TRENDS IN BIRD SPECIES RICHNESS IN THE MIDST OF DROUGHT

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ABSTRACT: Climate change is predicted to exacerbate the effects of disturbances such as drought on numerous wildlife communities. On the basis of surveys from 1981 to 2014, we investigated whether drought altered the species richness and composition of bird communities of coastal sage scrub in two protected areas of southern California. At one site, the Voorhis Ecological Reserve, Pomona, we found that the number of species of permanent residents, but not of summer and winter visitors, was lower during droughts than during periods of at least average rainfall. At the other site, the Bernard Field Station, Claremont, we found that the richness of resident species remained the same in both drought and nondrought periods, and richness of summer and winter visitors increased during times of drought. The difference in patterns between these sites may be explained by the presence of a constructed, permanent water source at the second site. Thus, supplemental water sources embedded in natural areas might be an important resource for native bird species during drought.

Climate change is predicted to increase the frequency of drought in arid regions, threatening avian populations and native ecosystems (National Wildlife Federation 2008, Mastrandrea and Luers 2012). There is a growing body of work on the effects of drought on birds that breed in arid and semi-arid habitats. For example, periods of drought or atypically low rainfall have led to lower levels of species richness and abundance in birds (Albright et al. 2010), reduction of birds' reproductive rates (McCreedy et al. 2015), reproductive failure of passerines (Bolger et al. 2005), a decline of over 60% in density of grassland birds (George et al. 1992), short-term declines in both resident and migratory species (Bock and Bock 1999), and smaller clutch sizes of the California Gnatcatcher (*Polioptila californica*; Patten and Rotenberry 1999).

Coastal sage scrub is a plant community found in coastal California and northern Baja California, largely below 300 m in elevation. Its species are adapted to winter rains and a summer dry period, in which many plants are deciduous, growing leaves during the wet winter and losing them during the dry summer. The dominant plant species consist of low-growing shrubs such as *Artemisia californica, Salvia mellifera*, and *Salvia apiana*. In this region annual variability in rainfall is high, and fire and drought are recurrent. Shrubs characteristic of coastal sage scrub experience increased mortality following drought (Minnich and Dezzani 1998). Of the numerous species of organisms in coastal sage scrub, approximately 100, both animals and plants, require conservation attention according to California and federal wildlife agencies (Atwood 1993, McCaull 1994). Among birds of coastal southern California, the California Gnatcatcher (designated as threatened by the U.S. Fish and Wildlife Service) and Cactus Wren (*Campylorhynchus brunneicapillus*), rely on coastal sage scrub for critical breeding habitat (Barr et al. 2015, Rubinoff

2001). As a result of urban development and fragmentation, this habitat is one of the most endangered in the United States, reduced to less than 10% of its original range (Taylor 2005), with many species relying on it in decline (Chase et al. 2000, Rubinoff 2001, Barr et al. 2015). The effects of climate change, including longer and more severe droughts, may further threaten southern California's declining, fragmented coastal sage scrub (Griffin and Anchukaitis 2014).

From 2012 to 2016, southern California experienced one of the most severe droughts in recorded history (Griffin and Anchukaitis 2014, Wang et al. 2014, Robeson 2015). The California Department of Water Resources (2015) declared it a "state of emergency" that caused significant economic losses and threatened native wildlife and ecosystems. Protecting and restoring native ecosystems affected by this drought poses a critical conservation challenge. Here, on the basis of long-term data on the bird community in two remnants of coastal sage scrub in Los Angeles County, we consider whether avian species richness changed significantly during drought. We predicted that species richness should decline during drought, especially richness of migratory species that might avoid drought-affected habitat (Albright et al. 2010).

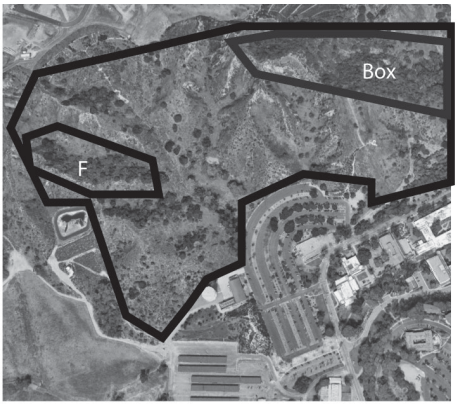
METHODS

Our study is focused on two patches of coastal sage scrub along the urban–wildland interface of inland Los Angeles County, the Voorhis Ecological Reserve and the Robert J. Bernard Biological Field Station (Figure 1). Precipitation averages 545 mm per year, although from the year 1900 through 2000 the number of days of rainfall per year decreased (36 to 29), while the average precipitation during each storm increased from 7 to 11 mm (U.S. Geological Survey 2005, Goldstein and Suding 2014). Both the Voorhis Ecological Reserve and the Bernard Field Station have experienced periodic wildfire.

