixel.[a]
Distance to $\geq$60% slope	Shortest distance (m) from every 30-m^2 pixel to a pixel with slope of $\geq$60% (we Box-Cox–transformed data after we added 15 m to all values due to presence of zero values).
Elevation	Elevation (m) of individual 30-m^2 pixel.[a]
Ruggedness	Index of ruggedness over a 150 m $\times$ 150 m area (22,500 m^2) centered on each 30-m^2 pixel.
Distance to ruggedness $\geq$0.02	Shortest distance (m) from every 30-m^2 pixel to a pixel with ruggedness of $\geq$0.02.[a]
Distance to water (conservative)	Shortest distance (m) from each 30-m^2 pixel to water sources (e.g., springs, streams) available yr-round in $\geq$75% of yr, based on local biologist knowledge.[a]
Distance to water (best scenario)	Shortest distance (m) from each 30-m^2 pixel to water sources (e.g., springs, streams) available yr-round in $\geq$25% of yr, based on local biologist knowledge, and those that have unknown status.[a]
Incident radiation	Index of incident radiation at each 30-m^2 pixel.[a]
Distance to roads	Shortest distance (m) from each 30-m^2 pixel to paved roads.[a]
Distance to forest	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as California Wildlife Habitat Relationships (CWHR) conifer or hardwood forest.[a]
Distance to hardwood woodland	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as CWHR hardwood woodland.[a]
Distance to conifer woodland	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as CWHR conifer woodland.[a]
Distance to shrub (including chaparral)	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as CWHR shrub.[a]
Distance to desert shrub	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as CWHR desert shrub.[a]
Distance to desert woodland	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as CWHR desert woodland.[a]
Distance to urban or agriculture	Shortest distance (m) from each 30-m^2 pixel to the nearest pixel classified as urban or agriculture.
Index of vegetation cover	Normalized difference vegetation index; reflectance based on satellite data.[a]

[a] We Box-Cox–transformed data.

slopes being warmer (McCune and Keon 2002). We calculated a ruggedness index for each cell at the scale of 150 $\times$ 150 m (5 $\times$ 5 30-m^2 cells) following methods developed by Sappington et al. (2007). This index ranges from zero to one, with a value of one indicating the highest ruggedness. In addition, a second eco-geographical variable, Distance to ruggedness $\geq$0.02, was calculated by measuring the shortest distance from each cell to the closest cell with ruggedness $\geq$0.02. We chose the value 0.02 based on a visual examination of GPS locations mapped relative to ruggedness values, which suggested that sheep locations tended to be associated with cells with a ruggedness index $\geq$0.02.

For the variable Distance to water, we identified all known water sources (based on existing maps and data sets, our knowledge of the area, and input from local biologists), and grouped them into 4 categories: sources that would provide bighorn sheep with water year-round during 1) $\geq$75% of years, 2) 25–75% of years, 3) <25% of years, and 4) sources whose status and reliability were unknown. Because of uncertainties about the relative importance of these water categories to bighorn sheep, we ran each model 2 ways; first using only water sources in category 1 (hereafter Conservative water) and then including water sources in categories 1, 2, and 4 (hereafter Best scenario water).

For land-cover data we used the Multi-source Land Cover Data (2002 v2) produced by the California Department of Forestry and Fire Protection. Using California Wildlife Habitat Relationship classes (California Department of Fish and Game 2009), we identified 7 vegetation and non-vegetated land-cover categories (Table 1). Although a more detailed vegetation data layer was available for ABDSP, our analysis required a vegetation layer that spanned the entire study area. We calculated distance from each cell in the study area to the nearest cell representing each of the 7 land-cover categories.

Model Development, Evaluation, and Selection

We used only GPS data for model development because non-GPS data had varying levels of precision and accuracy, were obtained according to multiple study protocols not necessarily designed for a habitat use study, and were possibly biased by the ability of field biologists to locate animals equally well in all terrain. We combined GPS data from 5 subpopulations (one in the Santa Rosa Mountains SE of Hwy 74, one in Coyote Canyon, 2 in the San Ysidro Mountains, and one in the Vallecito Mountains) for model development and training. Although Biomapper and GARP both incorporate internal methods of model testing, we randomly selected and held aside 30% of GPS data to evaluate resulting models, and used the remaining 70% for model development.

