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Research Article

Effects of habitat quality and wildfire on occupancy dynamics of Coastal California Gnatcatcher (*Polioptila californica californica*)

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ABSTRACT

Habitat Conservation Plans (HCPs) are a mechanism used for conserving land and often have an umbrella species associated with them. We conducted occupancy surveys for an umbrella species, the Coastal California Gnatcatcher (*Polioptila californica californica*), from 2004 to 2009 in San Diego County, California, focusing on preserve lands associated with HCPs. We investigated the effects of habitat quality classification, elevation, distance to coast, and heat load on gnatcatcher occupancy, extinction, and colonization probabilities. Our work focused on these factors throughout the range of this species in San Diego County where, through conservation agreements, a preserve system has been assembled addressing management considerations at a landscape scale. In addition, a large wildfire in 2003 burned 17,044 ha, roughly 1/3 of preserve lands, thus we were able to investigate the recolonization process associated with this event. We found that occupancy increased with habitat quality and over time, but decreased with elevation. Extinction probability was generally constant (~ 0.13), but colonization varied greatly, with probabilities being greater in higher quality habitat and at lower elevations. Gnatcatchers were more likely to colonize burned areas adjacent to high and very high quality habitat, sites that should receive priority conservation actions, particularly at lower elevations. Our work suggests that umbrella species, like the California Gnatcatcher, may reflect not just habitat quality, but may also be useful indicators of recovery after an unexpected event such as fire. Although not perfect, the use of multiple umbrella species in HCPs may lead to effective conservation and management of biodiversity hotspots.

Keywords: California gnatcatcher, colonization, extinction, fire impacts, HCP, biodiversity hotspot, umbrella species

Efectos de la calidad de hábitat y los fuegos silvestres en la dinámica de ocupación de *Polioptila californica californica*

RESUMEN

Los Planes de Conservación de Hábitat (PCHs) son un mecanismo usado para conservar tierras y usualmente tienen asociada una especie paraguas. Realizamos muestreos de ocupación de una especie paraguas, *Polioptila californica californica*, de 2004 a 2009 en el Condado de San Diego, California, enfocando en tierras conservadas asociadas con PCHs. Investigamos los efectos de la clasificación de la calidad del hábitat, la elevación, la distancia a la costa y la carga de calor en las probabilidades de ocupación, extinción y colonización de *P. c. californica*. Nuestro trabajo se enfocó en estos factores a lo largo del rango de este especie en el Condado de San Diego donde, a través de acuerdos de conservación, se ha montado un sistema de preservación que atiende consideraciones de manejo a la escala de paisaje. Adicionalmente, un gran fuego silvestre en 2003 quemó 17,044 hectáreas, aproximadamente 1/3 de las tierras conservadas, por lo que pudimos investigar el proceso de recolonización asociado a este evento. Encontramos que la ocupación aumentó con la calidad del hábitat y a lo largo del tiempo, pero disminuyó con la elevación. La probabilidad de extinción fue generalmente constante (~ 0.13), pero la colonización varió enormemente, con mayores probabilidades en los hábitats de alta calidad y a elevaciones bajas. Los individuos de *P. c. californica* presentaron una mayor probabilidad de colonizar áreas quemadas adyacentes a los hábitat de alta y muy alta calidad, sitios que deberían implementar acciones de conservación prioritarias, particularmente a elevaciones bajas. Nuestro trabajo sugiere que las especies paraguas, como *P. c. californica*, pueden reflejar no solo la calidad del hábitat, sino también ser indicadores útiles de recuperación luego de un evento inesperado como el fuego. Aunque no es perfecto, el uso de múltiples especies paraguas en PCHs puede permitir la conservación y el manejo efectivo de los sitios de alta biodiversidad.