Study Areas

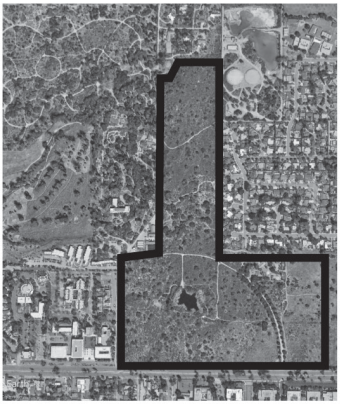
The Bernard Field Station is located in Claremont on an alluvial outwash from the San Gabriel Mountains (Figure 1; 34.11° N, 117.71° W, elevation 356 m). It covers approximately 35 ha and contains an artificial pond and wetland that are managed as a source of permanent water for wildlife. The wetland consists of 0.2 ha of marsh with water up to 2 m deep and a 0.4-ha pond up to 6 m deep. The pond is kept full, even during dry periods. The dominant plant community consists of coastal sage scrub and alluvial fan sage scrub, with some oak woodland and grassland. The reserve also contains small areas of riparian woodland and artificial vernal pools. The portion in coastal sage scrub is mostly undeveloped, with some areas categorized as "recovering" after 5.5 ha burned in an accidental fire in September 2013 (Wallace Meyer pers. comm.).

The 31-ha Voorhis Ecological Reserve is located in the middle of the San Jose Hills in Pomona (34.06° N, 117.83° W, elevation 300 m) approximately 22.5 km from the Bernard Field Station. It is an important wildlife corridor that connects the San Gabriel and Santa Ana mountains (Figure 1).



(A) Voorhis Ecological Reserve

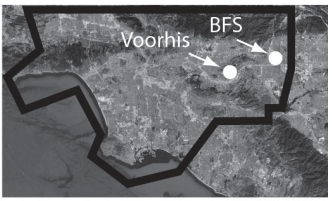
0.20 km



(B) Bernard Field Station

0.30 km

(C) California



(D) Los Angeles County

(E) F Canyon

Figure 1. Study areas in Los Angeles County, California (C, D; from Google Earth). (A) Voorhis Ecological Reserve, Pomona (34.059, –117.828, elevation 300 m). Polygons indicate Box Canyon and F Canyon survey sites. (B) Bernard Field Station, Claremont (34.110, –117.710, elevation 356 m). The permanent lake is shown in the center of the area. (E) View of F Canyon in the Voorhis Ecological Reserve, showing typical vegetation patterns.

Photo by Brian Myers

The Voorhis Reserve contains undeveloped coastal sage scrub and has been designated as a "significant ecological area" by Los Angeles County. Like the Bernard Field Station, the Voorhis Reserve is dominated by coastal sage scrub and mixed oak woodland, although the Voorhis Reserve also includes invasive annual plants and some chaparral species. It lacks permanent water but is adjacent to areas with artificial ponds and watered landscaping. The distance to the nearest water source is 0.55 km. The reserve has burned several times, most recently in 1981 (a portion of the reserve) and 1989 (the entire reserve). The 1989 fire was limited to the Voorhis Reserve and small adjacent areas; it did not significantly alter the composition of the reserve's bird community (Moriarty et al. 1985, Moriarty 2013).

Sampling

The results of monthly bird surveys of the Bernard Field Station by Catherine McFadden from 2000 to 2014 were recorded at www.ebird.org, from which we extracted these data. She completed a four-hour survey over the same route around the perimeter of the 35-ha site on each date (Catherine McFadden and Wallace Meyer pers. comm.). We used only presence/absence data to ensure comparability with results from the Voorhis Ecological Reserve.

From the Voorhis Reserve we used data by Moriarty (2013) based on 265 surveys from January 1983 to December 2003. Each survey covered two canyons (Box Canyon and F Canyon) from a fixed location in each canyon at approximately sunrise for 30 minutes each; which canyon was surveyed first each day alternated. In each canyon the area surveyed was approximately 1.25 ha, 0.4 km apart, south-facing, and similar in vegetation structure. According to the protocol of Moriarty (2013), species within the boundaries of the canyon were recorded as present, but birds flying above the canyon to another location were not counted. During a year of exceptional drought, approximately twice per week year round from February 2013 to February 2014, we replicated these surveys from nearly the same positions as Moriarty (2013), for a total of 89 surveys. We followed the same protocol, except in Box Canyon our survey point was about 9 m above that of Moriarty because recent growth of vegetation impaired visibility from the previous survey point. The large number of these surveys allowed us to examine how drought altered community diversity by month rather than just by season. Both sites were surveyed at the same time, allowing us to compare their species richness.