For ENFA models, we ran Biomapper with all eco-geographic variables included, and we used the geometric mean algorithm for calculating habitat suitability (Hirzel and Alettaz 2003). We used McArthur's broken-stick model as a guide for choosing the number of factors to be used in developing the predictive habitat model (Hirzel et al. 2002*b*). Program Biomapper evaluated the predictive power of the resulting suitability maps using the *k*-fold cross-validation process described by Boyce et al. (2002). For this analysis Biomapper uses all data available; however, animal locations are randomly partitioned into *k* identically sized data sets (10 partitions in our study) and $k - 1$ sets are used to compute a suitability map and the remaining data set is used to validate the map. The process is repeated *k* times, with each of the *k* subsets left out one at a time. Predictive power is evaluated by evaluating the relationship between observed and expected number of validation points at different habitat suitability values (Hirzel et al. 2006). We used the continuous Boyce index, with window size set at 20 for all model validations (Hirzel et al. 2002*b*).

In GARP, we used the same set of eco-geographic variables used in the ENFA analysis and allowed the model to consider all rule types (atomic, range rules, negated range rules, and logistic regression; Payne and Stockwell [no date]). Within GARP, occurrence data were divided evenly into training and intrinsic testing data, which were used for developing and testing rules, respectively. We ran 1,000 iterations (or until the model converged), and we iterated GARP 700 times to produce 700 models. Because of the stochastic nature of GARP algorithms, every model generated by GARP is unique, even when the same training data are used. Using guidelines presented by Anderson et al. (2003), we selected a best subset of 20 models by first choosing all models with intrinsic and extrinsic omission error <10% and then choosing the 20 models with commission error closest to the median commission error. We then combined this best subset of 20 models to predict a range-wide distribution, with a relative likelihood of presence rating of 0 to 20 (hereafter likelihood-of-presence categories) assigned to each cell in the study area, based on the number of models predicting presence in each cell (Anderson et al. 2003, Drake and Bossenbroek 2004).

Models based on true presence–absence data can be evaluated by methods such as a confusion matrix (Fielding and Bell 1997). However, these methods are problematic when models are based on presence-only data, because absences are not available for testing model predictions (Anderson et al. 2003). Although Programs Biomapper and GARP facilitate comparison of models derived within each program, we held back 30% of our data so that we could compare models derived by different methods using a suite of evaluation methods. We used a goodness-of-fit test (Sokal and Rohlf 1995) to test whether the 30% test data were distributed among habitat rating categories as predicted by the model. For this analysis, we used 5 equal-sized categories based on frequency-of-use and likelihood-of-presence assigned by ENFA and GARP, respectively, with expected values derived from the distribution of training data in each category. For evaluation and comparison of ENFA models, we also examined continuous Boyce indices generated by Program Biomapper. For GARP models, we evaluated how test data were distributed among the 20 likelihood-of-presence ratings in each model, by examining density of test data (locations/km^2) in each category, with the expectation that the highest rating (those areas identified as habitat by all 20 best subset models) should have the highest density of test locations. Finally, we also used receiver-operator characteristic (ROC) analysis (Hanley and McNeil 1982, Chen et al. 2007), implemented in a web-based calculator (J. Eng, John Hopkins University, http://www.jrocfit.org, accessed 26 May 2009), to evaluate ENFA and GARP models. The ROC analysis has been used to assess accuracy of predictive habitat models, by comparing test data to the predicted distribution of habitat ratings (Wiley et al. 2003, Iguchi et al. 2004, Chen et al. 2007). The ROC analysis is used to test sensitivity (absence of omission error) and specificity (absence of commission error) of the predicted habitat, in relation to its ability to successfully predict presence of test data (Wiley et al. 2003, Iguchi et al. 2004, Chen et al. 2007). The ROC scores are maximized when all test data fall into areas predicted as habitat by all models, giving a ROC score of 1.0, and are minimized when test locations are as likely to fall into predicted habitat as non-predicted habitat (a score of 0.50 indicates a random distribution relative to predicted habitat).