Palabras clave: colonización, especies paraguas, extinción, impactos del fuego, Planes de Conservación de Hábitat (PCH), *Polioptila californica californica*, sitios de alta biodiversidad

INTRODUCTION

In southern California, the Coastal California Gnatcatcher (*Poliophtila californica californica*) serves as the umbrella or flagship species associated with Habitat Conservation Plans (HCPs) used to establish a preserve system for species of concern in California coastal sage scrub. An effective HCP outlines monitoring and adaptive management plans across a landscape to manage development, species of concern, and threats to these species (Section 10(a) of the ESA–16 U.S.C. §1539(a); U.S. Fish and Wildlife Service 1996). In California coastal sage scrub, one threat is large wildfires. In sage scrub systems, fires impact the landscape without regard to preserve design and are difficult to mitigate, especially when relying on umbrella species.

Proper selection of umbrella species is paramount to HCP success (Chase et al. 2000, Roberge and Angelstam 2004). The Coastal California Gnatcatcher (hereafter gnatcatcher) fills this role (Fluery et al. 1998) by serving as a proxy for a suite of fauna dependent on coastal sage scrub. For conservation planners, habitat relationships of gnatcatchers are used for establishing conservation priorities relevant to protection of this biodiversity hotspot, the California Floristic Province (Myers et al. 2000).

Much of the protected land in Southern California is predicated on a habitat model (i.e. the Technology Associates International Corporation, or TAIC model) that identifies areas of gnatcatcher occupancy (TAIC 2002). This model focuses on the presence of sagebrush (*Artemisia californica*) and then categorizes habitat suitability for the gnatcatcher into low, medium, high, and very high strata based on patch size, slope, precipitation, and average minimum January temperature. In 2002, a survey was conducted across the range of the gnatcatcher in Orange and San Diego counties. The results of that study verified the usefulness of the TAIC categorization, with occupancy estimates of 0.00, 0.08, 0.28, and 0.48 in the low, medium, high, and very high strata, respectively (Winchell and Doherty 2008).

Based on the success of Winchell and Doherty's (2008) study, a similar survey protocol for the Multiple Species Conservation Program (MSCP) was established in a specific HCP in southwest San Diego County, California (San Diego County 1998). This survey was conducted in 2004 and then expanded in 2007 and 2009 to include all quasi-public, public, and preserve lands across San Diego County; data from these surveys can be used as a more rigorous evaluation of HCPs by including not just occupancy by the gnatcatcher, but also extinction and colonization across years.

A large wildfire occurred in Fall 2003, 5 months before the 2004 surveys, and burned 17,044 ha, roughly 1/3 of the

MSCP preserve area, allowing us to investigate occupancy patterns as the land recovers from the fire, an aspect of particular interest to the regulatory agencies and land managers who are responsible for the repercussions from unpredicted large fires. Previous work with gnatcatcher recovery following fire, at a much smaller scale, has led managers to believe that recolonization of burned areas by gnatcatchers can take place in 3–5, or possibly 10 or more years post burning (Akçakaya and Atwood 1997, Wirtz et al. 1997).

Underlying permanent landscape features might also influence occupancy. We were particularly interested in the effect of elevation and distance to the Pacific coast, as elevations < 150 m and areas closer to the coast have been suggested, anecdotally, to have higher gnatcatcher occupancy rates (Winchell personal observation). Winchell (2009) suggested this might be due to the higher levels of atmospheric moisture in these areas. Sites with a higher heat load (McCune and Keon 2002) might be more likely to be occupied by gnatcatchers, possibly due to these sites being warmer than other exposures.

We used surveys in 2004, 2007, and 2009 to examine occupancy dynamics and recovery from the 2003 fire across the MSCP area. We predicted that extinction probabilities would vary by habitat category (low, medium, high, very high, and burned) with higher probabilities in lower quality habitats. We predicted that extinction probabilities would also vary by year. We predicted colonization probabilities would vary by habitat category (higher quality having higher probabilities), year, elevation (lower elevations having higher occupancy rates), and the distance to the coast (areas closer to the coast have had higher occupancy rates and may serve as a source for colonizing gnatcatchers). We predicted that recolonization of large, burned areas would take longer than 5 years and that the carrying capacity at a landscape level would be affected. Our goal in estimating occupancy dynamics of the gnatcatcher was to evaluate how well preserve lands, planned around development, withstood the effects of an unforeseen event and what ecological factors should be considered in mitigation efforts to sustain gnatcatcher populations.

