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RESEARCH ARTICLE

## Restoring habitat for coastal California Gnatcatchers (*Poliioptila californica californica*)

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### ABSTRACT

One goal of Habitat Conservation Plans is to protect viable populations of animal species. Management actions included in such plans often focus on vegetation restoration to benefit the target animal species. Yet, such restoration activities are often uninformed by fine-scale animal survey data. Using the California Gnatcatcher (*Poliioptila californica californica*), we demonstrate how survey data can guide restoration toward the goal of improving gnatcatcher viability by identifying habitat conditions most favorable for gnatcatcher occupancy. We found that gnatcatcher presence and colonization probabilities tripled as the coverage of coastal sagebrush (*Artemisia californica*) increased from 10% to 40%. Coastal sagebrush was more likely to be present at low elevations, and was most closely associated with soil texture of 5%–20% clay, 40%–70% sand, and 20%–40% silt. Higher gnatcatcher extinction probabilities were associated with closed, dense habitat; optimal conditions were between 30% and 40% openness, creating a slightly closed canopy. Open habitat was associated with southern aspects, shallow slopes, and inland areas. An understanding of the soil types and physical parameters of the environment that affect vegetation, especially the amount of coastal sagebrush needed for high gnatcatcher occupancy and colonization rates, will help to define restoration target conditions. Using multiseason, occupancy-based surveys in conjunction with detailed habitat measurements will allow ornithologists and land managers to design powerful restoration prescriptions, even within narrowly defined ecosystems.

**Keywords:** California Gnatcatcher, coastal sage scrub, colonization, extinction, restoration, habitat

### Restauración del hábitat costero de *Poliioptila californica californica*

#### RESUMEN

Uno de los objetivos de los Planes de Conservación de Hábitat es proteger poblaciones viables de especies animales. Las acciones de manejo incluidas en dichos planes a menudo se enfocan en la restauración de la vegetación para beneficiar las especies animales seleccionadas. Sin embargo, tales actividades de restauración a menudo no cuentan con información de base derivada de censos de animales a escala fina. Usando la especie *Poliioptila californica californica*, demostramos cómo los datos de censos pueden orientar la restauración hacia el objetivo de mejorar la viabilidad de *P. c. californica* mediante la identificación de las condiciones del hábitat más favorables para la ocupación de esta especie. Descubrimos que la presencia de *P. c. californica* y las probabilidades de colonización se triplicaron a medida que la cobertura de *Artemisia californica* aumentó de 10% a 40%. *A. californica* presentó una mayor probabilidad de estar presente en las elevaciones más bajas y se asoció más estrechamente con la textura del suelo con 5% a 20% de arcilla, 40% a 70% de arena y 20% a 40% de limo. Las mayores probabilidades de extinción de *P. c. californica* estuvieron asociadas con hábitats densos y cerrados; las condiciones óptimas de apertura fueron de 30% a 40%, creando un dosel ligeramente cerrado. El hábitat abierto se asoció con las orientaciones sur, laderas poco profundas y áreas de interior. Comprender los tipos de suelo y los parámetros físicos del entorno que afectan a la vegetación, especialmente la cantidad de *A. californica* necesaria para altas tasas de ocupación y colonización por parte de *P. c. californica*, ayudarán a definir las condiciones de restauración deseadas. El uso de censos basados en la ocupación de varias estaciones, en conjunto con mediciones detalladas del hábitat, permiten a los ornitólogos y administradores territoriales diseñar prescripciones de restauración potentes, incluso dentro de ecosistemas estrechamente definidos.

**Palabras clave:** colonización, extinción, hábitat, matorral costero de *Artemisia californica*, *Poliioptila californica californica*, restauración

## INTRODUCTION

Implementation of Habitat Conservation Plans is commonly used to aid the recovery and persistence of species of concern (Kareiva et al. 1999). Monitoring of animal population trends is required to assess the effectiveness of these plans (Noss et al. 1997, Case and Fisher 2001). Even so, a disconnect exists between an understanding of the indirect effects of environmental factors that influence vegetation communities and the optimization of conditions for target species. Although habitat suitability models developed using broad-scale data, such as remote sensing, are useful for planning purposes, restoration projects, where the goal is the recovery of populations, are most effective when models are refined using covariates that vary at a smaller scale relative to species occupancy patterns in the field. For example, breeding sites selected for Black Terns (*Chlidonias niger*) using only landscape suitability indices had <20% occupancy (Wyman and Cuthbert 2016). In contrast, Taillie et al. (2015) used both local and landscape level predictors to explain the distribution patterns of Bachman's Sparrows (*Peucaea aestivalis*), and showed that small prescribed burns to control the density of high grass increased the predicted occupancy probability to 75%. This disconnect of scale between landscape-level planning and site-specific restoration often leaves a wide gap between vertebrate conservation and ecological restoration (Cabin 2007, Cabin et al. 2010, DeSimone 2013). Our goal was to lessen this gap by demonstrating an approach that provides guidance for restoring vegetation to benefit animals covered under conservation plans. As a case study, we focused on Habitat Conservation Plans for southern California that aim to preserve or restore habitat for the coastal California Gnatcatcher (*Polioptila californica californica*).

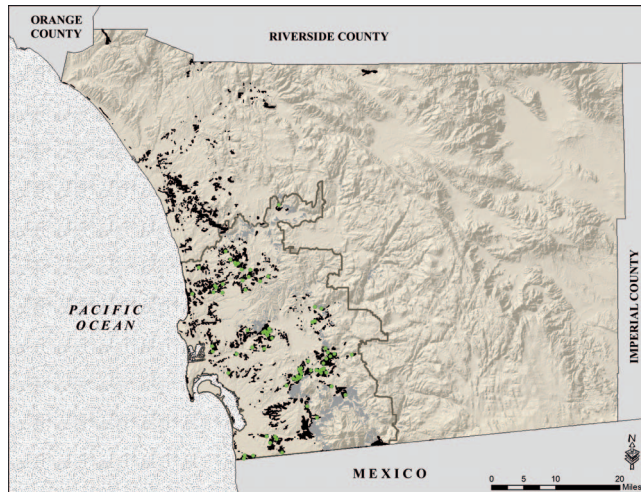
In southern California, the gnatcatcher serves as an umbrella and flagship species for many Habitat Conservation Plans (R.J. Meade Consulting 1996, San Diego County 1998, Dudek Consulting 2006). Past work (Winchell and Doherty 2008, 2014, TAIC 2002) has studied gnatcatcher occupancy as a function of climatic and landscape variables, but this work is of limited utility to restoration ecologists because of the coarse scale of inference. Nonetheless, from these studies we understand that gnatcatcher distribution west of the Peninsular Range Provinces (coastal mountains) is limited by steep slopes, too much precipitation, low temperatures, and high elevations. Thus, colonization is greater on relatively gentle slopes with dry, warm climates that occur mainly at comparatively low elevations. In addition, gnatcatcher occupancy has been found to be strongly dependent on the presence of coastal sagebrush (*Artemisia californica*; Bontrager 1991, Beyers and Wirtz 1997, Atwood et al. 1998).

Preserving and restoring coastal sagebrush has been a key component of actions to improve the viability of the gnatcatcher in southern California, but gnatcatcher monitoring activities have not been directly linked to coastal sagebrush restoration activities (e.g., Winchell and Doherty 2008, 2014). Questions about the optimal spacing and density of coastal sagebrush for gnatcatcher presence, whether nonnative plants affect gnatcatcher presence, and what vegetation characteristics are related to gnatcatcher occupancy, colonization, and extinction all need answers. Identifying suitable locales for restoring coastal sagebrush, and thus gnatcatchers, is the next step. In particular, identifying combinations of aspect, slope, and soil type that are most likely to produce optimal vegetation conditions can focus restoration. Our goal was to guide restoration at a scale relative to habitat usage by nesting pairs of gnatcatchers. We measured biological and environmental parameters to determine what covariates maximized sustained occupancy by gnatcatchers. Our objectives were to analyze gnatcatcher occupancy dynamics (occupancy, local colonization, and extinction) in relation to habitat covariates (e.g., vegetation and soil types) at a finer scale than has been done with previous models. This information can guide land managers toward more effective restoration and maintenance of gnatcatcher habitat.

