A Habitat-Based Metapopulation Model of the California Gnatcatcher

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Abstract: We present an analysis of the metapopulation dynamics of the federally threatened coastal California Gnatcatcher (Polioptila c. californica) for an approximately 850 km² region of Orange County, California. We developed and validated a habitat suitability model for this species using data on topography, vegetation, and locations of gnatcatcher pair observations. Using this habitat model, we calculated the spatial structure of the metapopulation, including size and location of habitat patches and the distances among them. We used data based on field studies to estimate parameters such as survival, fecundity, dispersal, and catastrophes, and combined these parameters with the spatial structure to build a stage-structured, stochastic, spatially-explicit metapopulation model. The model predicted a fast decline and high risk of population extinction with most combinations of parameters. Results were most sensitive to density-dependent effects, the probability of weather-related catastrophes, adult survival, and adult fecundity. Based on data used in the model, the greatest difference in results was given when the simulation's time horizon was only a few decades, suggesting that modeling based on longer or shorter time horizons may underestimate the effects of alternative management actions.

Modelo de Metapoblación Basado en el Hábitat de Polioptila c. Californica

Resumen: Presentamos un análisis de la dinámica metapoblacional de Polioptila c. californica, especie amenazada de extinción de las costas de California, para una región de aproximadamente 850 km² del condado de Orange, California. Describimos y validamos un modelo de ajuste para esta especie utilizando datos de topografía, vegetación y sitios de observación de la especie. Utilizando este modelo de hábitat, estimamos la estructura espacial de la metapoblación incluyendo tamaño y localización de parches de hábitat así como las distancias entre ellos. Utilizamos datos basados en estudios de campo para estimar parámetros tales como la supervivencia, fecundidad, dispersión y catastrofes, también se combinaron estos parámetros con la estructura espacial con la finalidad de construir un modelo metapoblacional estructurado por pasos, estocásico y espacialmente explícito. El modelo predijo una declinación rápida y un alto riesgo de extinción de la población con la combinación de la mayoría de los parámetros. Los resultados fueron más sensibles a efectos densodependientes, la probabilidad de catastrofes ocasionadas por el clima, la supervivencia de adultos y la fecundidad de los adultos. Basados en los datos utilizados en este modelo, las diferencias mayores en los resultados se produjeron cuando el horizonte de tiempo de las simulaciones fue de solo unas cuantas décadas, sugiriendo que el modelado basado en horizontes de tiempo largos o cortos pueden desestimar los efectos de acciones alternativas de manejo.

Introduction

The California Gnatcatcher’s northernmost subspecies (Polioptila c. californica) has declined due to extensive agricultural and urban development of coastal sage scrub, the species’ primary habitat type in southern California and northwestern Baja California (Atwood 1993). Listed in 1993 as threatened under the U.S. Endangered Species Act (ESA), protection of the gnatcatcher and its habitat has become a major focus in the inaugural application of the State of California’s Natural Community Conserva-
tion Planning (NCCP) program (Atwood & Noss 1994). This voluntary, regional land-use planning process, aimed at delineating core tracts of essential natural habitat while allowing economic development in areas of lower biological significance, has been described as a potential model for resolving conflicts between conservation and economic concerns (Reid & Murphy 1995). Because participation in the NCCP program was formally recognized as an alternative to the requirements for incidental “take” permits as authorized under Section 10(a) of the ESA, most NCCP efforts in southern California have revolved around planning decisions intended to conserve gnatcatchers and their habitat.

We analyzed the viability of a California Gnatcatcher metapopulation in central and coastal Orange County. Our aims were (1) to develop a habitat suitability model for California Gnatcatcher, (2) to demonstrate how this model can be linked to a metapopulation model for viability analysis, and (3) to analyze the sensitivity of the viability of this species to uncertainties in model parameters.

The NCCP plans that were recently prepared for central and coastal Orange County did not incorporate these results, in part because our analysis was not completed until after the planning process was well underway. Nonetheless, it is our hope that these results will contribute to future NCCP planning efforts elsewhere in southern California, as well as provide a basis for long-term habitat management within the NCCP coastal sage scrub reserve system in central and coastal Orange County.

The Model

We developed a spatially-explicit, stage-structured, stochastic model of the California Gnatcatcher metapopulation based on habitat suitability maps we developed and on demographic data from Atwood et al. (1995, unpublished manuscript). We used the population viability analysis program RAMAS/gis, which is designed to link landscape data from a geographic information system with a metapopulation model (Akçakaya 1995; for another application of the program see Akçakaya et al. 1995; for reviews see Kingston 1995 and Boyce 1996).

We used data on the current distribution of the species’ habitat to find the spatial structure of the metapopulation (i.e., to identify the location, size, and shape of habitat patches in which [sub]populations of the metapopulation exist). In addition to spatial structure, we incorporated parameters related to demography, such as carrying capacities, initial abundances and vital rates of each population, the amount of year-to-year variability in vital rates, as well as the rate of dispersal between patches and the degree of similarity of environmental fluctuations that different populations experience.