METHODS

We conducted this research on lands within San Diego County designated as public, quasi-public, or military lands. In general, this included preserve lands regulated under HCPs, other public lands regulated by local jurisdictions, and lands separately managed by Marine Corps Air Station Miramar and Naval Weapons Station Seal Beach, Detachment Fallbrook. Marine Corps Base Camp Pendleton, private lands, and Tribal lands were not included.

Surveys in 2004 included 29,210 ha (12,165 ha not burned; 17,045 ha burned) of lands within the planning area for the MSCP. Surveys in 2007 expanded to 42,139 ha (25,094 ha not burned; 17,045 ha burned) to include more lands within San Diego County (in addition to MSCP lands). We used a stratified sampling design (Thompson 2012) across the 4 TAIC habitat strata (very high, high, moderate, and low quality habitat) and followed the sampling methods in Winchell and Doherty (2008). In brief, potential sampling locations were identified as the center points of a 600 m \times 600 m grid randomly overlaid on the study area. Sampling effort was allocated proportionally to each stratum (Siniff and Skoog 1964). We had chosen these plots in summer 2003 for surveys the following spring. Large wildfires moved through the area in October 2003, after we designed the study, but before any surveys. Burning a plot in one stratum does not transform the plot into one of the other strata as a stratum designation is most strongly based on factors not affected by fire—namely variation in slope, average annual precipitation, and average annual temperature (TAIC 2002, Winchell and Doherty 2008). Fire removed the vegetation component of the habitat, leaving the physical components unaltered. Thus, after the fire we considered these burned plots a 5th stratum. Within the fire-affected stratum we only surveyed the previously categorized high and very high plots (a total of 86 plots) because we thought the previously categorized low and medium plots would have very low occupancy rates and we did not anticipate large changes in those plots. We surveyed 28, 77, 151, 261, and 86 plots in low, medium, high, very high, and burned strata, respectively. Of these 639 plots, 488 were in the established MSCP area and 151 were on preserve lands outside the MSCP area. All 86 burn plots were within the MSCP planning boundary. We visited each plot a maximum of 5 times in 2004 and 6 times in 2007 and 2009. We made visits between 15 March and 20 April in 2004, from 30 April to 30 June in 2007 and from 13 April to 22 June in 2009. During each visit the observer recorded temperature ($^{\circ}\text{C}$), relative humidity (%), average wind speed (km hr^{-1}), and cloud cover during the first 2 minutes prior to beginning gnatcatcher surveys. Surveys were not conducted at a point if the average wind speed exceeded 20 km hr^{-1} , precipitation was greater than a drizzle, or ambient temperature was lower than 4.5 $^{\circ}\text{C}$. At each visit we recorded whether a gnatcatcher was detected over an 18-minute period. During the first 15 min, an observer detected gnatcatchers either aurally or visually, while during the last 3 min a digital playback was used to aid detection. Only adult bird detections were used in the analysis and a point was either occupied or unoccupied. These records formed an encounter history for each plot.

We utilized an occupancy dynamics model (MacKenzie et al. 2003) to estimate occupancy, extinction, and

colonization while also estimating detection probability. If occupancy at time t , extinction, and colonization are estimated, then occupancy at time $t+1$ can be derived. Thus we chose to estimate the initial occupancy rate (in 2004), as well as time-specific extinction and colonization probabilities, and derived future occupancy parameters using Program MARK (White and Burnham 1999). Our surveys did not occur at equal intervals (2004, 2007, 2009). To address this, we standardized the modeling and estimation of extinction and colonization between surveys on an annual basis. Annual extinction and colonization probabilities for intervals between surveys were considered identical because of the lack of intervening survey data. For example, we had to assume extinction probabilities between 2007 and 2008, and between 2008 and 2009 were the same.