## METHODS

We worked within San Diego County, California, USA, on lands designated as public or quasi-public, and on some military lands (Figure 1). In general, the area included preserve lands regulated under Habitat Conservation Plans, other public lands designated as open space and regulated by local jurisdictions, and lands separately managed by Marine Corps Air Station Miramar or Naval Weapons Station Seal Beach, Detachment Fallbrook. All lands had some component that was distinctly managed for gnatcatcher conservation. Marine Corps Base Camp Pendleton, private lands, and Tribal lands were excluded from the sampling frame because of access limitations, logistic difficulties, and liability concerns.

We collected data on gnatcatchers and their habitat in 2004, 2007, and 2009 as part of the San Diego Multiple Species Conservation Program (San Diego County 1998). Each study year recorded below average rainfall for San Diego County. During our entire survey time frame, only 2005 had above average rainfall. Because we sought to use fine-scale data for our occupancy analyses, we focused on areas that were within strata labeled as high or very high quality by TAIC (2002), were generally within the preferred climatic and landscape conditions identified by previous analyses (Winchell and Doherty 2014), and were located where gnatcatchers were more likely to occur. These strata represented habitat covering 22,230 ha. In 2007, our study



**FIGURE 1.** Map shows San Diego County shaded in tan. Lands modelled as Very High and High quality California Gnatcatcher habitat is marked as black for unburned and dark gray habitat that burned during 2003 and 2007 wildfires. The black outline in the southwest corner is the boundary of the San Diego Multiple Species Conservation Program area within which are randomly positioned 76 sample points, marked as yellow dots.

area experienced a massive wildfire, reducing our area to 14,150 ha and our sample size to 76 survey point locations that were unburned and thus still likely to have gnatcatchers. Bird survey details have been previously described (Winchell and Doherty 2008, 2014); in brief, point locations were surveyed for gnatcatchers for 15 min during 5–6 visits each year during the breeding season. We included gnatcatcher observations within 50 m of survey points, with distance determined using a rangefinder. From these data, multiple season robust design occupancy encounter histories were constructed (MacKenzie et al. 2003), from which gnatcatcher occupancy, local colonization, local extinction, and detection probabilities were estimated.

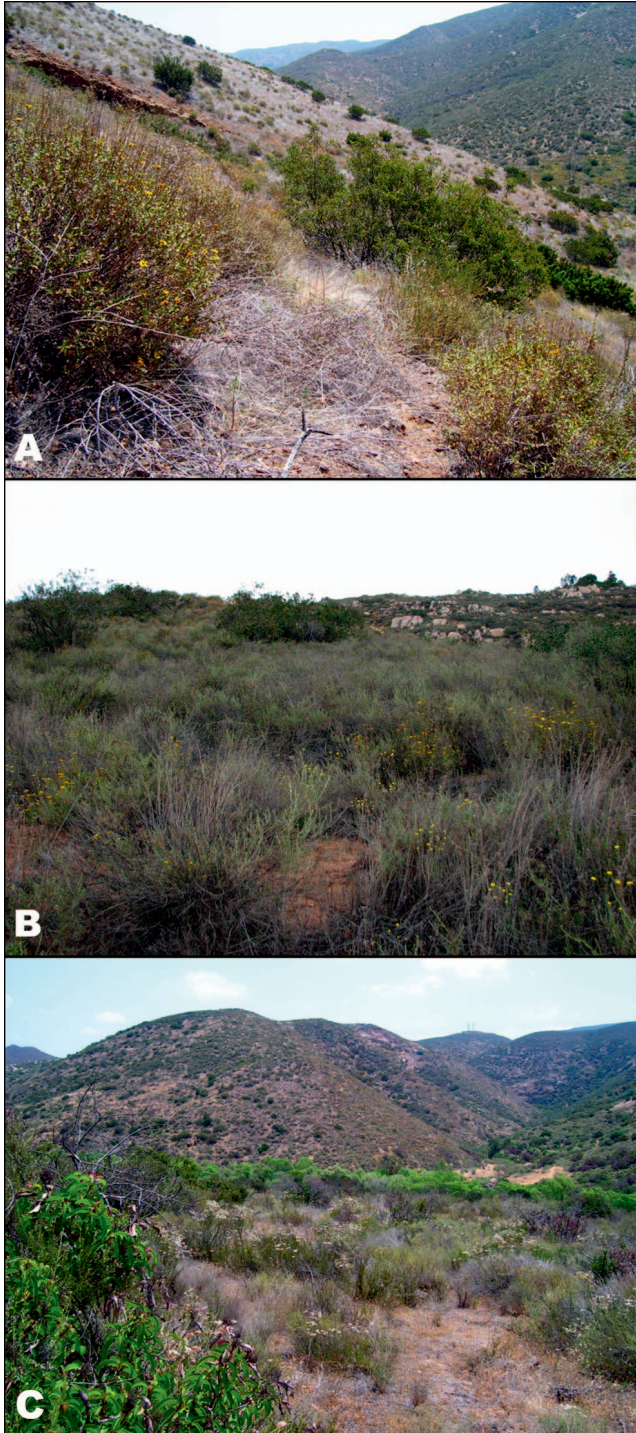
In 2007, we collected habitat data along two 50-m transects centered on each of the 76 survey points. The first transect was along a random azimuth, establishing a 50-m radius, whereas the second transect was along a random azimuth at least  $\pm 45^\circ$  from the first transect. We conducted habitat measurements every 2 m along each transect for a total of 50 sampling locations associated with each gnatcatcher survey point. At each of the 50 locations, we recorded the presence of any vegetation, as well as the presence of individual grass, herb, shrub, and tree species. We summarized these data as the proportion of the 50 locations at which no plant species occurred, the proportion at which a particular plant species or growth form (grass, herb, shrub, tree) occurred, as well as whether a plant species was detected at any of the locations. We also collected a soil sample at each survey point, from

which we derived the percentage of clay, sand, and silt (Bouyoucos 1962, Gee and Bauder 1979). Additionally, we collected soil samples at the end of each transect to determine whether soil texture was homogeneous within our 50-m radius area.

### Predictions and Analysis

We first tested predictions concerning gnatcatcher occupancy, colonization, extinction, and detection probabilities. Specifically, we thought that gnatcatcher occupancy and colonization probabilities would be positively associated with, and extinction probability would be negatively associated with, the proportion of coastal sagebrush coverage (ARCA; Figure 2). We also anticipated an optimal intermediate level of coastal sagebrush coverage, so we included a quadratic term for the proportion of coastal sagebrush (ARCA<sup>2</sup>; Figure 2). Similarly, we predicted that higher proportional coverage of invasive nonnative grasses or herbs, such as black mustard (*Brassica nigra*) and stork's bill (*Erodium* spp.), would be negatively associated with gnatcatcher occupancy and colonization probabilities, and positively associated with extinction probability, because invasives may compete for water with germinating native plants and may provide cover for predators. We predicted that higher proportional coverage of black sage (*Salvia mellifera*; SAME) would be negatively associated with gnatcatcher occupancy and colonization probabilities but positively associated with extinction probability were gnatcatchers to be averse to using black sage due to its dense structure and limited forage (Robinson and Holmes 1982, Roach 1989). We predicted that the presence of laurel sumac (*Malosma laurina*; MALA) would be positively associated with gnatcatcher occupancy and colonization, but negatively with gnatcatcher extinction, because laurel sumac is frost intolerant (Riggan et al. 1994) and gnatcatchers are sensitive to temperatures below 4.5°C (Root 1988, Mock 1998); thus, we viewed MALA as a fine-scale indicator of temperatures. We predicted that gnatcatchers might prefer more openness (proportion of locations with no trees or shrubs; Atwood and Bontrager 2001) in their territories (Figure 2). Thus, we thought that openness would be positively associated with occupancy and colonization probabilities and negatively associated with extinction probability, as gnatcatchers frequently forage for tiny insects by flying between shrubs rather than hopping from shrub to shrub, and can probably not forage as efficiently in dense vegetation. None of these predictor variables were correlated ( $r > |0.47|$ ), and, since all were proportions or binomial, we did not rescale the variables prior to analysis. Based on past analyses (Winchell and Doherty 2014), we predicted that detection probability would be constant among years ( $t$ ); we tested this prediction by including constant and annually variable detection structures in our modeling efforts.





