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*Avian Behavior, Ecology, and Evolution*

# Foraging preferences of the threatened coastal California Gnatcatcher (*Polioptila californica*) during the non-breeding season

## Preferencias de forrajeo durante la temporada no reproductiva de la especie amenazada de la costa de California, *Polioptila californica*

*Kevin B. Clark*[1], *Kimberly Ferree*[1], *Kylie Fischer*[2] *and Stephen J. Myers*

ABSTRACT. We studied the foraging behavior of the federally threatened coastal California Gnatcatcher (*Polioptila californica*), an obligate insectivore, during the non-breeding season, a period of reduced survivorship for this non-migratory passerine due to seasonal aridity and the onset of cold winter storms. During the seasonal dry period in fall (October–November), California Gnatcatchers preferentially foraged in fall-blooming shrubs such as coyote brush (*Baccharis pilularis*), and California brickelbush (*Brickellia californica*). Upon the onset of the wet winter period (December–January), foraging California Gnatcatchers demonstrated a seasonal shift toward drought deciduous shrubs then leafing out, especially coastal sagebrush (*Artemisia californica*). Our findings suggest that California Gnatcatchers shift their foraging preferences seasonally to track available food resources. Additionally, our findings point to the value of floristic diversity within California Gnatcatcher habitat to provide year-round foraging opportunities for this obligate insectivore.

RESUMEN. Estudiamos el comportamiento de forrajeo de *Polioptila californica*, una especie amenazada federalmente de la costa de California, insectívora obligatoria, durante la temporada no reproductiva, un periodo de reducción en la supervivencia para esta especie paseriforme no migratoria, debido a la aridez estacional y el comienzo de los inviernos fríos. Durante el periodo seco estacional en el otoño (Octubre-Noviembre), *Polioptila californica* forrajeó preferencialmente en arbustos que florecen durante el otoño como *Baccharis pilularis* y *Brickellia californica*. Con el inicio del periodo húmedo del invierno (Diciembre-Enero), el forrajeo de *Polioptila californica* mostró un cambio estacional hacia arbustos deciduos por sequía que estaban perdiendo sus hojas en ese momento, especialmente *Artemisia californica*. Nuestros resultados sugieren que *Polioptila californica* cambia sus preferencias de forrajeo estacionalmente para rastrear los recursos disponibles. Adicionalmente, nuestros resultados apuntan al valor de la diversidad florística dentro del hábitat de *Polioptila californica* para proveer oportunidades de forrajeo a través de año para esta insectívora obligada.

Key Words: *California Gnatcatcher; conservation; endangered species; foraging; habitat; non-breeding season, Polioptila californica*

## INTRODUCTION

Previous research into habitat use by birds has emphasized plant community structure (e.g., MacArthur and MacArthur 1961, MacArthur et al. 1966), but plant species composition can also determine habitat selection by birds in some settings (Holmes and Robinson 1981, Rotenberry 1985). Studies evaluating avian use of plant species for foraging among insectivores have found preferential use of some plant species over others, generally related to varying densities of preferred insect prey (Holmes and Robinson 1981, Narango et al. 2017). Understanding the foraging preferences of avian species that are of conservation concern is vital to targeted management actions and restoration efforts.

The federally threatened coastal California Gnatcatcher (*Polioptila californica*) is a year-round resident of coastal sage scrub habitats in Southern California. California Gnatcatchers breed from March–August, raising multiple broods in favorable years, but also suffer from high over-winter mortality and relatively short lifespans compared to other passerines (Atwood and Bontrager 2020). In the Mediterranean climate of coastal Southern California, characterized by cool wet winters and warm dry summers, the non-breeding season (September–January) overlaps with the period of summer and fall aridity, often resulting in periods of six months or more with essentially no precipitation (typically May–November; Rundel 2007). As an obligate insectivore with a high metabolism, California Gnatcatchers must continue to forage through the annual dry period in a time of presumed declining food availability. Therefore, foraging efficiency is crucial for maintaining enough caloric food intake to compensate for energy expenditures. Indeed, mortality has been found to be greatest during the fall and winter period, with periods of cold temperatures and wet weather resulting in population declines at monitored sites (Atwood et al. 1998, Erickson and Miner 1998).