In addition to habitat stratum and year, we included location (within the MSCP or not), elevation, distance to the coast, and heat load as predictors of gnatcatcher occupancy (Table 1). We set occupancy of burned plots to zero in 2004 as these plots had not recovered enough to have the gnatcatcher present. From preliminary analyses and examination of the data, we also set the initial occupancy of the low and moderate strata to zero. By doing so our models converged more easily. We modeled detection as either a constant or varying by year. We modeled combinations of factors as additive and used all possible combinations of factors (Doherty et al. 2012) to achieve a balanced model set. We relied upon Akaike's Information Criterion with small sample size correction (AIC_c) for model selection and for calculating cumulative AIC_c model weights for each predictor variable across our balanced model set (Burnham and Anderson 2002). We considered variables with cumulative AIC_c weights > 0.5 (Barbieri and Berger 2004) to have meaningful relationships with parameters of interest. We present model-averaged parameter estimates (Burnham and Anderson 2002) unless otherwise noted.

RESULTS

Our most supported model included effects of stratum and elevation on occupancy, extinction as a constant, colonization as a function of stratum, elevation, and year, and detection as a constant. This model also reflected the variables with the highest cumulative AIC_c weights across our model set (Table 2; Barbieri and Berger 2004).

Occupancy was estimated in 2004 and then derived from extinction and colonization estimates in following years. Occupancy was the highest in the very high and high strata. The moderate, low, and burned strata had lower occupancy and more uncertainty, especially in the low stratum (Figure 1). We found occupancy to decrease with elevation (Figure 2).

TABLE 1. Variables used to model occupancy, extinction, colonization, and detection of California Gnatcatchers in San Diego County, CA, from 2004 to 2009.

Variable	Occupancy in 2004	Extinction	Colonization	Detection
Constant	x	x	x	x
Habitat strata (low, medium, high, very high, burned)	x	x	x	
Year (2004, 2007, 2009)	x ¹	x ²	x ²	x ³
MSCP ⁴ (within plan area or not)	x	x	x	
Elevation (m)	x		x	
Distance to coast (m)	x		x	
Heat load ⁵	x			

¹ Occupancy was only estimated for 2004 and then derived in future years using estimates of extinction and colonization.

Occupancy was set equal to zero for the low, medium, and burned strata in 2004 based on the data.

² Extinction and colonization were considered identical for years between surveys.

³ Detection was set equal to zero for years in which surveys were not conducted.

⁴ MSCP is the Multiple Species Conservation Plan located in San Diego County, California, USA.

⁵ As defined by McCune and Keon (2002).

The model-averaged extinction probability varied little over strata (range: low 0.000–0.396, moderate 0.000–0.124, high 0.192–0.208, very high 0.163–0.178, burned 0.000–0.180), but our estimates were imprecise, especially for low, moderate, and burned strata. The model-averaged colonization varied by stratum with the highest colonization rates in the high (range 0.085–0.124) and very high (range 0.116–0.167) strata and the lowest in the moderate (range 0.016–0.025) and burned (range 0.018–0.027) strata with the most uncertain estimates in the low stratum (%CV ~90%). Annual colonization was highest at lower elevations and higher in 2007–2009 versus the 2004–2007 period (Figure 3), although confidence intervals for the 2 periods overlapped. Overall average extinction and colonization rates, from a model with constant extinction and colonization rates ($\Delta AIC_c > 65$), were 0.13 (95% CI 0.09, 0.18) and 0.06 (95% CI 0.05, 0.09), respectively.

DISCUSSION

Similar to Winchell and Doherty (2008), we found the strata of the TAIC model to reflect occupancy estimates well

(Figure 1). In addition to reconfirming the TAIC model, we estimated that occupancy within strata increased from 2004 to 2009, possibly as a result of precipitation patterns over this interval. Rainfall in southern California is highly variable, and species are probably affected by extremes. Population declines may be caused by extreme low rainfall years, whereas population maintenance, or increases, may be a function of rainfall adequate to support plant growth and insect populations, especially during the breeding season (Morrison and Bolger 2002, Oppel et al. 2013). For Southern California, the 3 months receiving the most rainfall are January, February, and March, which coincides with nest building and first-brood egg laying (Atwood and Bontrager 2001). Coastal sage plant species have evolved a drought deciduous phenology and shallow root systems (Barbour et al. 2007). Consistently below-average precipitation during the winter months can reduce photosynthetic capacity (Langan et al. 1997). Such a reduction in photosynthesis would lead to a corresponding reduction in insects that depend on leaf mass, which are the prey base for gnatcatchers.