**FIGURE 2.** Examples of proportional coastal sagebrush (*Artemisia californica*) coverage found at our survey points used to identify habitat conditions favorable for California Gnatcatchers in southern California, USA: (A) Open habitat with very little coastal sagebrush. This survey point was never occupied by gnatcatchers during all 3 survey years; (B) Closed habitat dominated by coastal sagebrush. This survey point was never occupied during all 3 survey years; and (C) Moderately open habitat with a diverse shrub community, of which 30%–40% is composed of coastal sagebrush. This survey point was occupied by gnatcatchers during all 3 survey years.

We incorporated the above predictions into models using the dynamic occupancy model of Mackenzie et al. (2003) in program MARK (White and Burnham 1999). This model permits estimates of occupancy, colonization, extinction, and detection probabilities. If occupancy at time  $t$ , colonization, and extinction are estimated, then occupancy at time  $t + 1$  can be derived. Thus, we estimated the initial occupancy probability (in 2004), as well as time-specific colonization and extinction probabilities, and derived future occupancy estimates. Our surveys did not occur at equal intervals (i.e. 2004, 2007, and 2009), so we standardized the modeling and estimation of colonization and extinction between surveys on an annual basis. We had to assume that annual colonization and extinction probabilities were identical within survey intervals because of the lack of intervening survey data. For example, we had to assume that the colonization probabilities from 2007 to 2008 and from 2008 to 2009 were the same. Considering the above parameters, hypotheses, and limitations, we constructed 92 submodels for colonization, 92 submodels for extinction, 46 submodels for occupancy, and 2 submodels for detection.

Model building and selection is challenging when using models with numerous submodels (e.g., occupancy, colonization, extinction, and detection) and many covariates due to the large number of possible models (Doherty et al. 2012, Bromaghin et al. 2013). To reduce the number of models, we used a strategy similar to that of Bromaghin et al. (2013) by focusing on a set of plausible submodels and variables and combining these submodels in all possible combinations to examine the effects of the remaining covariates. We first focused on each parameter (i.e. occupancy, colonization, extinction, and detection) by holding the other 3 parameters constant. This procedure forced the maximum amount of explainable variation into the focal parameter. For each focal parameter, we constructed models representing all possible additive combinations of predictor variables for a balanced model set and calculated cumulative Akaike model weights for each predictor variable (Burnham and Anderson 2002). Barbieri and Berger (2004) implied that variables with  $>0.5$  cumulative Akaike weights have meaningful relationships with parameters of interest; at this stage in our analysis, we used a more liberal cutoff of 0.4 cumulative Akaike weight to avoid eliminating variables. Using the reduced set of predictor variables for each parameter, we then constructed all possible additive combinations of models across all parameters for a final, balanced model set and used Akaike's information criterion with small sample size correction ( $AIC_c$ ) for model selection and for calculating cumulative Akaike weights for each predictor variable. Following Barbieri and Berger (2004), and maintaining our liberal 0.4 cumulative Akaike weight cutoff for consistency, we defined the model that contained

**TABLE 1.** Cumulative Akaike model weights for each variable used to model the occupancy, colonization, extinction, and detection rates of California Gnatcatchers in San Diego County, California, USA, in relation to habitat parameters. We constructed all possible additive combinations of variables for each parameter while holding the other 3 parameters constant. Variables with cumulative weights  $>0.4$  were used in further modeling. ARCA is the proportion of 50 transect intersections ('locations') associated with each gnatcatcher survey point ('point') with coastal sagebrush (*Artemisia californica*) as a linear term, and ARCA<sup>2</sup> is a quadratic model; Openness is the proportion of locations at a point with no vegetation; Invasive is the proportion of locations at a point with nonnative grasses (black mustard [*Brassica nigra*] or stork's bill [*Erodium* spp.]); SAME is the proportion of locations at a point with black sage (*Salvia mellifera*); MALA is the proportion of locations at points with laurel sumac (*Malosma laurina*) present (0 = absent, 1 = present). The range of values appears in parentheses after the variable name. Asterisks (\*) denote that variables were not considered for a particular parameter. Appendix Table 5 shows the top 10 models for each parameter.

Parameter	ARCA (0.00–0.37)	ARCA <sup>2</sup>	Openness (0.02–0.99)	Invasive (0.00–0.10)	SAME (0.00–0.63)	MALA (0, 1)	Year (2004–2009)
Occupancy	0.44	0.43	0.50	0.34	0.37	0.43	<sup>§</sup>
Colonization	0.60	0.35	0.15	0.29	0.30	0.21	0.86
Extinction	0.54	0.20	0.75	0.28	0.28	0.41	0.51
Detection	*	*	*	*	*	*	0.51

<sup>§</sup> Occupancy was estimated for the first year and derived in future years with estimates of extinction and colonization.

all independent variables with  $\geq 0.4$  cumulative Akaike weight as our predictor model from which to produce estimates.

The above analyses identified which vegetation parameters were correlated with gnatcatcher occupancy, colonization, and extinction probabilities. Understanding how vegetation is correlated with soil type and other variables can help to identify ideal locations for restoration, so we focused on explaining variation in the presence of coastal sagebrush, laurel sumac, and openness (i.e. lack of trees or shrubs). We focused on the 5 vegetation sampling locations along each transect nearest to our center-point soil sample, instead of all sampling locations, because we found that soil texture differed at the end of at least one transect at 17% of our survey points. We viewed the 10 locations as repeated vegetation measures associated with each center point and used a repeated measures logistic regression in which the dependent variable was the presence or absence of the plant species of interest. As independent variables, we considered soil texture, aspect, slope, elevation, and distance to the coast of the center point. Because soil texture has 3 components (percent clay, percent sand, percent silt) that sum to 100%, the 3 values are not independent. We followed Aitchison's (1986) advice for analyzing such compositional data: We used a log-ratio transformation of percent clay and percent sand relative to percent silt because percent silt showed the least variation across our sampled points. Aspect (degrees) can influence vegetation through the amount of solar radiation (Kirkby et al. 1990), so we transformed our aspect measures by taking the cosine of the radian to address the circular nature of the degree measurement, thus equalizing the gradient in aspect in both directions of north (Beers et al. 1966, McCune and Keon 2002). We thought that elevation (m), slope (degrees), and distance to the coast (m; because of the fog that can develop) could

predict where particular plant species grow. We constructed all possible additive combinations of predictor variables and relied upon AIC<sub>c</sub> for model selection and for calculating cumulative Akaike weights for each predictor variable. We report estimates and standard errors (SE) unless otherwise noted.

## RESULTS

Using gnatcatcher survey data (summarized in Appendix Table 4), our first set of analyses focused on each parameter (occupancy, colonization, extinction, and detection) separately and helped to reduce the number of predictor variables for further modeling. We identified ARCA, ARCA<sup>2</sup>, openness, and MALA as relevant for further analysis of occupancy; ARCA and year for analysis of colonization; ARCA, openness, MALA, and year for analysis of extinction; and year for analysis of detection (Table 1). We then constructed all possible combinations of these variables for our final model set and calculated cumulative Akaike model weights for each variable (Table 2). Influential predictors were ARCA, ARCA<sup>2</sup>, openness, and MALA for occupancy; ARCA and year for colonization; and openness and MALA for extinction (Table 2).