Initially, we developed separate models for males and females because male and female bighorn sheep are known to use habitat differently (Bleich et al. 1997). After we evaluated models, we chose the best male and female models (within ENFA and GARP) and merged them to produce a final sexes-combined ENFA model and a final sexes-combined GARP model. We merged sex-specific models by selecting the higher of the 2 (M vs. F) frequency-of-use and likelihood-of-presence categories in ENFA and GARP, respectively, for each cell. Although male and female bighorn sheep use habitat differently (e.g., Bleich et al. 1997), our intent was not to identify sex-specific habitat needs, but rather to delineate an overall inclusive habitat delineation, which requires habitat for both males and females.

Using the 30% test data, we evaluated and compared how well these 2 models and the expert-based model predicted habitat use in the large portion of the range southeast of Hwy 74. Because our GPS data set only represented habitat use during a 2-year period, we also evaluated the 3 models with non-GPS data (SE of Hwy 74) that encompassed more years of data (1940–2000 with most locations collected post–1990) and represented habitat use across a wider range of environmental conditions and population sizes. We compared the 3 models by examining the proportion of the 30% test data and non-GPS data located in predicted habitat. However, because a model predicting the entire study area as habitat (and likely not a very accurate model) would rate high in this respect, we also evaluated this measure in relation to the overall extent of predicted habitat, by creating a ratio of the proportion of test data located within predicted habitat to the overall size of the predicted habitat (indicating possible errors of commission). A larger value suggests a better model.

RESULTS

All 4 ENFA models (2 using the Conservative water variable and 2 using the Best scenario water variable, with a separate model for M and F in each case) had good fit according to the continuous Boyce index, with the index approaching its maximum value and having small standard deviations in all cases (Table 2). The ROC values also indicated a good fit of the 4 models, with values $\geq$0.78 in all cases. Goodness-of-fit tests revealed no difference between distribution of observed (test) and predicted distribution among frequency-of-use categories for male models, suggesting that both male models had good

Table 2. Continuous Boyce Index and receiver-operator characteristic (ROC) values for Ecological Niche Factor Analysis (ENFA) and Genetic Algorithm for Rule-set Production (GARP) habitat models for bighorn sheep in the Peninsular Ranges, California, USA, based on data collected during 2001–2003 (CW = Conservative water, BSW = Best scenario water).

		ENFA model				GARP model	
Model	Test data	Boyce Index	Boyce Index SD	ROC area	ROC area SD	ROC area	ROC area SD
M, CW		0.974	0.022				
	M			0.785	0.005	0.878	0.003
M, BSW		0.978	0.024				
	M			0.842	0.004	0.875	0.003
F, CW		0.996	0.003				
	F			0.877	0.002	0.895	0.011
F, BSW		0.996	0.003				
	F			0.876	0.003	0.927	0.013

predictive power (Table 3). Although male models developed with Conservative water and Best scenario water performed similarly, slightly higher ROC and Boyce Index values suggested that the model developed with the Best scenario water had slightly better predictive power than the model developed with Conservative water (Table 2). When we compared female models developed with different water variables, we observed little difference in ROC and Boyce Index values (Table 2). However, goodness-of-fit tests indicated that distribution of test data among frequency-of-use categories differed significantly ($P = 0.009$; Table 3) from the expected distribution when we used the Best scenario water variable. We therefore chose the male model created with the Best scenario water variable and the female model developed with the Conservative water variable as our best male and female models and merged these 2 models as our best ENFA model for sexes combined.