We accounted for uncertainties arising from measurement errors and lack of data by making three estimates of each parameter (i.e., estimating lower and upper bounds, in addition to a “medium” estimate). We used these ranges to estimate upper and lower bounds on the estimated viability of the species. In most cases the estimation of a range is quite arbitrary; we used ranges such as ±20% to 100% for parameters based on crude estimates and ranges such as ±5% to 10% for parameters based on more reliable data.

Habitat and Census Data

The habitat variables and census data that formed the basis of our analysis were provided by the GIAS lab of Southern California Edison in the form of digital raster (grid) maps with a resolution of 100 m. These maps described topography, vegetation, and gnatcatcher distribution in approximately 853 km² of central and coastal Orange County.

Topographical data layers included elevation, slope, and aspect, with each grid cell being represented by the value at the cell’s central point. The values for elevation map (named ELV) are elevation in meters above sea level, the values for the slope map (SLP) are in percentages (i.e., 0 for flat areas; 100 for a 45° incline), and the values for aspect (ASP) are in units of degrees from north (e.g., 180 for south, 90 for east and west, 0 for north), ranging from 0 to 180.

Vegetation maps, originally prepared by Jones and Stokes (1993) from color aerial photographs, were converted from ARC/Info coverages to grid (raster) format. Because field experience suggested that the Jones and Stokes (1993) classification of various coastal sage scrub subassociations might include a relatively high degree of subjective interpretation and because a preliminary analysis failed to detect any consistent patterns regarding presence or absence of gnatcatchers in different subassociations, we combined the original 20 subassociations of coastal sage scrub into a single, generalized map. The total amount of coastal sage scrub was calculated for each map cell, with values ranging from 0 m² (no coastal sage scrub) to 10,000 m² (full cover). Because of uncertainties regarding accuracy of the raw vegetation data, each cell in the coastal sage scrub (CSS) data layer was assigned the value of a 9-cell (3×3) moving average of these area estimates.

We also used the Jones and Stokes (1993) vegetation data to create maps of wetland vegetation (including riparian habitat), woody vegetation (combining chaparral, woodland, and forest categories), and grasslands. Based on these maps, we created three data layers describing distance of each cell to (1) the nearest cell with at least 10% cover of trees or other woody vegetation (DTR), (2) the nearest cell of grassland (DGR), and (3) the nearest

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cell of wetland or riparian vegetation (DWT). We believe that variables describing distance to woody vegetation or grassland provide a more objective characterization of coastal sage scrub subassociations than do the classifications used by Jones and Stokes (1993). For example, coastal sage scrub dominated by *Artemisia californica* generally occurs in closer proximity to grassland areas, whereas subassociations dominated by *Salvia mellifera* often occurs near chaparral or oak woodland (and distant from grassland). We truncated distance values greater than 2 km for these data layers.

In surveys of California gnatcatchers (conducted in Orange County in 1991–1992 and 1994), 325 pairs and 80 single individuals were found in 1991–1992, and 238 pairs and 80 single individuals were located in 1994. Cells where one or more pairs were recorded were assigned a value of 1 (present) \(n = 547\). In a separate data layer, which we used for validation purposes, we also assigned a value of 1 (present) to all cells \(n = 129\) where single birds were observed.

Finally, because distributional surveys did not certainly document gnatcatcher absence within the study area, we randomly added 273 (50% of the number of cells where pairs were observed) points intended to represent locations unsuitable for gnatcatchers. We selected these “absent” localities randomly, but with the following constraints. (1) “Absent” localities were not placed within 300 m of cells where pairs or single individuals were observed. Because the species’ territory size may be larger than one 1 ha (Atwood et al., unpublished manuscript), it is likely that cells surrounding an observation point would support suitable habitat even though no observations were obtained in these cells. Similarly, we consider it likely that many observations of single birds occurred in suitable breeding habitat and that areas near these points should not be used to characterize unsuitable habitat. (2) Absent localities were not placed within 300 m of other randomly-placed points because too much clustering would lead to redundancy and not add information to the analysis. (3) Absent localities were not placed in cells dominated by agricultural fields, water, rural development, or residential development. All of these habitat types are clearly not suitable gnatcatcher habitat, and their inclusion would not add information to the analysis.

### Habitat Suitability Map and Patch Structure

We used logistic regression (SAS Institute 1990) to calculate a habitat suitability function, which was then used to calculate an index of habitat suitability for each cell. Logistic regression is indicated in cases where the response (dependent) variable is binary (e.g., 0 or 1). We used a stepwise approach with a significance level of \(p = 0.05\) for adding and removing variables. After all variables were tested, we started adding interaction terms (and removing those that became non-significant). In this phase we retained all previously-added single variables, even if they were rendered not significant with the addition of an interaction term.

The link between the habitat map and the metapopulation model was characterized by two parameters. Threshold HS is the minimum habitat suitability (HS) value below which the habitat is not suitable for reproduction and/or survival. Neighborhood distance is used to identify nearby cells that belong to the same patch and may represent, for example, the foraging distance of the species. These parameters are used by a patch-recognition algorithm that delineates patches on the habitat map. Given these two parameters, the program finds clusters or groups of nearby cells (i.e., within the neighborhood distance of each other) that have HS values higher than or equal to the threshold HS and labels them as patches.