We found that gnatcatcher occupancy probability increased with proportional coastal sagebrush coverage (Figure 3), with  $>30\%$  coastal sagebrush coverage resulting in high occupancy probabilities. Occupancy was slightly negatively associated with the proportion of openness (i.e. lack of trees and shrubs;  $\beta = -1.95 \pm 1.46$ ) and with the presence of laurel sumac ( $\beta = -0.92 \pm 0.68$ ). Colonization probability increased with proportional coastal sagebrush coverage (Figure 4). Gnatcatcher colonization probability was greater in 2007–2009 than in 2004–2007. Extinction probability was negatively correlated with openness (Figure 5) and increased with the presence of laurel sumac



**TABLE 2.** Cumulative Akaike model weights for each variable used to model the occupancy, colonization, extinction, and detection rates of California Gnatcatchers San Diego County, California, USA, in relation to habitat conditions, from models with all possible additive combinations of the variables. See Table 1 for variable codes. Asterisks (\*) denote that variables were not considered for a particular parameter. The model containing all variables with  $\geq 0.4$  cumulative Akaike weight was the predictor model used in Figures 2–4. Appendix Table 6 shows the models with  $\Delta AIC_c < 2$ .

Parameter	ARCA	ARCA <sup>2</sup>	Openness	MALA	Year
Occupancy	0.44	0.42	0.40	0.40	<sup>s</sup>
Colonization	0.94	*	*	*	0.80
Extinction	0.29	*	0.82	0.49	0.30
Detection	*	*	*	*	0.27

<sup>s</sup>Occupancy was estimated for the first year and derived in future years with estimates of extinction and colonization.

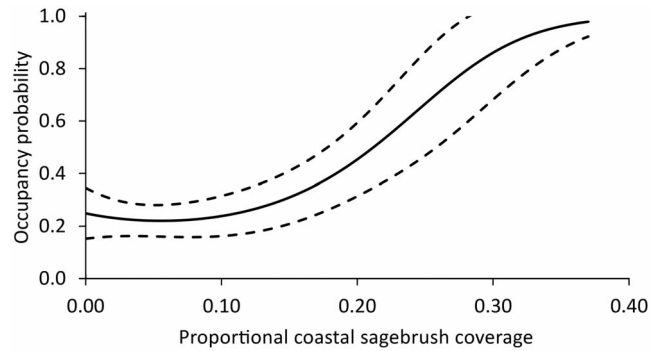
( $\beta = 1.16 \pm 0.76$ ). The detection probability of gnatcatchers was  $0.42 \pm 0.03$  per survey visit.

Following the above analysis, we investigated how the presence of coastal sagebrush, openness, and laurel sumac depended on soil texture, aspect, slope, elevation, and distance to the coast. We found that soil texture and elevation were useful predictors of the amount of coastal sagebrush coverage. Aspect, slope, and distance to the coast all had cumulative Akaike weights greater than 0.40 for predicting openness. None of our variables were useful predictors of laurel sumac presence (Table 3).

We primarily found coastal sagebrush in soil textures ranging from 5% to 20% clay, 40% to 70% sand, and 20% to 40% silt. These soils were more likely to be present at low elevations, although the relationship with elevation was not strong ( $\beta = -0.003 \pm 0.003$ ). Openness (absence of trees and shrubs) declined on steep slopes (Figure 6) and had a weak positive relationship with aspect ( $\beta = 0.305 \pm 0.248$ ). Upon further examination, distance to the coast

**TABLE 3.** Cumulative Akaike model weights for independent variables used to investigate the presence of coastal sagebrush (*Artemisia californica*; ARCA), laurel sumac (*Malosma laurina*; MALA), and the absence of trees and shrubs (Openness) at California Gnatcatcher survey points in San Diego County, California, USA. We constructed all possible additive combinations of independent variables for each dependent variable for a balanced model set. The range of values appears in parentheses after each variable name. Appendix Table 7 shows the top 10 models for each dependent variable.

Dependent variable	Soil texture	Elevation (24–386 m)		Distance to coast (1.37–34.35 km)	
		Aspect (0–360°)	Slope (0–35°)		
ARCA	1.00	0.43	0.31	0.32	0.29
MALA	0.34	0.39	0.35	0.38	0.37
Openness	0.14	0.37	0.45	0.96	0.42

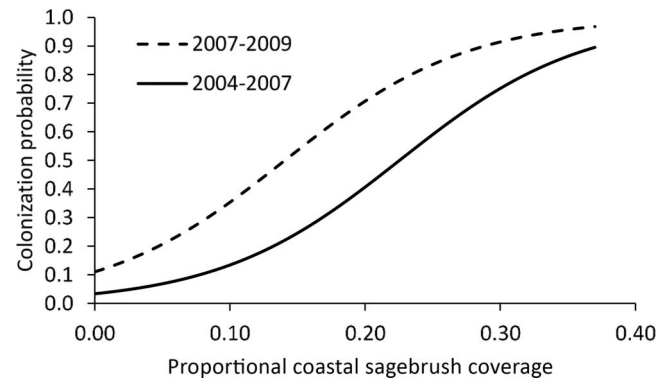


**FIGURE 3.** Occupancy ( $\pm 1$  SE) of surveyed points by California Gnatcatchers increased with the proportion of coastal sagebrush (*Artemisia californica*) present in southern California, USA.

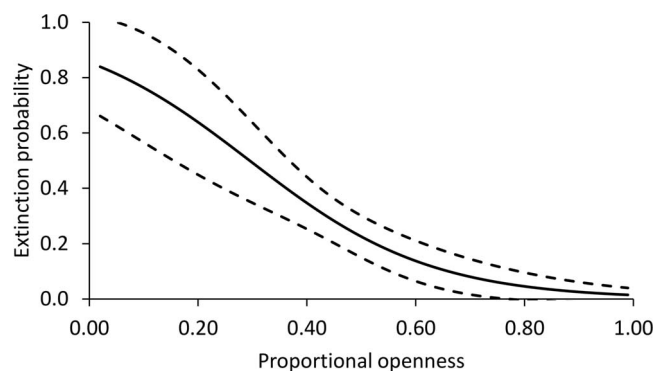
was found to be an uninformative parameter (Arnold 2010;  $\beta = 0.269E-4 \pm 0.201E-4$ ).

## DISCUSSION

Our results support the observation that coastal sagebrush strongly influences gnatcatcher presence (Figure 3; Atwood and Bontrager 2001). In turn, coastal sagebrush presence is influenced by soil texture and elevation. We also found that gnatcatcher colonization probabilities were most closely associated with coastal sagebrush (Figure 4). These results give some insight into the dynamic processes underlying gnatcatcher population dynamics. We found that gnatcatcher occupancy (Figure 3) and colonization (Figure 4) increased with coastal sagebrush coverage and were highest with coastal sagebrush coverage of 30%–40% of the plant community, the maximum values recorded at our sites. Restorationists might try to artificially increase coastal sagebrush coverage above 40% through plant pallet composition and irrigation, but we caution against such an approach as this may not be a situation found in natural



**FIGURE 4.** Colonization of unoccupied habitat by California Gnatcatchers increased with the proportion of coastal sagebrush (*Artemisia californica*) present in southern California, USA, and was greater in 2007–2009 than in 2004–2007.

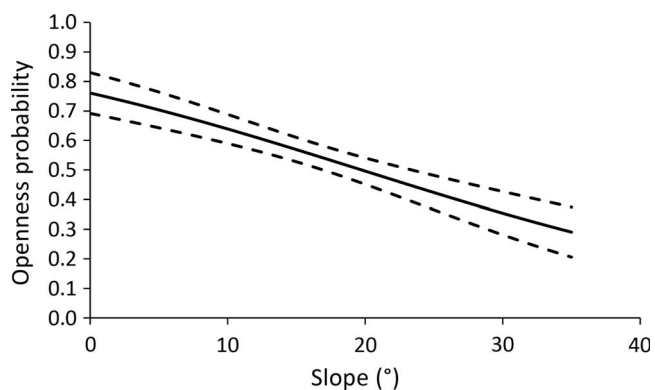


**FIGURE 5.** The extinction ( $\pm 1$  SE) probability for California Gnatcatchers decreased with an increasing proportion of openness (i.e. lack of trees and shrubs) in southern California, USA.

communities (Sproul et al. 2011). Instead, coastal sagebrush coverage of at least 30% might be a good target for restoration activities. In addition, we found that coastal sagebrush presence was most closely associated with a soil texture of low clay, moderate sand, and moderate silt, a type of soil most likely to be found at low elevations.