All 4 GARP models (2 using the Conservative water variable and 2 using the Best scenario water variable, with a separate model for M and F in each case) had good fit according to ROC values (≥ 0.87 in all cases; Table 2). Goodness-of-fit tests indicated that all 4 GARP models fit the data, with no significance between observed (test) and expected distributions (Table 4). The male model developed with Best scenario water tended to have higher predictive power, whereas female models developed with the 2 water variables had similar goodness-of-fit (Table 4). The ROC values were similar for both male models but suggested that the female model developed with the Best scenario water variable had better predictive power (Table 2). We therefore chose models developed with the Best scenario water variable as our best single-sex GARP models, and we merged these models to produce our best single (sexes combined) GARP model.

Goodness-of-fit tests of the final male and female models suggested that GARP models had better predictive power than ENFA models, based on test results for the best female ENFA model (developed with the Conservative water variable), which tended to approach significance ($P = 0.078$; Tables 3, 4). In addition, ROC scores were slightly higher for GARP models (Table 2). When we plotted the 30% GPS test data on the final sex-specific GARP maps, most test locations fell within areas predicted as habitat by all of the 20 models in the best-subset of GARP models (Fig. 2). For males, test data fell into all likelihood-of-presence categories, with density of locations increasing as likelihood-of-presence increased (Fig. 2A). For females, only some test data fell into the lower categories and most test data fell into areas predicted by all 20 best-subsets models (Fig. 2B).

When we compared our final sexes-combined ENFA model, GARP model, and expert-based model, we found that the ENFA model predicted the largest habitat extent and the expert-based model predicted the smallest extent (Table 5; Figs. 3 and 4). The areas predicted by each of the models encompassed $\geq 98.99\%$ of the 30% test GPS data and the non-GPS data, and the expert-based model captured these test data in the smallest area (Table 5; Fig. 5). Visually, the GARP and expert-based models were most similar, whereas the ENFA model tended to predict habitat extending farther west than the other 2 models (Figs. 3, 4).

Table 3. Expected and observed number of test data falling within each frequency-of-use category predicted by Ecological Niche Factor Analysis models of bighorn sheep habitat in the Peninsular Ranges, California, USA, based on data collected during 2001–2003 (CW = Conservative water, BSW = Best scenario water).

		Frequency-of-use categories (expected:observed)								
Model	Test data[a]	0	1–20	21–40	41–60	61–80	81–100	χ^2	df	P
M, CW	M	9:7	371:365	368:365	370:372	370:391	366:354	2.16	5	0.826
M, BSW	M	9:10	370:368	371:380	373:355	368:359	362:381	2.43	5	0.788
F, CW	F	14:17	588:575	591:582	595:627	595:543	589:628	9.92	5	0.078
F, BSW	F	14:16	588:576	593:570	592:643	597:536	587:630	15.19	5	0.009

[a] Test data used for goodness-of-fit test.

Table 4. Expected and observed number of test data falling within each likelihood-of-presence category predicted by Genetic Algorithm for Rule-set Production models of bighorn sheep habitat in the Peninsular Ranges, California, USA, based on data collected during 2001–2003 (CW = Conservative water, BSW = Best scenario water).

		Likelihood-of-presence categories (expected:observed)								
Model	Test data[a]	0	1–4	5–8	9–12	13–16	17–20	χ^{2b}	df	P
M, CW	M	22:28	66:78	42:40	56:42	65:53	1,602:1,612	9.69	5	0.085
M, BSW	M	14:18	58:61	43:46	64:51	70:75	1,604:1,602	4.51	5	0.479
F, CW	F	2:0	5:2	4:4	5:3	15:14	2,940:2,948	3.19	3	0.364
F, BSW	F	3:0	6:3	3:5	6:4	12:7	2,941:2,952	3.60	3	0.308

[a] Test data used for goodness-of-fit test.
[b] Categories were collapsed as necessary, to avoid expected values <5.