We used 0.5 (i.e., 50%) as the threshold HS; only those cells that had a habitat value of 0.5 or above were considered when habitat patches were analyzed. We used a neighborhood distance of 3 cells, which corresponds to the assumption that any two suitable locations within about 300 m of each other are in the same habitat patch. We analyzed the sensitivity of extinction risk to these two parameters by using a range of 0.45 to 0.55 for the threshold HS parameter and a range of 250 m to 350 m for the neighborhood distance parameter (Table 1).

### Carrying Capacities and Initial Abundances

The program allows the calculation of carrying capacities \(K\) based on the total habitat value of each patch (i.e., the sum of habitat values of all cells that are included in a patch). We estimated carrying capacities based on territory sizes, which were estimated to be 4.69 ha on average in Orange County (Bontrager 1991). We used \(1/4.69 (=0.213)\) as a scaling constant in calculating \(K\) of each patch by multiplying it with the total habitat value in each patch. We used total habitat value instead of the total area as the argument because the latter includes areas with low habitat value. The sum of habitat values in a patch is also related to the area of the patch, but weighted by the amount of habitat in each cell, so that territories in areas with low habitat value are assumed to be larger. We used \(\pm20\%\) of this parameter as the upper and lower limits. We excluded patches with \(K \leq 5\) because only larger populations would have at least one pair of adults at stable stage distribution.

We specified the initial number of individuals in each patch as a fixed proportion of the carrying capacity of that patch. We estimated this proportion based on the ratio of the total number of observed pair locations (for both 1992 and 1994, but excluding the 1994 locations within 150 m of 1992 locations) (503) to the number of pairs (629) predicted by the above calculation of the total carrying capacity. Thus, each patch had a population of 503/629, or 80%
of its carrying capacity at the beginning of the simulation. For the lower limit we used 52% (based on only the 1992 pairs), and for the upper limit we used 100% (assuming some of the singles represent pairs). For all simulations, we assumed the populations have a stable distribution of individuals to stages at the start of the simulation.

Stage Structure

We modeled the dynamics within each patch with a stage-structured, stochastic matrix model with two stages (juveniles and adults). In parameterizing this stage-structured model, we assumed (1) all reproduction in the population takes place in a relatively short breeding season (a post-reproductive census, Caswell 1989); (2) the population is censused immediately after each breeding season (a post-reproductive census, Caswell 1989); (3) all adults breed (so that the proportion of last year’s adults who are breeders this year is simply the survival rate of adults); (4) the maternity rate (number of fledglings per breeder) is the same whether none, one, or both of the breeders are nesting for the first time (i.e., were juveniles last year); and (5) the stage matrix is the same in all populations. With these assumptions, the stage matrix is

\[
\begin{pmatrix}
P_{JB} \cdot M & S_a \cdot M \\
S_j & S_a
\end{pmatrix},
\]

where \(S_a\) is survival rate of adults; \(S_j\) is survival rate of juveniles; \(P_{JB}\) is proportion of last year’s juveniles that are breeders this year; and \(M\) is maternity or fertility (number of fledglings per breeder).

The two elements in the first row of the matrix are fecundities. Adult fecundity \(F_a\) is equal to \(S_a \cdot M\), and juvenile fecundity \(F_j\) is equal to \(P_{JB} \cdot M\). We estimated \(P_{JB}, S_{ar}\), and \(S_j\) based on data from the California Gnatcatcher population on the Palos Verdes peninsula (Atwood et al., unpublished manuscript), and \(M\) based on data from Orange County (Woehler, unpublished manuscript; Bontrager et al., 1995). There were no comparable data on survival from Orange County. The data set represented three transitions: 1993–1994, 1994–1995, and 1995–1996.

The data for 1994–1995 suggests a sharp decline, which is what was observed on the Palos Verdes Peninsula (Atwood et al., unpublished manuscript), as well as in coastal Orange County (Erickson & Pluff, unpublished manuscript; Chambers Group and LSA Associates, unpublished manuscript; Mock, unpublished manuscript). If this is correct, the survival rates for 1994–1995 would be an exception rather than the rule. For this reason, we used the average of 1993–1994 and 1995–1996 transitions to estimate the average stage matrix and the 1994–1995 data as a basis for modeling catastrophes (Table 2).

To calculate upper and lower bound on vital rates, we assumed a measurement error of ±1 individual in the recovery (resighting) of banded individuals. The rationale for these limits is based on the assumption of birth-pulse population. The parameters are estimated assuming that the census is made exactly at the same time each year. If the census is actually made, say, one day earlier than this exact time, then the re-sighting might be an overestimate (if a bird actually dies before the “correct” time). At a practical level, ±1 number for re-sighting is more reasonable than, say, ±10% of the vital rate itself because the latter does not account for differences in sam-

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Table 1. Low, medium, and high estimates of parameters used in the model of the California Gnatcatcher metapopulation.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat-demography</td>
<td>Low</td>
</tr>
<tr>
<td>link Threshold HS</td>
<td>0.45</td>
</tr>
<tr>
<td>Neighborhood distance (m)</td>
<td>250</td>
</tr>
<tr>
<td>Carrying capacity (K) multiplier</td>
<td>0.170</td>
</tr>
<tr>
<td>Initial abundance (as % of K)</td>
<td>52</td>
</tr>
<tr>
<td>Mean dispersal distance (km)</td>
<td>2.5</td>
</tr>
</tbody>
</table>