Occupancy estimates from a 2002 survey, over a wider area (Winchell and Doherty 2008), were higher than 2004

TABLE 2. Cumulative Akaike's Information Criterion (AIC_c) weights for each predictor variable examined in dynamic occupancy models for California Gnatcatcher in San Diego County, California, USA, from 2004 to 2009.

Variable	Parameter			
	occupancy in 2004 ¹	Extinction	Colonization	Detection
Habitat strata	0.86	0.21	0.86	
Year		0.34	0.61	0.13
MSCP ²	0.24	0.24	0.24	
Elevation	0.78		0.69	
Distance to coast	0.33		0.28	
Heat load	0.34			

¹ Occupancy was only estimated in 2004 and then derived in future years from estimates of extinction and colonization.

² MSCP is the Multiple Species Conservation Plan located in San Diego County, California, USA.

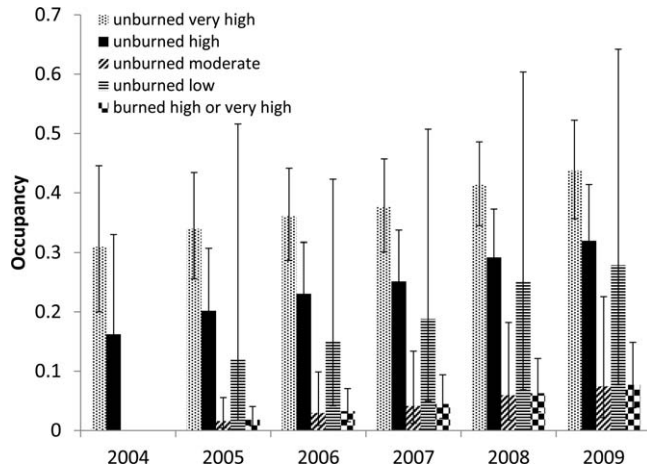


FIGURE 1. Model-averaged California Gnatcatcher occupancy estimates for 2004–2009 for the 5 habitat strata. Error bars are 95% confidence intervals.

and closer to 2009 estimates. High occupancy rates in 2002 may have been a result of conditions during previous years, with rainfall amounts within the 50th percentile of normal during the breeding season (Morrison and Bolger 2002). The year 2002 (July 1, 2001, to June 30, 2002) was the driest on record for San Diego County, with a total of 7.6 cm of precipitation at the coast (Western Regional Climate Center: <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca7740>). We assume this lack of precipitation resulted in high rates of nest failure and low juvenile survivorship (DeSante and Geupel 1987). Adult mortality post-survey, coupled with poor fecundity and low juvenile survivorship, could have reduced the population to low levels by the 2004 survey. Rainfall during the breeding seasons 2003 through 2009 showed an increasing pattern from 2002, with the lowest year (January–March 2007) still receiving nearly double the rainfall of 2002. This pattern of precipitation during the breeding season possibly triggered

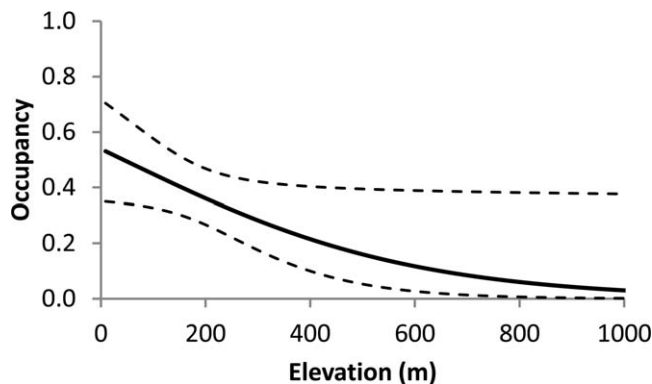


FIGURE 2. The relationship between occupancy and elevation for California Gnatcatcher plots in the very high quality habitat stratum. Dashed lines are the 95% confidence limits based on estimates from our top model.