Coastal sage scrub communities inhabited by California Gnatcatchers are floristically diverse, with shifting patterns of species dominance and high levels of endemism, which affect California Gnatcatcher densities (Weaver 1998, Rundel 2007, Sawyer et al. 2009). Within this diverse habitat, California Gnatcatchers densities are influenced by floristic patterns. For example, multiple studies have demonstrated a correlation between California Gnatcatcher presence and coastal sagebrush (*Artemisia californica*) density (Atwood et al. 1998, Winchell and Doherty 2008, Winchell and Doherty 2018). However, *Artemisia californica* is a drought deciduous shrub which loses its leaves during the dry period of summer and fall, likely limiting the amount of insect fauna it supports during this period. While significant effort has focused on defining the breeding season habitat preferences for this species and the preferred vegetative structure, relatively little is known about the habitat preferences in the non-breeding season in the fall and winter, as well as how gnatcatchers utilize the floristic diversity in their preferred habitats.

[1]San Diego Natural History Museum, [2]WSP USA

To what extent California Gnatcatchers forage within various plant species within their habitat during the fall is unknown. Preferred gnatcatcher prey items are primarily Hemipterans and spiders during the breeding season (Burger et al. 1999). An early study based on specimens collected across seasons found that gnatcatchers fed primarily on Hemiptera, followed in order of importance by adult Hymenoptera and Coleoptera (Beal 1907). We predicted that fall blooming shrubs would provide a resource peak during this critical dry period and would be selected for by California Gnatcatchers for foraging. We sought to define the foraging preferences of California Gnatcatchers during this fall/winter period of high mortality. This information is critical to managing and restoring the habitat of this rare species in the fragmented landscape of Southern California.

## METHODS

We conducted our study at Marine Corps Base Camp Pendleton (~125,000 acres), an active military training installation with a large population of California Gnatcatcher (373 pairs and territorial males; J. V. Hercules, unpublished report). As part of a larger study analyzing gnatcatcher home range in the non-breeding season (J. V. Hercules, unpublished report), we included gnatcatcher locations across the breadth of the installation, encompassing both coastal and interior sites, to incorporate the range of vegetation types utilized by gnatcatchers. Surveys for gnatcatcher pairs were consistent with accepted protocols (USFWS 1997). A subset of adults were uniquely color-banded to facilitate following the pairs in the non-breeding season, with a total of 45 pairs color-banded. All activities were authorized under approved permits (TE-804203; TE-117947).

Gnatcatchers were observed as they moved through the vegetation, and we recorded the location (observation point) and the plant species they were observed foraging in with the ArcGIS Application Collector© for smartphones. A new location and plant species were recorded each time the gnatcatcher moved from shrub to shrub, for as long as it remained in view. Often, a pair was observed foraging together. If they were observed in the same shrub, they were recorded as a single location, however, if they were observed using different shrubs, they were recorded separately. We spot mapped each pair on at least six separate occasions spaced at two-week intervals.

Vegetation measurements were collected concurrently with the home range mapping observational period. Following each observation session, vegetation was sampled at two 10-meter point-intercept transects (20 points total; Godínez-Alvarez et al. 2009, Toledo et al. 2010). Transects were established on the middle and last observation point of the session. For instance, if six observation points were collected, vegetation sampling was conducted at points three and six. Transect directions were established through a random number generator application. At each meter along the transect, the shrub species intersecting the point was recorded. If no shrub was intercepted, the observer recorded bare ground, grass, litter, or dead shrub. The point-intercept transect data estimate relative availability of shrub species for each gnatcatcher pair.

Home range and vegetation monitoring occurred from 1 October 2016 through 30 January 2017. During the study period, the first precipitation events occurred between 20–27 November, during which 0.82 in. of rain fell cumulatively, and then a second event 15–16 December, which resulted in 1.46 in. of precipitation (Wire Mountain RAWS weather station data; https://raws.dri.edu/). We observed drought deciduous shrubs leaf out rapidly after these rains, beginning in early December. We, therefore, divided our California Gnatcatcher shrub use observations into two periods, a dry period encompassing October–November and a wet period encompassing December–January. We refer to these periods as fall (October–November), and winter (December–January) in the results and discussion below.