Stage matrix

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile survival rate (S_j)</td>
<td>0.3275</td>
</tr>
<tr>
<td>Juvenile fecundity (F_j)</td>
<td>0.4901</td>
</tr>
<tr>
<td>Adult survival rate (S_a)</td>
<td>0.4650</td>
</tr>
<tr>
<td>Adult fecundity (F_a)</td>
<td>0.7975</td>
</tr>
</tbody>
</table>

Density dependence

<table>
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<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density dependence type</td>
<td>ceiling</td>
</tr>
<tr>
<td>Allee effects (local threshold as % of K)</td>
<td>0</td>
</tr>
<tr>
<td>Density-dependent dispersal</td>
<td>none</td>
</tr>
</tbody>
</table>

Stochasticity

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard deviations (S)</td>
<td>0.8 (S)</td>
</tr>
<tr>
<td>Correlation of fluctuations (b)</td>
<td>10</td>
</tr>
<tr>
<td>Catastrophe (weather) probability</td>
<td>0.07</td>
</tr>
<tr>
<td>Number of fires</td>
<td>1</td>
</tr>
<tr>
<td>Metapopulation extinction threshold</td>
<td>30</td>
</tr>
</tbody>
</table>

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*a This parameter is multiplied with the total habitat suitability value of the patch to calculate carrying capacity and initial abundance in the patch.

*b S represents the standard deviations given in Table 2.

"See text, page 426, for details."
ple size for different vital rates. The number 1 (instead of 2) is used as a minimum, but even this gave quite large uncertainties at the risk level. The resulting ranges are listed in Table 1.

Environmental and Demographic Stochasticity

We modeled environmental stochasticity by sampling the set of vital rates used to project the dynamics of each population from random (lognormal) distributions with means taken from the mean stage matrix and standard deviations taken from a “standard deviations matrix.” The sampling was done at each time step (in this case each year), thus the required standard deviation is one among years. We estimated these standard deviations based on the variability of survival rates and fecundities from the two transitions (1993–1994 and 1995–1996; Table 2). We used the 1994–1995 transition to model catastrophes, so we did not include this transition in estimating the standard deviations.

We incorporated demographic stochasticity by sampling number of survivors from a binomial distribution and number of offspring from a Poisson distribution (Akçakaya 1991). In addition, we incorporated demographic stochasticity in dispersal.

Catastrophes

One type of catastrophe that may affect species living in coastal sage scrub is fire. Coastal sage scrub is frequently subject to fire, especially in areas where the habitat occurs in close proximity to human population centers (Westman 1982; Keeley 1982). Two fires have occurred within the study area since 1948 (Fig. 5 in NCCP Habitat Conservation Plan prepared by R. J. Meade Consulting, Inc. 1995). In 1982 a fire was located in the area identified here as the second largest patch, and in 1993 one occurred in the area identified as the largest patch. The 1993 fire destroyed habitat occupied by approximately 127 gnatcatcher pairs (Atwood et al., unpublished manuscript), corresponding to about 48% of the initial abundance in the modeled population occupying the largest patch. Based on this we assumed two fires, one affecting the second largest patch in year 34 and the other affecting the largest patch in year 45 in the 50-year simulations of our model. We assumed that each fire will decrease $K$ by 48% and $K$ will increase to its original level in 10 years in each case. Although these assumptions ignore long-term affects of fires, such as potential conversion of coastal sage scrub to grassland (Anderson 1991), we believe they capture most of its short and medium-term effects on gnatcatcher populations. We analyzed the sensitivity of results to fire by running simulations with only one fire (in the largest patch), and with two additional fires affecting the largest and second largest patches in years 25 and 14, respectively.

Another type of catastrophe with direct impact on gnatcatcher populations may be extreme weather conditions, such as those that may have characterized the winter of 1994–1995. In this model, we used the demographic parameters estimated from 1994–1995 to model such catastrophes. We assumed that the effect of such a catastrophe is a sharp decline in vital rates beyond the normal year-to-year fluctuations (see Environmental and Demographic Stochasticity, above). After a catastrophe year, the vital rates are again sampled from the average stage matrix (estimated based on the average of 1993–1994 and 1995–1996 transitions) with the standard deviations given above.

The frequency of such extreme population fluctuations caused by weather conditions is difficult, if not impossible, to estimate because it is not clear which aspect of the weather makes the crucial difference. A statistical estimation is possible only after several years of vital rate estimates. In the absence of such information, we focused on the minimum temperatures in October through December. In the two weather stations closest to the study area (Tustin and Newport), frequency of average of the three monthly minimum temperatures less than or equal to that in 1994 was about 14% in the last 98 years. Thus we chose the annual catastrophe probability of 0.14. We used the range 0.07–0.28 to evaluate the sensitivity of results to this assumption.