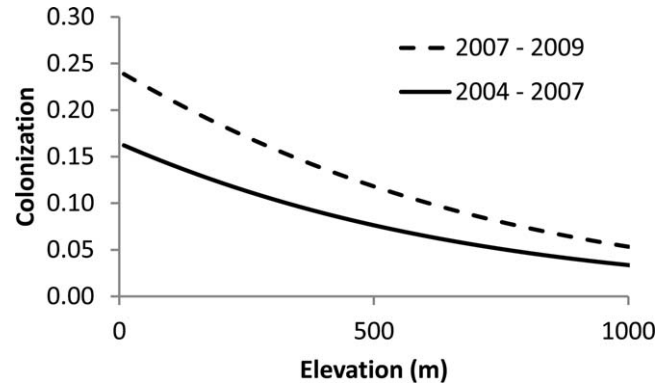


FIGURE 3. The relationship between annual colonization probability, elevation, and year for California Gnatcatcher plots in very high quality habitat stratum.

a recovery of the population that we detected in the 2007 and 2009 surveys.

We also found occupancy to decrease with increasing elevation. This was different from our prediction, leading us to examine meteorological data to help explain this result. Based on average yearly rainfall and average daily minimum low temperature for the month of January for 26 weather stations within the general geography of our sample frame (www.wrcc.dri.edu), we found that low-elevation areas receive less annual rainfall (<30.5 cm) than higher elevations (>40.6 cm) and have milder winter low temperatures (>1.1°C). Lower amounts of rainfall would favor the scrub habitat preferred by gnatcatchers, and higher rainfall would favor dense chaparral that gnatcatchers do not favor. Warmer winter temperatures would favor birds with high surface-to-volume ratios such as gnatcatchers (Root 1988, Mock 1998) and may also influence the abundance of small insects available for food during winter months. Thus, the relative amount of precipitation and temperature may explain the occupancy patterns we detected associated with elevation.

Beyond occupancy patterns, we were able to investigate extinction and colonization dynamics of gnatcatchers across our survey area. We found that extinction rates were relatively constant across our variables of interest. However, colonization rates varied by habitat strata, year, and elevation. Survey points considered high or very high quality had high colonization probabilities, especially at low elevations. Colonization was also higher from 2007 to 2008 than in 2004–2007 (Figure 3). This may be because the population was expanding during our survey period as it recovered from the 2002 drought. An increasing population would supply dispersing juveniles that would preferentially select very high and high quality habitat in which to establish territories.

We showed occupancy increased within the preserve areas of San Diego County during our study. This may be a

combined factor of higher colonization rates for habitat modeled as “high” and “very high” and the removal of 16% of these same habitats due to the 2003 wildfire. If the population of gnatcatchers was increasing due to precipitation patterns between 2002 and 2009, then this increased population would be concentrated into a smaller area of available preferred habitat, leading to higher occupancy rates. We do not assume that birds displaced from the wildfire found refugia in unburned areas.

Fire is an important factor shaping the structure and dynamics of habitats for many bird species (Brawn et al. 2001, Smucker et al. 2005), and we found that fire also plays a role in the occupancy dynamics of the gnatcatcher. We found our 5th stratum, the burned high and very high quality plots, to become occupied over time, but at a slow rate. No gnatcatchers were observed on burn plots during the 2004 breeding season following the October 2003 fire. We have some observations that show the pattern of recolonization of burned plots. In 2007, gnatcatchers colonized 3 points within the 2003 fire perimeter, all within 617 m of the edge, and all adjacent to unburned “very high” strata. In 2009, gnatcatchers were detected at 9 points up to 1,972 m from the perimeter. Six of these points were adjacent to habitat modeled as “very high.” Birds that disperse into burned areas appear to move in from the fire perimeter, rather than colonizing the center of the burned area immediately, and the quality of unburned habitat nearest to the burn may increase the likelihood of dispersal (Watson et al. 2012). These 2 factors, the quality of the habitat burned, and the proximity of the burned habitat to higher quality unburned areas, may be important when evaluating recovery of habitats and their avifauna after wildfire (Saab et al. 2004). If very high and high quality habitats burn and the burn area borders lower quality habitat types, the carrying capacity of the population across the preserve may decrease and be less likely to recover. This would be especially true for gnatcatchers if the burned areas converted to an exotic grassland system (Weitz et al. 1997, Talluto and Suding 2008).