### Data Analysis

We quantified California Gnatcatcher shrub preferences by 1) summing the total number of observation points in a shrub species for each pair and season, 2) calculating the proportional availability of shrubs by dividing the number of available points for each shrub by the total number of available points for all species of shrubs for each pair, and 3) estimating the expected number of available points for each shrub species by multiplying the proportional availability of shrubs by the total number of observation points in a shrub for each pair. We calculated proportional use as the ratio: ([total number of foraging observations in a shrub] / [total number of foraging observations in a shrub] + [total number of expected shrub points]) by pair and season. The ratios give a quantitative estimate of California Gnatcatcher proportional use by comparing shrub use versus shrub availability. Thus, when shrubs are used in proportion to availability, proportional use = 0.5. When shrubs are used more frequently than expected (proportional use > 0.5) or less frequently than expected (proportional use < 0.5) gnatcatchers are suggested to have a preference (or avoidance) to a shrub. For each pair, male and female observation points were pooled for analysis. Proportional availability was calculated for the entire study period because shrub composition was not expected to vary by season.

Pairs with a minimum of 20 observation points (10 each in fall and winter) and a minimum of 40 vegetation points (fall and winter combined) were included in the analyses. To evaluate the effect of season on gnatcatcher shrub use, we used a paired sample t-test to compare mean proportional use in fall and winter. For plant species that did not vary in proportional use by season, data were combined for fall and winter to test whether a plant species was used proportionally or more/less than what was available during both fall and winter. We used a one-sample t-test to evaluate differences in mean proportional plant species use and the null model ($\mu = 0.5$) for fall and winter. If mean proportional plant species use was not equal to the null model, then the plant species was used proportionally more/less than what was available. We considered $P < 0.05$ to be significant for all statistical tests. All statistical tests were performed using R (R Core Team 2021).

## RESULTS

Foraging observation points were recorded for 155 California Gnatcatcher pairs, of which 129 pairs reached the minimum threshold to be included in the analyses (mean = 83 points, SD = 22, range = 22–137). Measurements collected at vegetation transects ranged from 40–160 vegetation points per pair (mean = 97 points, SD = 36).

Shrub species included in the analyses were *Artemisia californica*, coyote brush (*Baccharis pilularis*), California brickelbush

(*Brickellia californica*), California encelia (*Encelia californica*), California buckwheat (*Eriogonum fasciculatum*), bladder pod (*Peritoma* [*Isomeris*] *arborea*), coast goldenbush (*Isocoma menziesii*), laurel sumac (*Malosma laurina*), coast prickly pear (*Opuntia littoralis*), lemonadeberry (*Rhus integrifolia*), white sage (*Salvia apiana*), black sage (*Salvia mellifera*), and elderberry (*Sambucus cerulea*) (Fig. 1). These 13 species were the most common shrub species observed being used by gnatcatchers during the study.

**Fig. 1.** The thirteen plant species most frequently encountered in our study area. These species are divided into three ecological groupings: drought deciduous, which are mostly leafless in the fall period; fall bloomers, which are leafed out and blooming in the fall period; and evergreen shrubs, which do not drop their leaves though are generally senescent in the fall period.


Across the entire study period (1 October 2016 to 30 January 2017), California Gnatcatchers were observed foraging in four species less frequently than expected given the shrub species' observed availability, including three drought deciduous species: *Encelia californica*, *Eriogonum fasciculatum*, and *Salvia mellifera*, and one evergreen shrub, *Malosma laurina* (Fig. 2, Table 1). California Gnatcatcher were observed more frequently than expected in only one species, *Opuntia littoralis*, throughout the entire study period (Table 1). California Gnatcatcher observations in *Artemisia californica* and *Baccharis pilularis* varied significantly by season ($P < 0.05$) compared to these species' availability and, therefore, were analyzed separately by season.

**Table 1.** Results from one-sample t-test investigating California Gnatcatcher (*Polioptila californica*) plant species use across the study period (fall and winter combined). Plant species that were used proportionately more/less than what was available ($P < 0.05$) are shown in bold. Sample size (N) is the number of gnatcatcher pairs in fall or winter, by plant species. Sample sizes vary by season and the species composition within a gnatcatcher territory.