DISCUSSION

Our assessment indicated that ENFA and GARP models both produced meaningful predictions of bighorn sheep habitat in the Peninsular Ranges, but that GARP models tended to have higher predictive power. This pattern was also observed by Tsoar et al. (2007) in a comparison of 6 modeling methods, in which GARP showed a small (though statistically significant) advantage over ENFA in predictive accuracy. The ability of both methods to produce meaningful predictions is consistent with the conclusion of Elith et al. (2006) that use of presence-only data was an effective means of predicting species distributions. In their comparison of 16 modeling methods (which did not include ENFA), Elith et al. (2006) concluded that more recently developed models (e.g., max. entropy models and a new open modeler implementation of GARP) may produce even more accurate results than GARP implemented in Program DesktopGARP. However, Tsoar et al. (2007) and Elith and Burgman (2002) concluded that model performance may be influenced by species distributional characteristics, and that this could account for considerable differences in model performance.

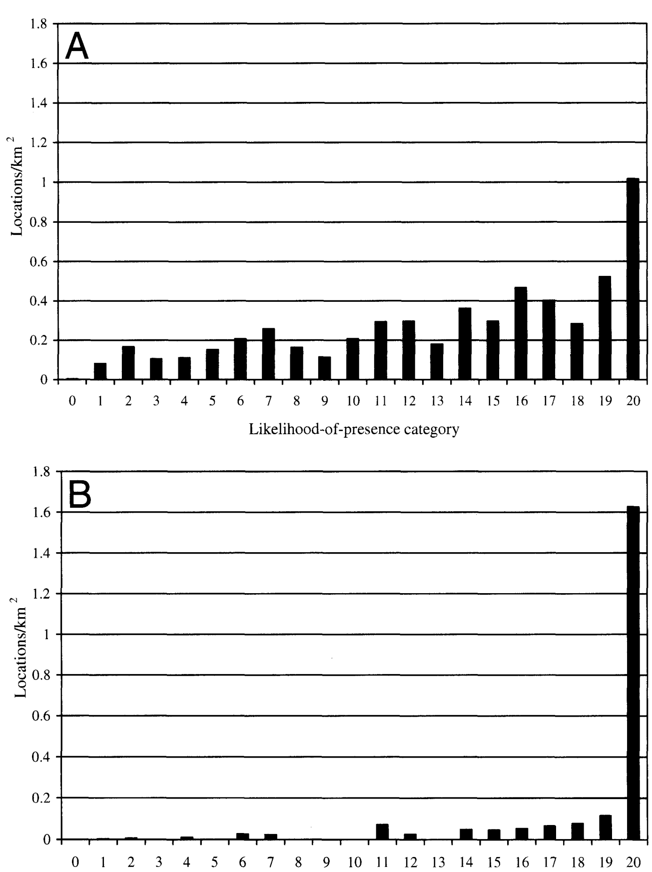

Figure 2. Distribution of (A) male and (B) female 30% Global Positioning System test data across 20 likelihood-of-presence categories predicted by Genetic Algorithm for Rule-set Production (GARP) models for bighorn sheep in the Peninsular Ranges, California, USA, based on data collected during 2001–2003. Categories 0–20 indicate how many of the 20 best-subsets GARP models predicted a particular pixel as habitat.

Our model evaluations based on ROC values and continuous Boyce indices showed that all 4 sex-specific ENFA models provided useful predictions, but the slightly higher ROC values of the GARP models suggested they provided better predictions (Table 2). Goodness-of-fit tests indicated that ENFA models had lower predictive power for females than for males, possibly because habitat use by female bighorn sheep is more restricted than that of males (Bleich et al. 1997), and consistent with the suggestion that species distributional characteristics may influence model performance. Based on goodness-of-fit tests, GARP models were able to predict female habitat use patterns more effectively than were ENFA models (Tables 3, 4). Nevertheless, goodness-of-fit tests did not reveal a difference between expected and observed distributions among habitat classes in our final male and female ENFA models, and we therefore merged the sex-specific models to produce the final sexes-combined ENFA model for comparison with the final sexes-combined GARP model and the expert model.