Density Dependence and Allee Effects

For most simulations we assumed a ceiling-type density dependence model for each population and used the carrying capacities calculated based on habitat data as population ceilings. This model allows the populations to fluctuate independent of the population size ($N$), according to the stage matrix and the standard deviations matrix, until the population reaches the ceiling. The population then remains at this level until a population fluctuation takes it below the ceiling. We also modeled density dependence with a contest model (which uses the Beverton-Holt equation) with the assumption that

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### Table 2. Stage matrix parameters: juvenile survival rate ($S_j$), proportion juveniles that become breeders ($P_{jB}$), juvenile fecundity ($F_j = P_{jB} \cdot M$), adult survival rate ($S_a$), and adult fecundity ($F_a = S_a \cdot M$).

<table>
<thead>
<tr>
<th>Year</th>
<th>M</th>
<th>$S_j$</th>
<th>$P_{jB}$</th>
<th>$F_j$</th>
<th>$S_a$</th>
<th>$F_a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>1.7</td>
<td>0.2568</td>
<td>0.1757</td>
<td>0.2986</td>
<td>0.5200</td>
<td>0.8840</td>
</tr>
<tr>
<td>1994</td>
<td>2.3</td>
<td>0.1588</td>
<td>0.0909</td>
<td>0.2102</td>
<td>0.1892</td>
<td>0.4375</td>
</tr>
<tr>
<td>1995</td>
<td>1.9</td>
<td>0.4314</td>
<td>0.4118</td>
<td>0.7766</td>
<td>0.4750</td>
<td>0.8958</td>
</tr>
<tr>
<td>Average for (93,95)</td>
<td>0.3441</td>
<td>0.2937</td>
<td>0.5376</td>
<td>0.4975</td>
<td>0.8899</td>
<td></td>
</tr>
<tr>
<td>SD for (93,95)</td>
<td>0.0873</td>
<td>0.1180</td>
<td>0.2390</td>
<td>0.0225</td>
<td>0.0059</td>
<td></td>
</tr>
</tbody>
</table>

*Woehler (unpublished manuscript)

*Average of M from Woehler (unpublished manuscript) and Bontrager, et al. (1995)

*Atwood et al. (1995, unpublished manuscript)
each population grows with a rate of 15% when $N$ is low and is stable with 0% growth when $N = K$.

Allee effects, which may cause a reduction in vital rates when population size becomes very small, are not well-studied for this species. In the current model we incorporated Allee effects by specifying a local extinction threshold for each population. Once any population falls to or below its local threshold, the model assumes the population to be extinct by setting the abundance to zero. The patch then remains unoccupied, unless it is colonized by dispersers from another patch. We set the local thresholds at 0%, 2%, and 4% of the carrying capacity of the patch. By considering a population to be extinct once it reaches or falls below its threshold, the model need not accurately predict the dynamics of the populations at these low abundance levels.

In addition, we specified a metapopulation extinction threshold of 30, 60, or 120 individuals (about 1%, 2%, and 4% of the total initial metapopulation size) and calculated the viability results in terms of falling below this threshold.

### Metapopulation Dynamics: Correlation-distance Function and Dispersal

Parameters related to dynamics at the metapopulation level include the interdependence of environmental fluctuations among populations and patterns of dispersal. The relatively small study area (with the maximum distance between any two patches about 40 km) and the apparent dependence of gnatcatcher biology to weather conditions suggests that weather patterns such as those seen in southern California (affecting substantial areas) impose a correlation structure on the metapopulation dynamics. In a study of the southern California metapopulation of the Spotted Owl, LaHaye et al. (1994) found strong, distance-dependent spatial autocorrelation among rainfall and used this relationship between rainfall and distance as a basis for setting correlation among population dynamics. In our model we used the mid-point of each distance class (in km) as the independent variable ($d$) in the exponential model $M = a \cdot \exp(-d/b)$.

The parameter $b$ is the average dispersal distance. The model was fitted with $a = 0.4$ and $b = 2.5$ km (Fig. 2). In addition, the above equation was modified to reflect a maximum dispersal distance of 15 km. Because of the relative isolation and small size of the Palos Verdes peninsula where these data were collected, we used the fitted function to model minimum dispersal, and set the average dispersal distance to 3.0 and 3.5 km for medium and high dispersal. The distance metric we used in this study is one between the center of the source population to the edge of the target population. The asymmetry of this measure of distance allows for more realistic modeling of dispersal between a large and a small patch.

We assumed adults have negligible dispersal among populations (they can disperse within the same patch) and used dispersal parameters discussed above only for the juvenile stage. We incorporated demographic stochasticity in dispersal among populations by sampling the number of dispersers from a binomial distribution with sample size equal to the number of juveniles in the source population and probability equal to the dispersal rate based on distance.

We modeled density dependence in dispersal for each population such that the dispersal rate was directly proportional to population size. We modeled two levels of published manuscript), who report the number of juveniles that dispersed different distances. We divided the number of dispersing juvenile birds in each distance class by the total sample size (32) to obtain proportion dispersing, and used this as the dependent variable. We used the mid-point of each distance class (in km) as the independent variable ($d$) in the exponential model $M = a \cdot \exp(-d/b)$. In our model $M$ is the dispersal rate, $d$ is the distance (km), and $a$ and $b$ are model parameters. The parameter $b$ is the average dispersal distance. The model was fitted with $a = 0.4$ and $b = 2.5$ km (Fig. 2). In addition, the above equation was modified to reflect a maximum dispersal distance of 15 km. Because of the relative isolation and small size of the Palos Verdes peninsula where these data were collected, we used the fitted function to model minimum dispersal, and set the average dispersal distance to 3.0 and 3.5 km for medium and high dispersal. The distance metric we used in this study is one between the center of the source population to the edge of the target population. The asymmetry of this measure of distance allows for more realistic modeling of dispersal between a large and a small patch.