Identifying highly suitable locations for sagebrush and testing soil texture prior to restoration will likely lead to increased probabilities of coastal sagebrush restoration success. Gnatcatcher extinction probability was highest in dense vegetation (Figure 5). Restoration activities close to the coast and on slopes less than  $20^\circ$  (Figure 6) are likely to lead to vegetation characteristics preferred by gnatcatchers. Sites with these characteristics have extinction probabilities  $<50\%$ . We recommend that land managers evaluate the physical parameters of the ecosystem, namely soil, slope, and elevation, and use these factors to predict where coastal sagebrush will best thrive and thereby provide habitat for gnatcatchers. Although we focused on occupancy and related parameters to define important habitat used by birds, other demographic parameters such as abundance, survival, and reproduction should also be considered. However, demographic parameters are often difficult to estimate. In the absence of such parameter estimates, especially when management funds are limited and disjointed, we believe that relying on occupancy-related parameters can lead to successful restoration.

One of our original predictions was that laurel sumac would be positively correlated with occupancy because gnatcatchers are frost intolerant. We found the opposite: Gnatcatcher extinction probability increased with the presence of laurel sumac. This result may have been a factor of scale and location. Gnatcatcher occupancy increased closer to the coast. Near the coast, laurel sumac is located on moist, cool, northern-aspect slopes (Holland 1986, Bartolome et al. 2007) and is a primary component of chaparral-type communities, where gnatcatchers have



**FIGURE 6.** The probability ( $\pm 1$  SE) of openness (no trees or shrubs) declined on steep slopes in southern California, USA.

low occupancy probabilities (Winchell and Doherty 2008). Inland, laurel sumac sparsely populates midelevation valleys where coastal sage scrub occurs and frost is a rare event. Laurel sumac may be a good indicator of gnatcatcher habitat in areas away from the coast; however, such areas are limited as interior land was converted to avocado farms early in the 20<sup>th</sup> century (Coit 1963, Shepherd and Bender 2001).

The composition of other shrubs may not be as significant as the presence of coastal sagebrush for gnatcatcher habitat. We found that our predictions pertaining to invasive plants and black sage were not supported, perhaps because other plants in the communities dominated by coastal sagebrush can be quite variable. For example, Westman (1981) found a high degree of variability in species diversity in coastal sage scrub plant communities. Eastern Mojave buckwheat (*Eriogonum fasciculatum*), the second most dominant plant in coastal sage scrub (Roach 1989), is not necessarily present in sites used by gnatcatchers (Atwood 1990). However, all of Atwood's (1990) sites contained coastal sagebrush. Decreased diversity of perennials may increase nest success, at least within plots with a certain amount of perennial heterogeneity (Braden et al. 1997).

Although we found that gnatcatcher occupancy probability slightly increased as the proportion of openness decreased and cover became denser, a stronger relationship existed with extinction probability: Gnatcatcher extinction probability was highest in the least open sites, and exceeded 50% with openness  $<30\%$  (Figure 5). Bontrager (1991) and Braden et al. (1997) reported that areas of dense vegetation had fewer gnatcatchers, and that fledging success increased with increasing cover of grasses and forbs. For restoration, it may be important to balance extinction probability and occupancy probability with a shrub density between 30% and 40% openness, maintaining a slightly closed canopy. Managing openness requires constant maintenance, such as cutting or prescribed fire.



Once the desired shrub density is established, we recommend maintaining 40% coastal sagebrush composition within the shrub community.

Coastal sage scrub is associated with steeper topography, with grasslands in flatter areas (Westman 1982, Bartolome et al. 2007). This relationship may explain the association that we found between slope and openness, wherein steeper slopes were less open. Areas with slopes  $>20^\circ$  had  $<50\%$  probability of being open (Figure 6). None of our sites had slopes greater than  $35^\circ$ ; steep slopes in Mediterranean climates tend to be highly erodible (Morgan 2005) and unable to support stable plant communities such as coastal sage scrub. We did not sample these steep slopes, as they did not include scrub vegetation.

Restoration projects in coastal sage scrub habitats should start with targeting loam or sandy loam soils. Loamy sands should be given a lower priority and clay soils (clay loam, sandy clay loam, and sandy clay) should generally be avoided. Next, low-elevation sites with southern exposures should be given priority. Sites with elevations  $<100$  m have a  $>50\%$  chance of coastal sagebrush being present. If low-elevation sites, which are typically nearer to the coast, are not available, then sites with sparse laurel sumac could be restored, as gnatcatchers are limited by winter temperatures below  $1.1^\circ\text{C}$  (Root 1988). Finally, areas with greater topographic relief should be selected over flatter areas because steeper areas are associated with coastal sage scrub. Communities dominated by coastal sagebrush should be a goal of restoration for gnatcatchers. Areas should be managed to maintain 30%–40% coastal sagebrush coverage, thus revegetative plantings should be dominated by coastal sagebrush, but include a diversity of other shrubs found in occupied sites, such as Eastern Mojave buckwheat, torhleaf goldeneye (*Viguiera laciniata*), common deerweed (*Lotus scoparius*), coyotebrush (*Baccharis pilularis*), laural sumac, or black sage.

Habitat Conservation Plans (HCP) are predicated on maintaining viable populations of animal species of concern, with management actions focused on supporting this goal. In southern California, HCPs have been established to maintain flagship or umbrella species that represent the rich biodiversity of the California Floristic Province (Myers et al. 2000). As in many other systems, vegetation restoration is a common management action, but is seldom informed by animal survey data. Our results demonstrate how occupancy surveys combined with vegetation and abiotic measurements can inform both site selection and management actions that may be beneficial to California Gnatcatchers and potentially the diverse suite of species under the umbrella of their HCP.

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## LITERATURE CITED

- Aitchison, J. (1986). *The Statistical Analysis of Compositional Data*. Chapman and Hall, London, UK.
- Atwood, J. (1990). Status Review of the California Gnatcatcher (*Poliioptila californica*). Manomet Bird Observatory, Manomet, MA, USA.
- Atwood, J. L., and D. R. Bontrager (2001). California Gnatcatcher (*Poliioptila californica*), version 2.0. In *The Birds of North America* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.574>
- Atwood, J. L., S. H. Tsai, C. A. Reynolds, and M. R. Fugagli (1998). Distribution and population size of California Gnatcatchers on the Palos Verdes Peninsula, 1993–1997. *Western Birds* 29: 340–350.
- Barbieri, M. M., and J. O. Berger (2004). Optimal predictive model selection. *Annals of Statistics* 32:870–897.
- Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson (2007). Valley grassland. In *Terrestrial Vegetation of California*, third edition (M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, Editors). University of California Press, Berkeley, CA, USA. pp. 367–393.
- Beers, T. W., P. E. Dress, and L. C. Wensel (1966). Notes and observations: Aspect transformation in site productivity research. *Journal of Forestry* 64:691–692.
- Beyers, J. L., and W. O. Wirtz, II (1997). Vegetative characteristics of coastal sage scrub sites used by California Gnatcatchers: Implications for management in a fire-prone ecosystem. In *Fire Effects on Rare and Endangered Species and Habitats*. Proceedings of a conference held in Coeur d'Alene, Idaho, November 13–16, 1995 (J. M. Greenlee, Editor). International Association of Wildland Fire, Fairfield, WA, USA. pp. 81–89.
- Bontrager, D. R. (1991). Habitat requirements, home range and breeding biology of the California Gnatcatcher (*Poliioptila californica*) in south Orange County, California. Unpublished technical report prepared for the Santa Margarita Company, Rancho Santa Margarita, CA, USA.