| Species | Plant Type | N | Mean Prop. Use | CI | t | df | P |
|---|---|---|---|---|---|---|---|
| Artcal | Drought Deciduous | 220 | 0.51 | 0.015 | 1.483 | 219 | 0.14 |
| **Enccal** | Drought Deciduous | 16 | 0.37 | 0.091 | -2.943 | 15 | **0.01** |
| **Erifas** | Drought Deciduous | 36 | 0.41 | 0.056 | -3.369 | 35 | **<0.01** |
| Isoarb | Drought Deciduous | 17 | 0.54 | 0.109 | 0.759 | 16 | 0.46 |
| Salapi | Drought Deciduous | 25 | 0.55 | 0.072 | 1.431 | 24 | 0.17 |
| **Salmel** | Drought Deciduous | 19 | 0.41 | 0.091 | -2.150 | 18 | **0.05** |
| Bacpil | Fall Bloomer | 117 | 0.52 | 0.034 | 1.202 | 116 | 0.23 |
| Isomen | Fall Bloomer | 25 | 0.55 | 0.067 | 1.651 | 24 | 0.12 |
| Brical | Fall Bloomer | 24 | 0.53 | 0.070 | 0.839 | 23 | 0.41 |
| **Mallau** | Evergreen Shrub | 26 | 0.43 | 0.063 | -2.414 | 25 | **0.02** |
| Rhuint | Evergreen Shrub | 28 | 0.49 | 0.061 | -0.443 | 27 | 0.66 |
| Sambucus | Evergreen Shrub | 16 | 0.58 | 0.102 | 1.611 | 15 | 0.13 |
| **Opulit** | Cactus | 29 | 0.59 | 0.080 | 2.401 | 28 | **0.02** |

Splitting the data into two seasons, the dry fall (1 October to 30 November 2016) and wet winter (2 December 2016 to 30 January 2017), revealed interesting patterns (Fig. 3). In the fall, California Gnatcatcher were observed foraging less frequently than expected given their availability for two species, *Artemisia californica* and *Encelia californica*, both drought deciduous shrubs that are mostly leafless during this period. In the dry season, California Gnatcatchers were observed foraging more in *Baccharis pilularis*, and *Brickellia californica* more frequently than expected given the occurrence of these fall blooming species. The third fall blooming shrub in our study, *Isocoma menziesii*, was used more frequently than expected given its occurrence but not at a $P < 0.05$ level ($P = 0.06$, Table 2). The cactus *Opuntia littoralis* was also foraged in more frequently than expected in the dry fall period ($P = 0.05$).

In contrast to these foraging preferences in fall, the relatively wet winter period (December–January) revealed different patterns. In this season, gnatcatchers foraged in four species significantly less

**Fig. 2.** California Gnatcatcher (*Polioptila californica*) mean proportional plant species use (95% CI) across the study period (fall and winter combined). Four species: Encelia californica, Eriogonum fasiculatum, Salvia mellifera, and Malosma laurina have non-overlapping 95% CI with 0.5 (vertical dashed line) indicating that use of these plants was significantly less than what was available (P < .05). One species, Opuntia littoralis, was used significantly more than its availability.

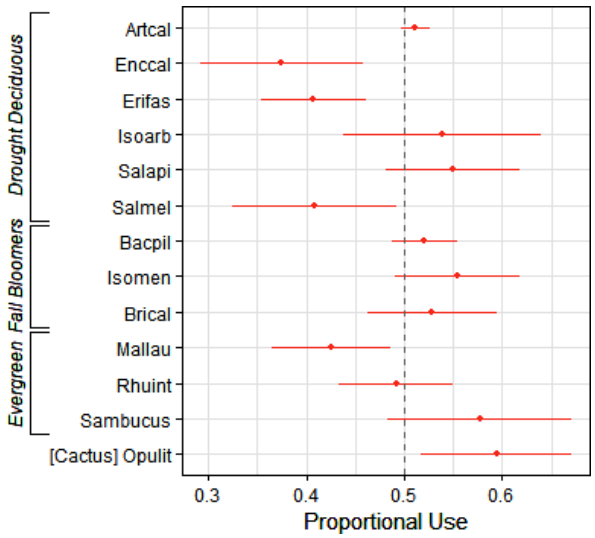


**Fig. 3.** California Gnatcatcher (*Polioptila californica*) mean proportional plant species use (95% CI) comparing fall and winter seasons. Species with non-overlapping 95% CI with 0.5 (vertical dashed line) indicate that use of these plants was significantly more/less than what was available (P < 0.05). Two species, Artemisia californica and Baccharis pilularis have non-overlapping 95% CI indicating that use of these shrubs was significantly different between fall and winter.