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![Figure 1. Correlation-distance functions $y = \exp(-x/b)$ used in the model. The function gives the correlation between the vital rates of two populations separated by the indicated distance.](image-url)
density dependence in dispersal, in addition to density-independent dispersal (Fig. 3). Under strong density-dependent dispersal, when the population size \( N \) is lower than the carrying capacity \( K \), the proportion dispersing is lower in proportion to the ratio of \( N/K \). When dispersal is density-independent ("none" on the graph), the dispersal rate is \( M \) regardless of abundance.

**Analysis and Viability Measures Used**

The analysis of the dynamics of the California Gnatcatcher metapopulation with the model described above consisted of a series of simulations. Each simulation consisted of 10,000 replications, and each replication projected the abundance of each population for 50 time steps (years). At each time step the number of juveniles and adults at each population were projected using a set of vital rates drawn from a random (lognormal) distribution.

The mean values of these vital rates (survival and fecundity) were taken from the stage matrix, and the standard deviation of vital rates are those given by the standard deviation matrix. The sampled stage matrices of different populations were correlated according to one of three sets of correlations, whereas the elements of the stage matrix within a population were perfectly correlated. The number of individuals in each stage of each population, as well as the number of dispersers were always integer numbers. These calculations followed the algorithm described by Akçakaya (1995).

To analyze the sensitivity of model results to each parameter, we ran three simulations for each parameter, using the lower, medium, and upper estimates of that parameter and the medium estimates of all the other parameters (Table 1). We used three measures to express the predicted viability of the metapopulation: (1) median time to fall below the metapopulation extinction threshold, (2) risk of falling below the metapopulation threshold anytime within 20 years, and (3) risk of falling below the threshold anytime within 50 years.

**Results**

**Habitat Suitability Map**

The results of the logistic regression analysis are summarized in Table 3. The goodness of fit statistics given at the end of the table show that the regression is highly significant, and the probability column shows that regression coefficients are also statistically significant. Slope, aspect, and distance from wetlands were non-significant.

The frequency distribution of habitat suitability values in the landscape is given in Fig. 4. Only 24% has habitat values of 0.5 or above, and the average habitat suitability is about 0.30. The locations where gnatcatcher pairs were observed have habitat values ranging from 0.14 to 1.00, with an average of 0.86. The frequency distribution of the habitat suitability values of locations with gnatcatcher observations is given in Fig. 5a. About 95% of the observations are in locations with habitat values of 0.5 or above.
Validation of the Habitat Function

Despite the highly significant fit of the data, and the obvious difference between the distribution of habitat suitability (HS) values at all locations and at locations with gnatcatcher observations, this analysis does not provide an independent validation of the habitat function because these are the observations we used in the statistical analysis. One method of validation is to separate the current observations in two and use only one set for estimation and the other set for testing. We separated the observation locations and random points into two sets, dividing the map roughly in half with all coastal observations in the southern half, with all inland observations in the northern half. We re-estimated the habitat function with the northern half of the data set, which gave a slightly different equation from the one estimated with the whole data set. We used this equation to predict the habitat suitability values of observed pair locations in the southern half of the data set, which gives a slightly different equation from the one estimated with the whole data set. We used this equation to predict the habitat suitability values of observed pair locations in the southern half of the data set. Because these observations were not used in the estimation of the function, they can be used to validate the model.

The results of this validation (Fig. 5b) show the frequency distribution of the habitat suitability (HS) values of locations where California Gnatcatcher pairs were observed in all of the study area (a) and in the southern part of the study area (b). The HS values in (b) are predicted using data only from the northern half of the data set, and thus are used as one of three validations of the habitat function.

We made two additional types of validation. We used the function estimated with the location of pairs to pre-
dict the HS values of locations of single birds. About 89% of the single locations were predicted to have a HS value of 0.5 or more. We used a function estimated with the location of pairs in 1992 to predict the HS values of locations of pairs in 1994. About 82% of the pair locations in 1994 were predicted to have a HS value of 0.5 or more. The habitat function estimated with observations of pairs successfully predicted the observations of singles, and the habitat function based on 1992 pairs successfully predicted the observations of 1994 pairs.

**Patch Structure**

Given the habitat map and the (medium) parameter estimates described above the program found 13 habitat patches (clusters of suitable cells within the neighborhood distance of each other). The 2 largest patches made up about 84% of the total area of all patches (Table 4, Fig. 6). Not all cells within the patch boundaries are suitable at the threshold level of 0.5, as discussed above. In other words, the patches have “holes” in them, as represented by the lighter gray regions within patches (Fig. 6). Such areas are not counted in the area of patches, and the habitat values in these areas are not used in the calculation of carrying capacities ($K$) or initial abundances ($N_0$) reported in Table 4. The total carrying capacity was 3357 birds, or (at stable distribution) 629 adult pairs. The total initial abundance was 2952 birds, or 553 adult pairs.