All 3 sexes-combined models (ENFA, GARP, and the expert model) captured nearly all ($\geq$98%) of the 30% test data and the non-GPS data within predicted habitat, indicating that omission errors were low for all models. Omission errors represent false negatives, areas where the model predicts no use where use actually occurs. In contrast, commission errors, or false positives, represent areas where the model predicts presence but the species is not present in these areas (Anderson et al. 2003). The final ENFA model predicted the largest overall habitat extent. Although the size of predicted habitat does not indicate habitat quality, this size difference suggested that commission error could potentially be greatest in the ENFA model.

We depicted habitat classes (frequency-of-use classes for ENFA and likelihood-of-presence classes in GARP) in 5 categories. Rather than implying any biological cut-points among habitat classes, we used these categories simply for

Table 5. Comparison of sexes-combined Genetic Algorithm for Rule-set Production (GARP), Ecological Niche Factor Analysis (ENFA), and expert-opinion models developed for bighorn sheep in the Peninsular Ranges, California, USA, based on data collected during 2001–2003 (GARP and ENFA models).

Model	Total predicted habitat area (km^2)[a]	Proportion of 30% Global Positioning System (GPS) test data located within predicted area[b]	Ratio of proportion of 30% GPS data located within predicted area to total predicted area[b]	Proportion of non-GPS data located within predicted area[b]	Ratio of proportion of non-GPS data located within predicted area to total predicted area[b]
ENFA (final M and F models merged)	4,315.48	0.993	0.00023	0.990	0.00023
GARP (final M and F models merged)	3,728.00	0.999	0.00027	0.997	0.00027
Expert-based model (for M and F)	3,166.99	0.999	0.00032	0.997	0.00031

[a] For ENFA and GARP models, this includes all pixels with rating >0.
[b] Areas and data NW of Highway 74 were excluded from this analysis.

analysis and map-representation purposes. However, most areas predicted as habitat by GARP fell into the highest GARP category, indicating that model prediction was consistent for these areas (Fig. 4). Most areas predicted as habitat by the expert-based model were also scored as the highest GARP category. Most female GPS test locations fell into the highest category, but male test data, although also falling primarily into the highest category, were distributed more widely across lower categories (Fig. 2). This pattern is consistent with sex-based habitat use differences, with males using a wider range of habitats than females (Bleich et al. 1997), and provides further support for the GARP model.

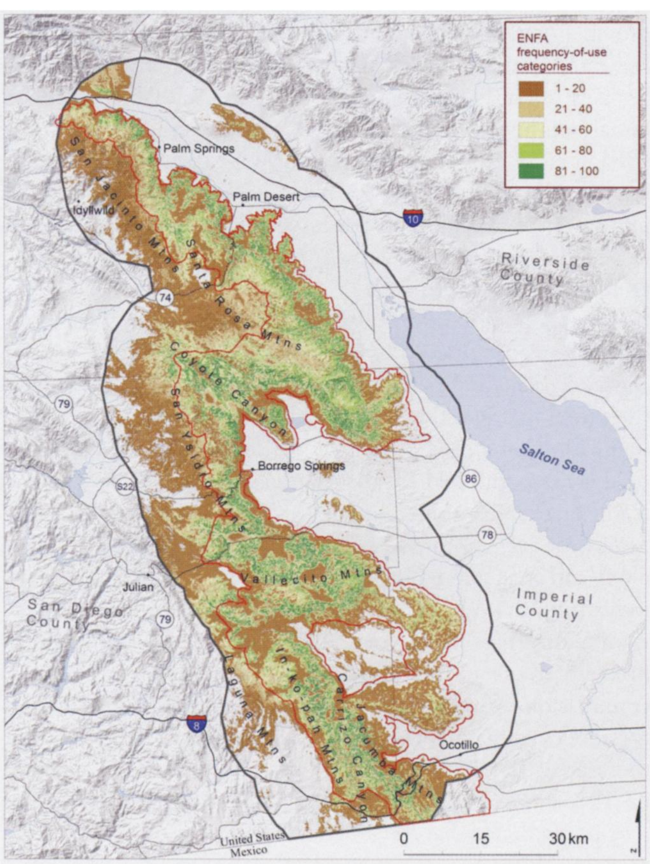

Figure 3. Habitat predicted by Ecological Niche Factor Analysis (ENFA) for male and female bighorn sheep (sexes combined) in the Peninsular Ranges, California, USA, based on data collected during 2001–2003. Five frequency-of-use categories are shown. The study area is indicated with a thick grey line and the expert-based model boundary is shown as a red dashed line.