Classification

Following Moriarty (2013), we categorized the surveys as summer (April through September) or winter (October through March), defining the seasons by the most significant differences observed in the presence and absence of migratory birds. We classified each species as a year-round resident, transient, or migrant, and separated migrants into two subcategories, summer visitors and winter visitors. Migratory birds were classified as summer visitors if found within or near our field sites during the summer season and classified as winter visitors if normally observed within or near our field sites during the winter season, on the basis of information provided in the Los Angeles

Breeding Bird Atlas (Allen et al. 1994) and occurrence records at www.eBird.org). We categorized species as breeding at our sites (resident or summer) if recorded adjacent to or within atlas block "SAD" in Allen et al. (1994). Further descriptions within each species account assisted with classification as resident or summer breeding birds. For species that were ambiguous, not listed in the atlas, or for those that breed in habitats beyond our study sites, we first consulted Allen et al. (1994), then eBird for the time of year in which a species was observed most often. This was necessary for several species, including the Pacific-slope Flycatcher (*Empidonax difficilis*), Townsend's Warbler (*Setophaga townsendi*), and Phainopepla (*Phainopepla nitens*).

The distributions of some species changed through the course of our study, as in the cases of the Allen's Hummingbird (*Selasphorus sasin*), Eurasian Collared-Dove (*Streptopelia decaocto*), Dark-eyed Junco (*Junco hyemalis*), and Mountain Chickadee (*Poecile gambeli*). For these species, which have all recently forged their way into our study areas, we based categorizations on current distributions and patterns, because these species were either never observed in any survey at either site before they colonized the area and became residents (Eurasian Collared-Dove, Allen's Hummingbird), or were observed with the same regularity at our study sites before and after their expansion (Eurasian Collared-Dove and Mountain Chickadee; eBird). We categorized birds as transient if they were observed only intermittently passing through a site during migration. Our use of "migrants" unqualified encompasses summer visitors and winter visitors combined. We included only birds using coastal sage scrub, excluding those found in other habitats at the Bernard Field Station, to ensure that comparisons with the Voorhis Reserve were meaningful.

Drought

To quantify the effect of drought, we adapted the Palmer Drought Index, based on monthly departures of precipitation and temperature data from long-term averages (Palmer 1965). Values of –4 and below represent "extreme drought," –3 to –3.99 "severe drought," –2 to –2.99 "moderate drought," –1.99 to 2.99 "mid-range," 2–2.99 "moderately moist" conditions, 3–3.99 "very moist," and 3–3.99 "extremely moist." The Palmer Drought Index is a widely used way to analyze fluctuations in drought data over time (Palmer 1965, NOAA 2017). To simplify the index, we reduced the values to categories, then ranked them on a scale from 0 to 6, 0 for extremely moist, 1 for very moist, 2 for moderately moist, 3 for mid-range, 4 for moderate drought, 5 for severe drought, and 6 for extreme drought.

Data Analysis

We used three datasets to examine the effects of drought and season on species richness: (1) long-term data from the Bernard Field Station, 2000–2014, (2) long-term data from the Voorhis Reserve, 1983–2003, and (3) 2013–2014 data from both sites. For the Voorhis Reserve we pooled results from the two canyons for each date to generate a single list of species. We tested separate models for the following dependent variables: total richness of bird species, richness of resident species, and richness of migratory species in each long-term dataset (1 and 2). At both sites the sampling on which

the long-term data were based was not consistent from month to month. To standardize the data for variation in sampling effort, we calculated the mean species richness over all sampling dates for each month, then used the value for each month as one data point.

We used general linear mixed models to test the effects of the factors drought level (adapted Palmer Index), season, and year on species richness from the two long-term datasets. We included year as a random variable; all other factors were fixed. We also included the interaction term season × drought level because drought might have a greater effect on the community in winter or summer. We tested the models with the data from the two sites separately and log-transformed data when needed to improve the normality and homogeneity of variance. We analyzed all models in R version 3.4.3 (R Core Team 2015).