**Viability**

With most parameter combinations, the model predicted a fast decline and a high risk of extinction of the gnatcatcher populations. With medium estimates of all variables, the risk of falling below the metapopulation threshold of 60 individuals was about 19% in 20 years and about 76% in 50 years. The median time to fall below the threshold was about 34 years. The sensitivities of these three results to each parameter are listed in Table 5. These sensitivity results are taken from cumulative time to decline curves (as in Fig. 7). The results were most sensitive to the probability of weather-related catastrophes, and also very sensitive to adult fecundity, juvenile fecundity, and parameters related to density dependence (the type of density dependence, and Allee effects that describe density effects at low abundances). All five parameters caused more than 10 years difference in median time to extinction and/or a difference of more than 0.2 in risk of extinction (falling below the metapopulation threshold) in 50 years.

The results showed moderate sensitivity to seven other parameters: juvenile survival, adult survival, metapopulation extinction threshold, threshold habitat suitability, carrying capacities, standard deviation of fluctuations in vital rates, and density dependence in dispersal. The results were not sensitive to neighborhood distance, initial abundances, dispersal distance, correlation among population fluctuations, and the number of fires.

<table>
<thead>
<tr>
<th>Rank</th>
<th>$K$</th>
<th>Init. abund.</th>
<th>Area (km$^2$)</th>
<th>Area as percentage of patches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1721</td>
<td>1514</td>
<td>101.0</td>
<td>49.82</td>
</tr>
<tr>
<td>2</td>
<td>1130</td>
<td>994</td>
<td>68.8</td>
<td>33.92</td>
</tr>
<tr>
<td>3</td>
<td>133</td>
<td>117</td>
<td>8.2</td>
<td>4.03</td>
</tr>
<tr>
<td>4</td>
<td>124</td>
<td>109</td>
<td>8.8</td>
<td>4.53</td>
</tr>
<tr>
<td>5</td>
<td>72</td>
<td>63</td>
<td>4.3</td>
<td>2.10</td>
</tr>
<tr>
<td>6</td>
<td>39</td>
<td>34</td>
<td>3.1</td>
<td>1.51</td>
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<td>36</td>
<td>32</td>
<td>2.5</td>
<td>1.21</td>
</tr>
<tr>
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<td>32</td>
<td>28</td>
<td>2.1</td>
<td>1.05</td>
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<td>2.0</td>
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<td>11</td>
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<td>7</td>
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<td>2952</td>
<td>202.7</td>
<td>100.00</td>
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dispersal. We used these types of natural variation (environmental and demographic stochasticity in reproduction, survival, and fecundities) and as natural catastrophes. We also modeled a form of randomly distributed vital rates (survivals and fates) due to year-to-year environmental fluctuations and Allee effects. We thus incorporated uncertainty that results from lack of knowledge in the form of parameter ranges. We used these ranges to estimate upper and lower bounds on the estimated viability of the species. In other words, we used natural variability to estimate risks and uncertainties to estimate the uncertainty of these risk estimates.

The sensitivity of results to catastrophe probability is not surprising. Because we did not have enough data to correlate vital rates with weather-related variables, we used a wide range for this parameter. The deterministic, long-term growth rate (eigenvalue, $\lambda$) predicted by the stage matrix (with medium values of vital rates) was above 1.0, and declines and extinctions occurred mostly due to catastrophic declines in the vital rates, as well as year-to-year environmental fluctuations and Allee effects. The declines predicted by the model also explain the insensitivity of metapopulation viability to fires. We modeled fires as causing a decrease in carrying capacity ($K$), but the populations were most of time well below $K$ and thus were not affected by a decline in $K$ caused by fires.

A surprising result was the negative (but weak) effect on the results of three types of validation of the habitat suitability function suggest the function is a good estimator of the quality of habitat in occupied locations. However, the major weakness of this function is the lack of data on absences (locations where gnatcatchers are absent), which forced us to use random locations. This might have caused an overestimation of habitat quality in certain locations. If such data become available, the function may be narrowed, excluding some of the areas now included as habitat in the patches. Another limitation of the habitat map is its geographic coverage. The coastal sage scrub in the study area may be connected to similar habitat in southern Orange county and elsewhere. One of potential improvements to the model involves expanding it to include the populations of California Gnatcatcher in other areas.

One of the specific aims of this analysis was to demonstrate how uncertainty and variability can be incorporated in models for determining the threat a species faces. We incorporated natural variation (resulting from temporal fluctuations in environmental factors) in the form of randomly distributed vital rates (survivals and fecundities) and as natural catastrophes. We also modeled demographic stochasticity in reproduction, survival, and dispersal. We used these types of natural variation (environmental and demographic) to express the model results in probabilistic terms (e.g., risk of decline).

Most parameters are not precisely known because of measurement errors and lack of data. In such cases, we made three estimates of the parameter; estimating lower and upper bounds, in addition to a “medium” estimate. We thus incorporated uncertainty that results from lack of knowledge in the form of parameter ranges. We used natural variability to estimate risks and uncertainties to estimate the uncertainty of these risk estimates.
of dispersal distance on viability, which can be explained by a type of source-sink dynamics. Although all populations in our model had the same vital rates (hence the same $\lambda$), the smaller populations were more prone to extinction as a result of demographic stochasticity. Increased dispersal distance meant a larger number of dispersers going from the more stable larger populations to these smaller and more extinction-prone populations.