Conservation decisions should be partly driven by habitat quality. We found high and very high quality areas (especially at lower elevations) to have higher occupancy probabilities and to be more likely to be colonized by gnatcatchers. Thus these areas should receive priority for being incorporated into preserve systems. Gnatcatchers will recolonize burned areas categorized as high and very high quality, especially at lower elevations, but to reach pre-burn levels will take many years (more than the 5 years post-burn we have monitored), at least when no habitat rehabilitation programs are implemented. Managers should consider directing habitat rehabilitation efforts toward areas of habitat that are modeled as either very high or high quality prior to a fire to increase recolonization

rates, or at least to assure the habitat reestablishes to pre-fire conditions. If funding is limited, then habitat rehabilitation efforts could be concentrated in concentric bands bordering the perimeter of the fire and adjacent to habitat modeled as very high. Likewise, rehabilitation efforts could shift away from the perimeter of burned areas over time, as gnatcatcher pairs do better in older stands of habitat (Atwood 2001).

Colonization and extinction rates demonstrate that the distribution of gnatcatchers changes across the landscape through time (Donner et al. 2010). Areas that support gnatcatchers one year may not the next, and vice versa, although we did not have consecutive years of data so we could not evaluate this idea directly. Nonetheless, there may be conservation value in having a sufficient amount of habitat available for the dynamics of colonization and extinction processes to function. In particular, preserving undisturbed, high quality habitat, regardless of occupancy status in a single survey year, will be important as this high quality habitat can facilitate maintenance of a source population (e.g., Breininger et al. 1995). This result also suggest that relying too strictly on a single umbrella species may not be wise as all species would have to have similar dynamics across a landscape for the umbrella species concept to work (e.g., Rubinoff 2001).

The use of umbrella species, or conservation surrogates, is often predicated by the untested assumption that a single species represents the stability of the preserved habitat. In our case, the California gnatcatcher was assigned the role of umbrella species representing coastal sage scrub habitat. Our findings upheld this assumption, as higher quality habitat supported higher occupancy rates. However, Rubinoff (2001) found that gnatcatchers were not a good umbrella species for invertebrates. His finding indicated that several invertebrate species were not represented in the overall community when patch size decreased. This contradiction can be explained by the fact that Winchell and Doherty (2008) found patch size does not influence gnatcatcher occupancy. We believe that gnatcatchers are relatively patch-size insensitive from an occupancy point of view. We recommend when selecting umbrella species that assumptions are tested, and that habitat requirements and behavior constraints are considered for the species thought to be under the “umbrella.” We believe that gnatcatchers probably represent a suite of species that are dependent on coastal sage scrub, but that are not influenced by patch size.

Our results suggest that restoration efforts of habitat for Coastal California Gnatcatcher should be directed toward lower elevation sites close to the coast and that priority should be given to patches considered as high and very high quality habitat. However, we recognize a number of challenges. As with many conservation plans with limited conservation dollars, we have to choose foci (e.g., Weller

2008). One of our foci is gnatcatcher occupancy, but we have neglected demographic parameters, such as fecundity, survival, and individual movement, that ultimately control population dynamics. To the extent possible, we suggest that demographic parameters be investigated to develop a comprehensive management plan directed at sustaining habitats supporting gnatcatcher populations.

At the larger coastal sagebrush community scale, we also rely on the shortcut concept of umbrella species (Chase et al. 2000, Roberge and Angelstam 2004) for conservation, because we do not have enough resources to investigate all the species we care about. Even though we realize that each of the covered species in the MSCP will not function as an umbrella equally for all species (e.g., Rubinoff 2001), we hope that, as a group, the list of covered species will perform adequately in conserving biodiversity in this hotspot. In the end, we suggest that effective conservation and management of biodiversity hotspots can be accomplished by applying lessons like those learned from the California Gnatcatcher and maintaining flexibility to respond to our changing world.

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