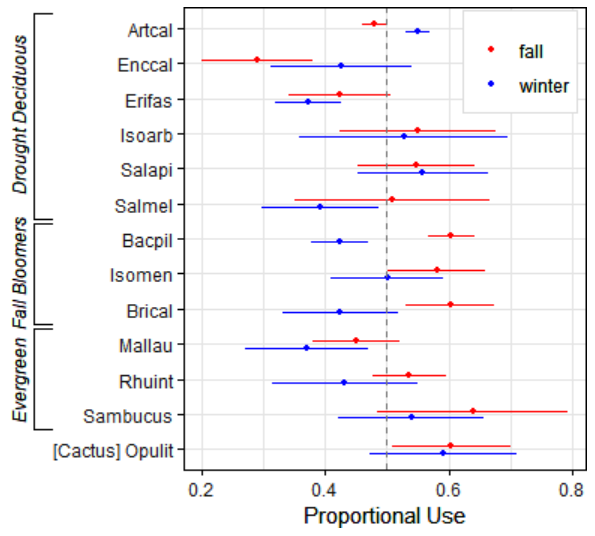


**Table 2.** Results from one-sample t-test investigating California Gnatcatcher (*Polioptila californica*) plant species use during fall and winter. Plant species that were used proportionally more/less than what was available (P < 0.05) are shown in bold. Sample size (N) is the number of gnatcatcher pairs in fall or winter, by plant species. Sample sizes vary by season and the species composition within a gnatcatcher territory.

| Species | Season | Plant Type | N | Mean Prop. Use | CI | t | df | P |
|---|---|---|---|---|---|---|---|---|
| **Artcal** | fall | Drought Deciduous | 122 | 0.48 | 0.020 | -2.001 | 121 | **0.05** |
| **Enccal** | fall | Drought Deciduous | 7 | 0.29 | 0.118 | -4.586 | 6 | **<0.01** |
| Erifas | fall | Drought Deciduous | 20 | 0.42 | 0.089 | -1.816 | 19 | 0.09 |
| Isoarb | fall | Drought Deciduous | 9 | 0.55 | 0.149 | 0.764 | 8 | 0.47 |
| Salapi | fall | Drought Deciduous | 13 | 0.55 | 0.104 | 0.998 | 12 | 0.34 |
| Salmel | fall | Drought Deciduous | 9 | 0.51 | 0.186 | 0.106 | 8 | 0.92 |
| **Bacpil** | fall | Fall Bloomer | 64 | 0.60 | 0.039 | 5.368 | 63 | **<0.01** |
| Isomen | fall | Fall Bloomer | 17 | 0.58 | 0.084 | 2.022 | 16 | 0.06 |
| **Brical** | fall | Fall Bloomer | 14 | 0.60 | 0.080 | 2.783 | 13 | **0.02** |
| Mallau | fall | Evergreen Shrub | 16 | 0.45 | 0.077 | -1.356 | 15 | 0.20 |
| Rhuint | fall | Evergreen Shrub | 17 | 0.54 | 0.063 | 1.217 | 16 | 0.24 |
| Sambucus | fall | Evergreen Shrub | 6 | 0.64 | 0.202 | 1.769 | 5 | 0.14 |
| **Opulit** | fall | Cactus | 14 | 0.60 | 0.106 | 2.120 | 13 | **0.05** |
| **Artcal** | winter | Drought Deciduous | 98 | 0.55 | 0.020 | 4.972 | 97 | **<0.01** |
| Enccal | winter | Drought Deciduous | 10 | 0.43 | 0.131 | -1.279 | 9 | 0.23 |
| **Erifas** | winter | Drought Deciduous | 15 | 0.37 | 0.059 | -4.598 | 14 | **<0.01** |
| Isoarb | winter | Drought Deciduous | 8 | 0.53 | 0.202 | 0.316 | 7 | 0.76 |
| Salapi | winter | Drought Deciduous | 11 | 0.56 | 0.120 | 1.077 | 10 | 0.31 |
| **Salmel** | winter | Drought Deciduous | 11 | 0.39 | 0.110 | -2.212 | 10 | **0.05** |
| **Bacpil** | winter | Fall Bloomer | 53 | 0.42 | 0.047 | -3.261 | 52 | **<0.01** |
| Isomen | winter | Fall Bloomer | 8 | 0.50 | 0.110 | 0.015 | 7 | 0.99 |
| Brical | winter | Fall Bloomer | 10 | 0.42 | 0.108 | -1.568 | 9 | 0.15 |
| **Mallau** | winter | Evergreen Shrub | 11 | 0.37 | 0.115 | -2.536 | 10 | **0.03** |
| Rhuint | winter | Evergreen Shrub | 10 | 0.43 | 0.138 | -1.142 | 9 | 0.29 |
| Sambucus | winter | Evergreen Shrub | 10 | 0.54 | 0.136 | 0.660 | 9 | 0.53 |
| Opulit | winter | Cactus | 15 | 0.59 | 0.130 | 1.503 | 14 | 0.16 |