To demonstrate that the smaller populations indeed act as sink populations, we ran two other simulations, with the ninth largest and fifth largest populations, by simply deleting the smaller populations. The results of these simulations showed that when the smaller populations were excluded, the risk of decline to any level was lower (Fig. 8). We made this comparison only to demonstrate that small populations can act as sink populations, even if their vital rates are the same as the larger populations. However, this result should not be interpreted in terms of reserve design because we also assumed there was no dispersal to the patches we deleted from the model (i.e., dispersal was only to the patches that remained in the model). There is, of course, no guarantee that gnatcatchers would not attempt to disperse to these areas whether or not they are part of a reserve system.

Increased dispersal had a similar effect of increasing extinction risk in another model: Akçakaya and Baur (1996) concluded that when some populations were modeled as being subject to more severe catastrophes than others, it created a type of source-sink dynamics, which caused this effect. When catastrophes were evenly distributed, increased dispersal caused a decrease in extinction risks.

Two of the model parameters, threshold habitat suitability and metapopulation extinction threshold, have necessarily arbitrary values. The rationale for selecting any value for these thresholds is similar to the one used in deciding a probability level for statistical significance. Just as the level of statistical significance depends on priorities (e.g., whether one wants to minimize Type I or Type II error), so do these parameters. Threshold habitat suitability reflects a compromise between making sure that no suitable habitat is left out and making sure that unsuitable habitat is not included in patches. Similarly, the extinction threshold depends on whether it is more important not to overestimate or not to underestimate extinction risks. It is therefore positive that the results were only moderately sensitive to these parameters.

The results point to a need to better estimate two groups of ecological parameters. One group is the vital rates (especially fecundity) and the frequency and amount of change in vital rates caused by catastrophes. The other group includes density dependence parameters, including Allee effects. Detailed data on vital rates may also help estimate these parameters, for example by comparing fecundities in regions with different density of gnatcatchers. Such a data set may also help link the vital rates to local habitat suitability, eliminating one of the stronger assumptions of our model (that vital rates are the same for all populations).

The sensitivity of results suggests that the results should not be interpreted in absolute terms. Specifically, it would be inappropriate to use the results of this

Figure 7. Sensitivity of risk of decline to adult fecundity ($F_a$). The curves show the probability of falling below the metapopulation threshold as a function of time. The vertical dashed lines show the median time to decline. The arrows show four sensitivity results: the difference between median time to decline (A), the difference in risk of decline in 20 years (B) and 50 years (C), and the maximum difference in risk of decline (D), which in this case occurred around year 40.

Figure 8. Risk of decline (by 80% to 100% from the initial metapopulation abundance) predicted by models with 13, 9, and 5 populations. The vertical line marks the metapopulation extinction threshold of 60 individuals.
model to conclude that gnatcatcher populations in Central/Coastal Orange County are either threatened by extinction or secure from such a threat. There is simply too much uncertainty about most of the parameters to predict with confidence what the population size will be in 50 years or what the risk of extinction might be. Despite this uncertainty, we believe the model can have practical use in two areas.

The sensitivity analysis described is one potential use of modeling in the conservation and management of the coastal sage scrub community; it gives information about which parameters need to be estimated more carefully. Once a model is developed, it can be improved with such analyses carried out at least once a year to incorporate new data collected during that year.

The second use of such a model is to rank management options in terms of their predicted effect on the viability of target species. Results of population viability models such as this one are less reliable if interpreted as absolute predictions than if interpreted as relative to other sets of assumptions or scenarios. Even if results of a model are sensitive to various model parameters, it is possible that relative rankings of management options will not be as sensitive. In other words, the specific predictions of the model may change as a function of parameters and assumptions, but all assumptions may still predict that a particular management option ranks better than its alternatives in terms of the viability of the species. This would make such a relative ranking a much more reliable prediction than a prediction of exactly what the population size would be 50 years from now.

In principle, all possible management actions can be represented as changes in habitat suitability or demographic parameters (including their variances and the initial values of variables such as abundances in each stage and each population). The consequences of these parameter sets can be estimated by the model in terms of the viability of the species and then used to rank alternative management actions, to prioritize conservation measures, and to evaluate the importance of different parameters.

The uncertainty of model results depends on the time horizon of the simulation. The cumulative time to quasi-extinction results showed that the greatest difference between the results given by different parameter combinations occurred around 30 to 40 years. This suggests that the results are most sensitive to changes in parameters when the time horizon is only a few decades. This might be an appropriate time horizon if the model is used in the future to compare alternative management options. Longer or shorter time horizons may underestimate the effects of management actions because the model results may not be as sensitive to changes in parameters (as a function of the simulated effect of the management action). As more demographic and ecological data accumulate, it will become possible to make assessments with longer time horizons.

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Note Added in Proof

Various data in this paper are from submitted, but as yet unpublished, manuscripts. These papers are available from the authors.

Literature Cited