- Bouyoucos, G. J. (1962). Hydrometer method improved for making particle size analysis of soils. *Agronomy Journal* 54: 464–465.
- Braden, G. T., R. L. McKernan, and S. M. Powell (1997). Association of within-territory vegetation characteristics and fitness components of California Gnatcatchers. *The Auk* 114:601–609.
- Bromaghin, J. F., T. L. McDonald, and S. C. Amstrup (2013). Plausible combinations: An improved method to evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. *Open Journal of Ecology* 3:11–22.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second edition. Springer-Verlag, New York, NY, USA.
- Cabin, R. (2007). Science-driven restoration: A square grid on a round earth? *Restoration Ecology* 15:1–7.
- Cabin, R. J., A. Clewell, M. Ingram, T. McDonald, and V. Temperton (2010). Bridging restoration science and practice: Results and analysis of a survey from the 2009 Society for Ecological Restoration International Meeting. *Restoration Ecology* 18:783–788.
- Case, T. J., and R. N. Fisher (2001). Measuring and predicting species presence: Coastal sage scrub case study. In *Spatial Uncertainty in Ecology: Implications for Remote Sensing and GIS Applications* (C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case, Editors). Springer-Verlag, New York, NY, USA. pp. 47–71.
- Coit, J. E. (1963). *The California Avocado Society: A Historical Sketch*. Special Publication of the California Avocado Society, San Juan Capistrano, CA, USA.
- DeSimone, S. A. (2013). Restoration and science: A practitioner/scientist's view from rare habitat restoration at a southern California preserve. *Restoration Ecology* 21:149–152.
- Doherty, P. F., G. C. White, and K. P. Burnham (2012). Comparison of model building and selection strategies. *Journal of Ornithology* 152 (Suppl. 2):317–323.
- Dudek Consulting (2006). Southern Orange County subregion natural community conservation plan/master streambed alteration agreement/habitat conservation plan. County of Orange Planning and Development Services Department, Santa Ana, CA, USA.
- Gee, G. W., and J. W. Bauder (1979). Particle size analysis by hydrometer: A simplified method for routine textural analysis and a sensitivity test of measurement parameters. *Soil Science Society of America Journal* 43:1004–1007.
- Holland, R. F. (1986). Preliminary Descriptions of the Terrestrial Natural Communities of California. State of California, The Resources Agency, Department of Fish and Game, Sacramento, CA, USA.
- Kareiva, P., S. Andelman, D. Doak, B. Elderd, M. Groom, J. Hoekstra, L. Hood, F. James, J. Lamoreux, G. LeBuhn, C. McCulloch, et al. (1999). *Using Science in Habitat Conservation Plans*. National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA, USA, and American Institute of Biological Sciences, Washington, DC, USA.
- Kirkby, M. J., K. Atkinson, and J. Lockwood (1990). Aspect, vegetation cover and erosion on semi-arid hillslopes. In *Vegetation and Erosion: Processes and Environments* (J. B. Tornes, Editor). John Wiley and Sons, Chichester, West Sussex, UK. pp. 25–39.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- McCune, B., and D. Keon (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.
- Mock, P. J. (1998). Energetic constraints to the distribution and abundance of the California Gnatcatcher. *Western Birds* 29: 413–420.
- Morgan, R. P. C. (2005). *Soil Erosion and Conservation*, third edition. John Wiley & Sons, New York, NY, USA.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent (2000). Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Noss, R. F., M. A. O'Connell, and D. D. Murphy (1997). *The Science of Conservation Planning: Habitat Conservation Under the Endangered Species Act*. Island Press, Washington, DC, USA.
- Riggan, P. J., S. E. Franklin, J. A. Brass, and F. E. Brooks (1994). Perspectives on fire management in Mediterranean ecosystems of southern California. *Ecological Studies* 107:140–162.
- R.J. Meade Consulting (1996). *Natural Community Conservation Plan & Habitat Conservation Plan: County of Orange Central & Coastal Subregion, Parts I & II: NCCP/HCP*. Final (administrative record copy) report prepared for County of Orange Environmental Management Agency, Santa Ana, CA, USA.
- Roach, J. D. (1989). The influence of vegetation structure and arthropod abundance on the reproductive success of California Black-tailed Gnatcatchers, *Polioptila melanura californica*. M.S. thesis, San Diego State University, San Diego, CA, USA.
- Robinson, S. K., and R. T. Holmes (1982). Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- Root, T. (1988). Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- San Diego County (1998). *Final Multiple Species Conservation Program MSCP Plan*. California Department of Fish and Wildlife, Habitat Conservation Planning Branch, Sacramento, CA, USA. <https://www.wildlife.ca.gov/Conservation/Planning/NCCP/Plans/San-Diego-MSCP>
- Shepherd, J., and G. Bender (2001). A history of the avocado industry in California. *California Avocado Society Yearbook* 85:29–50.
- Sproul, F., T. Keeler-Wolf, P. Gordon-Reedy, J. Dunn, A. Klein, and K. Harper (2011). *Vegetation Classification Manual for Western San Diego County*. Prepared for San Diego Association of Governments by AECOM, California Department of Fish and Game Vegetation Classification and Mapping Program, and Conservation Biology Institute.
- TAIC (Technology Associates International Corporation) (2002). *California Gnatcatcher habitat evaluation model for USFWS*. Digital Data. U.S. Fish and Wildlife Service, Carlsbad, CA, USA.
- Taillie, P. J., M. N. Peterson, and C. E. Moorman (2015). The relative importance of multiscale factors in the distribution of Bachman's Sparrow and the implications for ecosystem

- conservation. *The Condor: Ornithological Applications* 117:137–146.
- Westman, W. E. (1981). Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology* 62:439–455.
- Westman, W. E. (1982). Coastal sage scrub succession. In *Proceedings of the Symposium on Dynamics and Management of Mediterranean-Type Ecosystems* (C. E. Conrad and W. C. Oechel, Technical Coordinators). USDA Forest Service General Technical Report PSW-58. pp. 91–99.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Winchell, C. S., and P. F. Doherty, Jr. (2008). Using California Gnatcatcher to test underlying models in Habitat Conservation Plans. *The Journal of Wildlife Management* 72:1322–1327.
- Winchell, C. S., and P. F. Doherty, Jr. (2014). Effects of habitat quality and wildfire on occupancy dynamics of Coastal California Gnatcatcher (*Polioptila californica californica*). *The Condor: Ornithological Applications* 116:538–545.
- Wyman, K. E., and F. J. Cuthbert (2016). Validation of landscape suitability indices for Black Terns (*Chlidonias niger*) in the U.S. Great Lakes region. *The Condor: Ornithological Applications* 118:613–623.



**APPENDIX TABLE 4.** Raw detection data (0 = not detected, 1 = detected) for coastal California Gnatcatchers (*Poliophtila californica californica*; CAGN) in 2004, 2007, and 2009 at survey points in San Diego County, California, USA, along with the associated Proportion Openness (the proportion of vegetation transect intercepts ['locations'] at a gnatcatcher survey point ['point'] with no vegetation); Proportion invasive (the proportion of locations at a point with nonnative grasses, i.e. black mustard [*Brassica nigra*] or stork's bill [*Erodium* spp.]); Proportion ARCA (proportion of locations at a point with coastal sagebrush [*Artemisia californica*]); Proportion SAME (proportion of locations at a point with black sage [*Salvia mellifera*]); and Presence of MALA (indicates whether laurel sumac [*Malosma laurina*] was present at any locations associated with points).