than their availability, including the fall blooming: *Baccharis pilularis*; two drought deciduous shrubs, *Eriogonum fasciculatum* and *Salvia mellifera*; and the evergreen shrub, *Malosma laurina*. The only shrub that gnatcatchers preferentially foraged in during the winter was the drought deciduous shrub, *Artemisia californica*.

## DISCUSSION

*Baccharis pilularis* and *Brickellia californica*, the shrub species that California Gnatcatchers showed a preference for during the fall season, are notable in being fall bloomers (Rundel 2007, Sawyer et al. 2009). As most other shrub species are either leafless or not actively growing during the fall dry season, our results

suggest that these shrubs may support higher densities of preferred arthropod prey in the non-nesting season. This is supported by our personal observations of pollinating insects utilizing the flowers of these species during our surveys. Another fall blooming shrub, *Isocoma menziesii*, was not preferred for foraging at a $P < 0.05$ level, though gnatcatchers did show some preference for foraging in this species (Table 2). Campbell et al. (1998) also noted increased use of certain plant species by gnatcatchers in the non-breeding season, including *Sambucus* and *Baccharis*. Our data suggests *Sambucus* is foraged in at a level proportional to its availability in our study area.

California Gnatcatchers were observed using *Artemisia californica* more frequently during the winter months (December–January) than during the fall (October–November). This is likely due to the phenology of this shrub, which is drought deciduous and remains leafless through the summer and fall until the first rains of the winter, after which the plants leaf out and quickly flower. The first significant precipitation events of fall during the study period occurred in late November and again in mid-December (0.82 and 1.46 in. of precipitation respectively). Thus, in early December, *Artemisia californica* began its active growth phase and leafed out and bloomed. Several studies have shown a close relationship between California Gnatcatcher occurrences and the presence of *Artemisia californica* (Atwood et al. 1998, Winchell and Doherty 2008, Winchell and Doherty 2018).

California gnatcatchers foraged less than would be expected in several shrub species, including the evergreen shrub *Malosma laurina* and drought deciduous shrubs such as *Encelia californica, Eriogonum fasciculatum*, and *Salvia mellifera*. It may be that these shrubs do not support high densities of preferred gnatcatcher prey items during these seasons, though this has yet to be established. Winchell and Doherty (2018) also found a negative correlation at a landscape scale with California Gnatcatcher densities and *Malosma laurina* presence.

It should be noted that while we found these shrubs to be foraged in less than their prevalence on the landscape during the fall and winter seasons, they may be important during other seasons or for other components of California Gnatcatchers' life history needs. For instance, *Salvia mellifera* and *Eriogonum fasciculatum* are preferred shrubs for nest placement during the breeding season, and gnatcatchers are often observed foraging in *Eriogonum* during its summer blooming period (Roach 1989).

Our results show that California Gnatcatchers preferentially select certain plant species while foraging. Thus, floristic composition is an important factor when defining California Gnatcatcher habitat. These data will be useful in habitat restoration efforts, where success is often defined in terms of percent cover of all shrubs, rather than prevalence of preferred foraging plant species or overall floristic diversity.

These results provide the first data on the floristic preferences of foraging gnatcatchers during the critical fall and winter seasons, when limited insect prey and the initiation of cold, wet winter storms begins a period of high mortality. The preference for *Artemisia californica* in the non-breeding season further emphasizes the importance of this shrub within the U.S. range of this threatened bird (i.e., Pratt and Mooney 2013, Winchell and Doherty 2018). In addition, our findings that a variety of other shrubs were also favored, including common fall blooming species, point to the value of floristic diversity within California Gnatcatcher habitat.