Although GARP models tended to have stronger predictive power, models developed with ENFA had good predictive power based on continuous Boyce indices. The ENFA model predicted a larger total area of habitat than GARP or the expert-based model, with the most obvious differences along the western edge, where ENFA models predicted large areas in the lowest of our 5 frequency-of-use categories (Fig. 3). This western extension supports populations of mule deer (*Odocoileus hemionus*) and mountain lions (*Puma concolor*), and predation risk may limit this western distribution of bighorn sheep. These areas may currently also represent marginal habitat for bighorn sheep because of increased vegetation cover due to lack of recent fires, in areas where habitat conditions dynamically change in response to wildfires. Although bighorn sheep in our study area have infrequently been found at elevations >1,800 m or in forested areas, use of these habitat types has been documented in the Peninsular Ranges south of the United States–Mexico border, where vegetation cover at higher elevations may differ due to different fire patterns (Minnich et al. 2000). The ENFA model may, therefore, indicate potential for expanded habitat use along the western edge of our study area under different environmental conditions or predator densities.

Habitat delineations predicted by GARP and by the expert-based model were similar in overall size and configuration, with some differences (Fig. 4). The GARP model did not predict habitat at the extreme southeastern corner of the expert-based habitat delineation, where bighorn sheep were historically observed, because our study area delineation did not include that area (because we had excluded historic sightings that had only general locational attributes from our non-GPS data set, which we used to delineate the study area). Likewise, GARP models did not predict some areas along the eastern edge of the expert-

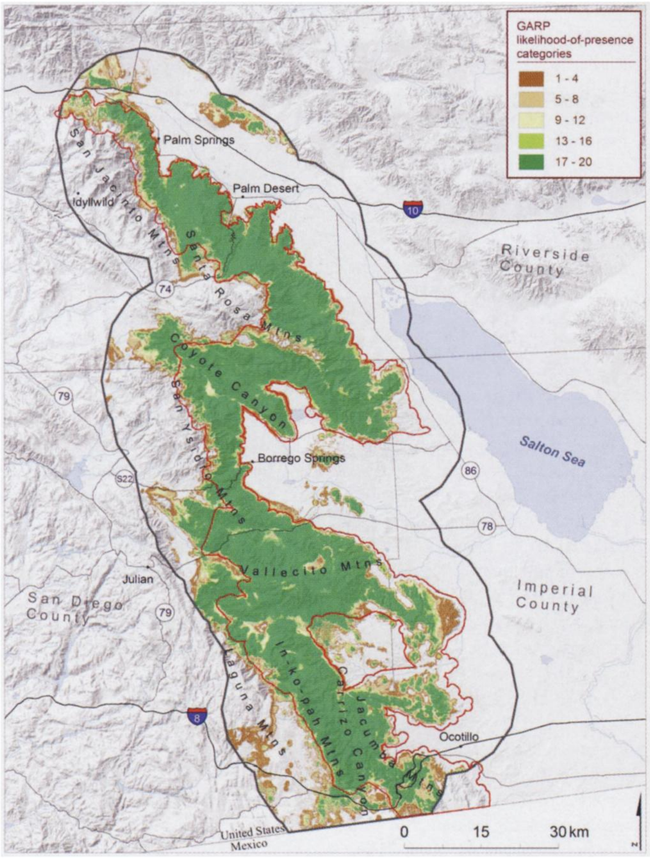

Figure 4. Habitat predicted by Genetic Algorithm for Rule-set Production (GARP) for male and female bighorn sheep (sexes combined) in the Peninsular Ranges, California, USA, based on data collected during 2001–2003. Five likelihood-of-presence categories are shown. The study area is indicated with a thick grey line and the expert-based model boundary is shown as a red dashed line.