CAGN detected 2004	CAGN detected 2007	CAGN detected 2009	Proportion openness	Proportion invasive	Proportion ARCA	Proportion SAME	Presence of MALA
0	0	0	0.99	0.04	0.01	0.00	0
0	0	0	0.29	0.00	0.06	0.11	1
0	1	1	0.77	0.00	0.05	0.00	1
0	0	1	0.75	0.00	0.16	0.00	0
0	0	1	0.26	0.00	0.14	0.32	1
1	0	0	0.37	0.00	0.02	0.24	1
0	0	1	0.31	0.00	0.00	0.01	0
0	1	1	0.61	0.00	0.15	0.00	1
0	0	1	0.20	0.00	0.01	0.63	1
0	0	0	0.89	0.02	0.00	0.00	0
1	0	0	0.38	0.02	0.25	0.00	1
0	0	0	0.24	0.00	0.00	0.16	1
1	0	1	0.02	0.01	0.14	0.00	1
0	0	0	0.54	0.03	0.03	0.00	0
0	0	0	0.78	0.01	0.02	0.05	0
1	1	1	0.36	0.00	0.00	0.11	0
0	0	0	0.44	0.00	0.09	0.03	0
1	0	1	0.23	0.00	0.01	0.06	0
0	0	0	0.20	0.00	0.00	0.21	0
0	0	0	0.09	0.00	0.06	0.09	0
0	0	0	0.69	0.06	0.08	0.00	1
0	0	0	0.68	0.06	0.01	0.00	1
1	0	1	0.35	0.07	0.02	0.00	1
0	0	0	0.47	0.08	0.09	0.00	1
0	0	0	0.34	0.00	0.00	0.15	1
0	0	0	0.35	0.00	0.02	0.14	0
0	0	0	0.45	0.00	0.00	0.11	1
0	0	0	0.55	0.00	0.00	0.20	0
0	0	0	0.31	0.00	0.00	0.05	1
0	1	1	0.44	0.00	0.15	0.02	0
0	1	0	0.44	0.00	0.22	0.01	1
0	1	0	0.42	0.02	0.08	0.00	1
0	0	0	0.33	0.00	0.14	0.21	1
1	1	1	0.64	0.03	0.14	0.00	0
1	0	1	0.19	0.00	0.09	0.04	0
0	0	0	0.64	0.06	0.02	0.00	0
1	1	1	0.44	0.02	0.35	0.02	1
1	1	1	0.46	0.10	0.25	0.11	1
1	0	1	0.42	0.00	0.11	0.00	1
0	0	0	0.53	0.01	0.01	0.00	1
0	0	0	0.10	0.00	0.03	0.21	1
0	0	0	0.69	0.07	0.02	0.00	1
0	0	1	0.30	0.00	0.07	0.00	1
0	0	0	0.40	0.02	0.04	0.00	1
0	0	1	0.37	0.03	0.13	0.01	1
0	1	0	0.50	0.00	0.07	0.00	1
0	0	0	0.41	0.01	0.10	0.00	1
0	0	0	0.51	0.00	0.26	0.00	1
0	0	0	0.93	0.08	0.02	0.00	0
0	0	0	0.56	0.01	0.09	0.00	1
0	0	1	0.32	0.02	0.09	0.00	1
1	0	1	0.22	0.00	0.37	0.00	1
1	0	0	0.55	0.01	0.07	0.00	0

**APPENDIX TABLE 4.** Continued.

CAGN detected 2004	CAGN detected 2007	CAGN detected 2009	Proportion openness	Proportion invasive	Proportion ARCA	Proportion SAME	Presence of MALA
1	0	1	0.41	0.01	0.14	0.00	1
0	0	0	0.40	0.00	0.16	0.00	1
0	0	0	0.51	0.01	0.10	0.03	0
0	0	0	0.36	0.00	0.15	0.00	1
0	1	1	0.65	0.01	0.01	0.00	1
0	1	1	0.66	0.00	0.10	0.00	1
1	1	0	0.56	0.00	0.23	0.00	1
1	1	1	0.53	0.00	0.15	0.00	1
0	1	1	0.60	0.05	0.26	0.00	1
1	1	1	0.21	0.02	0.22	0.00	1
0	1	0	0.64	0.10	0.00	0.00	0
0	1	1	0.60	0.01	0.11	0.00	0
0	0	0	0.81	0.00	0.03	0.00	0
0	0	0	0.93	0.08	0.05	0.00	0
0	0	1	0.41	0.05	0.05	0.00	1
1	1	0	0.53	0.06	0.00	0.00	0
0	0	1	0.37	0.00	0.05	0.00	0
1	1	1	0.51	0.00	0.00	0.09	0
1	0	1	0.80	0.06	0.00	0.00	0
1	1	1	0.63	0.01	0.03	0.00	0
0	0	1	0.42	0.00	0.27	0.00	0
0	0	1	0.77	0.08	0.09	0.00	0
1	1	1	0.83	0.06	0.04	0.00	0

**APPENDIX TABLE 5.** Table of results for the first stage of model construction and selection to determine the influence of habitat variables on California Gnatcatcher occupancy, colonization, extinction, and detection in coastal California, USA. Each parameter (occupancy, colonization, extinction, and detection) was first considered separately while keeping the other 3 parameters constant. Variables included in models were: ARCA (the proportion of 50 transect intersections ('locations') associated with each gnatcatcher survey point ('point') with coastal sagebrush [*Artemisia californica*] as a linear term), and ARCA<sup>2</sup> as a quadratic model; Openness (the proportion of locations at a point with no vegetation); Invasive (the proportion of locations at a point with nonnative grasses, black mustard [*Brassica nigra*] or stork's bill [*Erodium* spp.]); SAME (the proportion of locations at a point with black sage [*Salvia mellifera*]); MALA (the proportion of locations at a point with laurel sumac [*Malosma laurina*]); and Year. For each parameter, we show the top 10 models as well as the intercept only model and the global model. For each model, we show the difference in Akaike's information criterion with small sample size correction from the focal model and the top model ( $\Delta AIC_c$ ), the Akaike weight ( $w_i$ ), the model likelihood, the number of parameters in the model ( $K$ ), and the deviance associated with each model.

Parameter	Model	$\Delta AIC_c$	$w_i$	Likelihood	$K$	Deviance
Occupancy	ARCA <sup>2</sup>	0.00 <sup>a</sup>	0.07	1.00	6	213.98
	ARCA	0.03	0.07	0.98	5	216.12
	ARCA + MALA	0.76	0.05	0.69	6	214.74
	ARCA <sup>2</sup> + MALA	1.03	0.04	0.60	7	212.88
	Openness + ARCA + MALA	1.12	0.04	0.57	7	212.97
	Openness + ARCA <sup>2</sup>	1.29	0.04	0.53	7	213.14
	Openness + ARCA	1.34	0.04	0.51	6	215.32
	ARCA <sup>2</sup> + Openness + MALA	1.42	0.03	0.49	8	211.12
	ARCA <sup>2</sup> + SAME	1.54	0.03	0.46	7	213.40
	Openness + Invasive + ARCA + MALA	1.57	0.03	0.46	8	211.28
	Intercept only	2.46	0.02	0.29	4	220.65
Global (= Openness + Invasive + ARCA <sup>2</sup> + SAME + MALA)	3.17	0.01	0.21	10	208.52	
Colonization	Year + ARCA	0.00 <sup>b</sup>	0.21	1.00	6	207.57
	Year + ARCA <sup>2</sup>	1.49	0.10	0.48	7	206.93
	Year + ARCA + SAME	1.91	0.08	0.38	7	207.35
	Year + ARCA + Invasive	2.07	0.08	0.36	7	207.51
	Year + ARCA <sup>2</sup> + SAME	3.48	0.04	0.18	8	206.77
	Year + ARCA <sup>2</sup> + Invasive	3.58	0.04	0.17	8	206.87
	Year + ARCA <sup>2</sup> + MALA	3.64	0.03	0.16	8	206.93
	Year + ARCA + SAME + MALA	4.03	0.03	0.13	8	207.32
	ARCA	4.05	0.03	0.13	5	213.74
	Year + ARCA + SAME + Invasive	4.05	0.03	0.13	8	207.35
	Global (= Openness + Invasive + ARCA <sup>2</sup> + SAME + MALA)	13.10	0.00	0.00	11	209.83
Intercept only	20.10	0.00	0.00	4	231.87	
Extinction	Openness + ARCA	0.00 <sup>c</sup>	0.06	1.00	6	213.54
	Year + Openness + ARCA	0.09	0.06	0.96	7	211.49
	Openness + ARCA + MALA	0.35	0.05	0.84	7	211.76
	Openness	0.64	0.04	0.73	5	216.28
	Year + Openness + ARCA + MALA	0.71	0.04	0.70	8	209.96
	Year + Openness	1.16	0.03	0.56	6	214.69
	Year + Openness + ARCA + Invasive	1.87	0.02	0.39	8	211.13
	Openness + ARCA + Invasive	1.90	0.02	0.39	7	213.31
	Openness + ARCA + SAME	1.93	0.02	0.38	7	213.34
	Year + ARCA	2.02	0.02	0.36	6	215.56
	Year + ARCA + MALA	2.02	0.02	0.36	7	213.43
Intercept only	2.91	0.01	0.23	4	220.65	
Global (= Openness + Invasive + ARCA <sup>2</sup> + SAME + MALA)	6.00	0.00	0.05	11	208.69	
Detection	Year	0.00 <sup>d</sup>	0.51	1.00	6	874.65
	Intercept only	0.06	0.49	0.97	4	878.92

<sup>a</sup>  $AIC_c$  value of the top model = 884.63.