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**Data Availability:**

*The data/code that support the findings of this study are available on request from the corresponding author (KBC). This study was funded by the Department of Defense, and the data are not authorized for public distribution but can be shared for the purposes of peer review and to interested researchers. All research activities were authorized by the U.S. Fish and Wildlife Service and USGS Bird Banding Laboratory.*

**LITERATURE CITED**

Atwood, J. L., and D. R. Bontrager. 2020. California Gnatcatcher (Polioptila californica), version 1.0. Pages in A. F. Poole and F. B. Gill, editors. Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.calgna.01

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.

Beal, F. E. L. 1907. Birds of California in relation to the fruit industry. Part 1. USDA, Biological Survey, Bulletin No. 30. Government Printing Office: Washington, DC, USA.

Burger, J. C., M. A. Patten, J. T. Rotenberry, and R. A. Redak. 1999. Foraging ecology of the California Gnatcatcher deduced from fecal samples. Oecologia 120:304-310. https://doi.org/10.1007/s004420050862

Campbell, K. F., R. A. Erickson, W. E. Haas and M. A. Patten. 1998. California Gnatcatcher use of habitats other than coastal sage scrub: conservation and management implications. Western Birds 29:421-433.

Erickson, R. A., and K. L. Miner. 1998. Six years of synchronous California Gnatcatcher population fluctuations at two locations in Coastal Orange County, California. Western Birds 29:333-339.

Godínez-Alvarez, H., J. E. Herrick, M. Mattocks, D. Toledo, and J. Van Zee. 2009. Comparison of three vegetation monitoring methods: their relative utility for ecological assessment and monitoring. Ecological Indicators 9:1001-1008. https://doi.org/10.1016/j.ecolind.2008.11.011

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31-35. https://doi.org/10.1007/BF00346985

MacArthur R. W., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598. https://doi.org/10.2307/1932254

MacArthur R. W., H. Recher, and M. L. Cody. 1966. On the relation between habitat selection and species diversity. American Naturalist 100:319-332. https://doi.org/10.1086/282425

Narango, D. L., Tallamy, D. W., and P.P. Marra. 2017. Native plants improve breeding and foraging habitat for an insectivorous bird. Biological Conservation 213:42-50. https://doi.org/10.1016/j.biocon.2017.06.029

Pratt, J. D. and K. A. Mooney. 2013. Clinal adaptation and adaptive plasticity in Artemisia californica: implications for the response of a foundation species to predicted climate change. Global Change Biology 19:2454-2466. https://doi.org/10.1111/gcb.12199

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Roach, J. D. 1989. The influence of vegetation structure and arthropod abundance on the reproductive success of California Black-tailed Gnatcatchers. M.S. Thesis, San Diego State University, San Diego, CA, USA.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67 (2):213-217. https://doi.org/10.1007/BF00384286

Rundel, P. W. 2007. Sage Scrub in M. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial Vegetation of California. 3rd edition. University of California Press, Oakland, CA, USA. https://doi.org/10.1525/california/9780520249554.003.0008

Sawyer, J., T. Keeler-Wolf, and J. M. Evens. 2009. A Manual of California Vegetation. 2nd ed. California Native Plant Society, California, USA.

Toledo, D.P., J. E. Herrick, and L. A. Abbott. 2010. A comparison of cover pole with standard vegetation monitoring methods. Journal of Wildlife Management 74(3):600-604. https://doi.org/10.2193/2009-136

USFWS (U.S. Fish and Wildlife Service). 1997. Coastal California Gnatcatcher (Polioptila californica californica) Presence/Absence Survey Guidelines. Report from Carlsbad Field Office, Carlsbad, CA, USA.

Weaver, K. L., 1998. Coastal sage scrub variations of San Diego County and their influence on the distribution of the California gnatcatcher. Western Birds 29:392-405.

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(6), pp.1322-1327. https://doi.org/10.2193/2006-356

Winchell, C. S., and P. F. Doherty Jr. 2018. Restoring habitat for coastal California Gnatcatchers (Polioptila californica californica). The Condor: Ornithological Applications 120(3):581-595. https://doi.org/10.1650/CONDOR-17-221.1