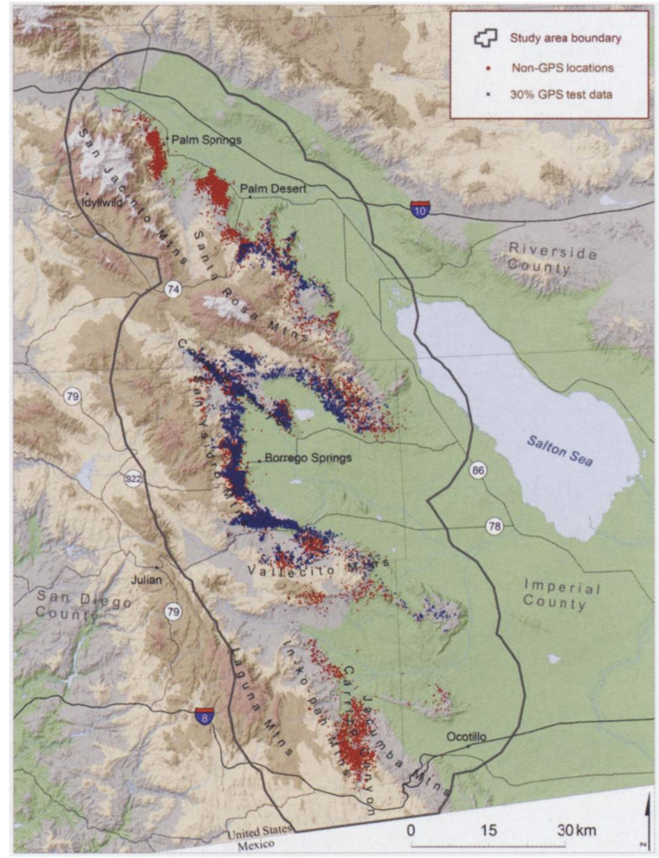

Figure 5. Locations of bighorn sheep as represented by 30% Global Positioning System (GPS) test locations (blue x-marks, 2001–2003) and non-GPS locations (red dots, 1940–2000 with most data collected post-1990) in the Peninsular Ranges, California, USA.

based model boundaries where bighorn sheep have been observed, possibly because our 2-year GPS data set did not capture the range of use necessary to predict habitat suitability. These differences, like those described above for the ENFA models and the western boundary, emphasize that model predictions should be interpreted with caution. Models are tools that must be placed in context with an understanding of the species' ecology, behavior, and history. An advantage of quantitative predictive models is that they can help identify potential habitat that is not recognized by expert opinion, and they can identify potential habitat not represented by current distribution. Both ENFA and GARP have been used to identify a species' fundamental niche, indicating areas where species may be reintroduced, where biological invasions may occur, or where factors other than habitat (e.g., predation) may preclude presence of the species (Hirzel et al. 2004, Chen et al. 2007).

MANAGEMENT IMPLICATIONS

Our evaluation indicated that the expert-based model, referred to as essential habitat in the Recovery Plan for bighorn sheep in the Peninsular Ranges (USFWS 2000), provides an objective, defensible, and valuable habitat delineation for guiding continued recovery efforts. A key commonality among the GARP, ENFA, and expert models is the continuity of habitat throughout the United States Peninsular Ranges. All 3 models predicted a narrow north–south band of habitat with habitat connectivity from the northern extent in the San Jacinto Mountains south to the international border. The Recovery Plan for this population identified the maintenance and restoration of habitat connectivity throughout the United States Peninsular Ranges as a high-priority recovery action, and our habitat models and assessment indicate that the potential to maintain connectivity still exists, thereby suggesting that this is an appropriate recovery goal. All 3 models reveal several constrictions where this band of habitat is narrow (≤ 10 km in some cases), emphasizing the vulnerability of habitat connection in this mountain range. Encroachment by urban development, primarily along the eastern edges, global climate change, and habitat modifications could have significant implications by threatening habitat connectivity for bighorn sheep in these mountains. Habitat protection will, therefore, be key to maintaining this tenuous connection.

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