<sup>b</sup>  $AIC_c$  value of the top model = 878.22.

<sup>c</sup>  $AIC_c$  value of the top model = 884.19.

<sup>d</sup>  $AIC_c$  value of the top model = 887.03.



**APPENDIX TABLE 6.** Models with  $\Delta AIC_c < 2$  from the second stage of model construction and selection in which the variables and parameters from the first step were combined in all possible additive combinations to determine the influence of habitat variables on California Gnatcatcher occupancy, colonization, extinction, and detection in coastal California, USA. Parameters included occupancy ( $\psi$ ), extinction ( $\epsilon$ ), colonization ( $\gamma$ ), and detection ( $p$ ). Variables included ARCA (the proportion of 50 transect intersections ('locations') associated with each gnatcatcher survey point ('point') with coastal sagebrush [*Artemisia californica*] as a linear term), and ARCA<sup>2</sup> as a quadratic model; Openness (the proportion of locations at a point with no vegetation); Invasive (the proportion of locations at a point with nonnative grasses, black mustard [*Brassica nigra*] or stork's bill [*Erodium* spp.]); SAME (the proportion of locations at a point with black sage [*Salvia mellifera*]); MALA (the proportion of locations at a point with laurel sumac [*Malosma laurina*]); and Year. For each model, we show the difference in Akaike's information criterion with small sample size correction from the focal model and the top model ( $\Delta AIC_c$ ), the Akaike weight ( $w_i$ ), the model likelihood, the number of parameters in the model ( $K$ ), and the Deviance associated with each model.

Model	$\Delta AIC_c$	$w_i$	Likelihood	$K$	Deviance
$\psi(\text{ARCA}^2) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	0.00 <sup>a</sup>	0.02	1.00	10	193.21
$\psi(\text{ARCA}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	0.08	0.02	0.96	9	195.48
$\psi(\text{ARCA}^2) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	0.10	0.02	0.95	9	195.51
$\psi(\text{ARCA}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	0.11	0.02	0.94	8	197.68
$\psi(\text{ARCA} + \text{MALA}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.01	0.01	0.60	9	196.41
$\psi(\text{ARCA} + \text{MALA}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.03	0.01	0.60	10	194.25
$\psi(\text{ARCA}^2 + \text{MALA}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.21	0.01	0.55	11	192.21
$\psi(\text{ARCA}^2 + \text{MALA}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.27	0.01	0.53	10	194.48
$\psi(\text{ARCA}^2 + \text{Openness}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.31	0.01	0.52	11	192.31
$\psi(\text{ARCA} + \text{Openness} + \text{MALA}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.33	0.01	0.51	10	194.55
$\psi(\text{ARCA} + \text{Openness} + \text{MALA}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.37	0.01	0.51	11	192.37
$\psi(\text{ARCA} + \text{Openness}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.40	0.01	0.50	10	194.61
$\psi(\text{ARCA}^2 + \text{Openness}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.40	0.01	0.50	10	194.61
$\psi(\text{ARCA} + \text{Openness}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.43	0.01	0.49	9	196.83
$\psi(\text{ARCA}^2 + \text{Openness} + \text{MALA}) \epsilon(\text{Openness} + \text{MALA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.56	0.01	0.46	12	190.34
$\psi(\text{ARCA}^2 + \text{Openness} + \text{MALA}) \epsilon(\text{Openness}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.60	0.01	0.45	11	192.61
$\psi(\text{ARCA}^2) \epsilon(\text{Openness} + \text{ARCA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.90	0.01	0.39	10	195.12
$\psi(\text{ARCA}) \epsilon(\text{Openness} + \text{ARCA}) \gamma(\text{ARCA} + \text{Year}) p(\text{constant})$	1.98	0.01	0.37	9	197.38

<sup>a</sup> The  $AIC_c$  value of the top model = 872.50.

**APPENDIX TABLE 7.** Top 10 models from a repeated measures logistic regression used to investigate the presence of coastal sagebrush (*Artemisia californica*; ARCA), laurel sumac (*Malosma laurina*; MALA), and the absence of trees and shrubs (Openness) as a function of soil texture, aspect, slope, elevation, and distance to the coast. For each model, we show the difference in Akaike's information criterion with small sample size correction from the focal model and the top model ( $\Delta AIC_c$ ), the Akaike weight ( $w_i$ ), the model likelihood, the number of parameters in the model ( $K$ ), and the Deviance associated with each model.

Dependent variable	Model	$\Delta AIC_c$	$w_i$	Likelihood	$K$	Deviance
ARCA	Soil texture	0.00 <sup>a</sup>	0.20	1.00	4	411.98
	Soil texture + Elevation	0.79	0.14	0.68	5	410.74
	Soil texture + Aspect	1.57	0.09	0.46	5	411.53
	Soil texture + Slope	1.86	0.08	0.39	5	411.82
	Soil texture + Distance	1.97	0.08	0.37	5	411.93
	Soil texture + Elevation + Slope	2.06	0.07	0.36	6	409.98
	Soil texture + Elevation + Aspect	2.56	0.06	0.28	6	410.48
	Soil texture + Elevation + Distance	2.66	0.05	0.26	6	410.59
	Soil texture + Aspect + Slope	3.41	0.04	0.18	6	411.33
	Soil texture + Aspect + Distance	3.53	0.04	0.17	6	411.45
MALA	Intercept only	0.00 <sup>b</sup>	0.09	1.00	2	195.47
	Elevation	0.11	0.08	0.95	3	193.56
	Slope	0.40	0.07	0.82	3	193.85
	Distance	0.42	0.07	0.81	3	193.87
	Soil texture	0.85	0.06	0.65	4	192.28
	Slope + Distance	1.23	0.05	0.54	4	192.66
	Elevation + Aspect	1.42	0.04	0.49	4	192.85
	Elevation + Distance	1.55	0.04	0.46	4	192.98
	Elevation + Slope	1.60	0.04	0.45	4	193.03
	Aspect	1.63	0.04	0.44	3	195.08
Openness	Slope	0.00 <sup>c</sup>	0.15	1.00	3	937.91
	Slope + Distance	0.16	0.14	0.92	4	936.05
	Aspect + Slope	0.50	0.12	0.78	4	936.39
	Elevation + Slope	0.63	0.11	0.73	4	936.52
	Aspect + Slope + Distance	0.77	0.10	0.68	5	934.63
	Elevation + Aspect + Slope	0.92	0.10	0.63	5	934.78
	Elevation + Slope + Distance	1.94	0.06	0.38	5	935.80
	Elevation + Aspect + Slope + Distance	2.41	0.05	0.30	6	934.24
	Soil texture + Slope	3.85	0.02	0.15	5	937.71
	Soil texture + Slope + Distance	3.88	0.02	0.14	6	935.71

<sup>a</sup>  $AIC_c = 420.04$ .

<sup>b</sup>  $AIC_c = 199.48$ .

<sup>c</sup>  $AIC_c = 943.94$ .