RESULTS

The numbers of species of year-round residents, winter migrants, summer migrants, transients, and all categories pooled were higher at the Bernard Field Station than at the Voorhis Reserve (Figure 2). The 93 species observed from 2013 to 2014 at the Bernard Field Station comprised 48 resident species, 29 migrants (16 winter visitors, 13 summer visitors), and 16 transient species. The 66 species observed over the same interval at the Voorhis Reserve encompassed 41 residents, 20 migrants (8 winter visitors and 12 summer visitors), and 5 transient species. Ninety-nine species were observed over 265 surveys from 1983 to 2003 in the Voorhis Reserve (55 residents, 12 winter visitors, 11 summer visitors, and 21 transients); 122 species were observed over 160 surveys from 2000 to 2014 at the Bernard Field Station (62 residents, 16 winter visitors, 14 summer visitors, and 30 transients). Several species, both residents and migrants, at both the Bernard Field Station and the Voorhis Reserve, were observed during surveys before the drought but not after the drought (Table 1).

Species Richness

At the Voorhis Reserve, total species richness varied by season, being higher in summer than in winter (Table 2; significant effect of season). There were no other significant factors affecting richness of total species at either study site, although the effect of drought level on richness of resident species was significant at both sites (Table 2). The number of resident species was higher during wet conditions (drought indices 0–2) and lower during drought conditions (drought indices 4–6), with the trend more pronounced at the Voorhis Reserve than at the Bernard Field Station (Figure 3a, d). The number of migrant species recorded at the Voorhis Reserve did not differ significantly by drought level, whereas at the Bernard Field Station it was higher during drought (index classes 5 and 6) than during wetter conditions (Table 2, Figure 3e). The number of migrant species was higher in summer than in winter at both sites (Table 2, significant effect of season, Figure 3b, e). Overall, richness of resident species was higher during wetter periods than during drought at both study sites, while that of migrant species at the Voorhis Reserve in drought and nondrought periods did not differ.

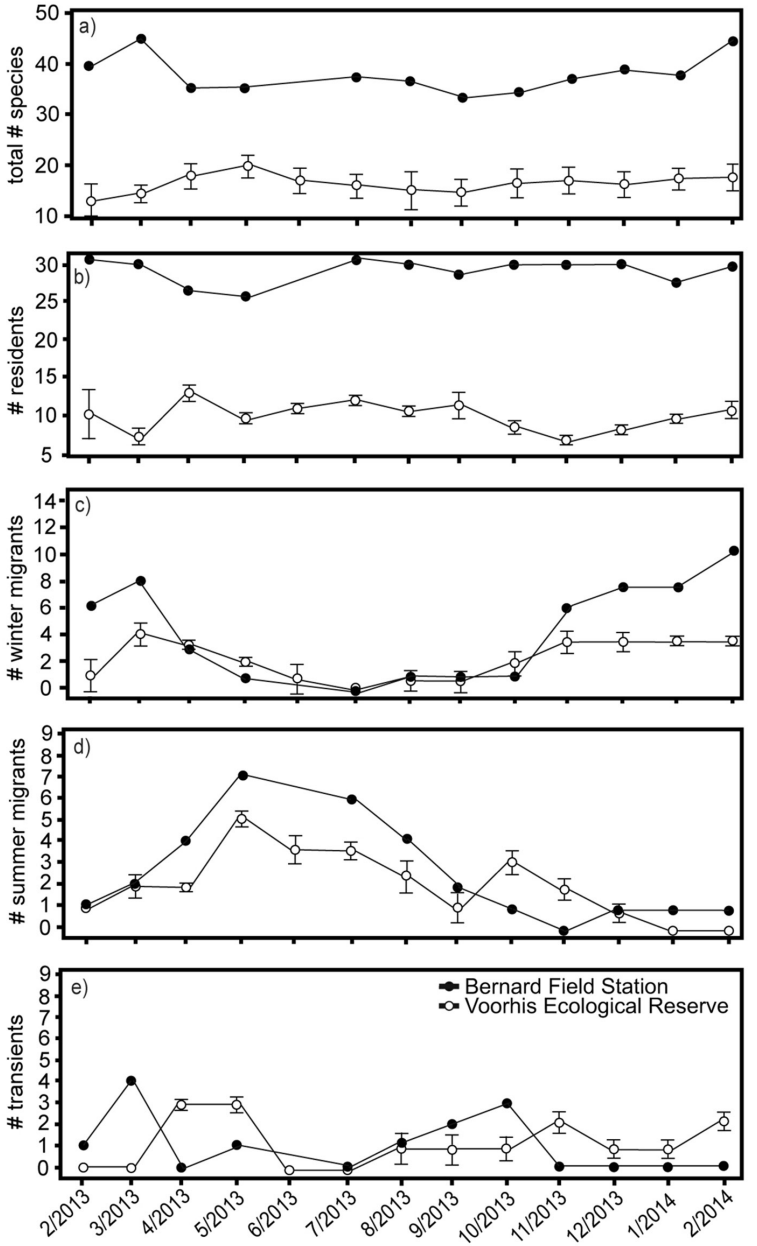


Figure 2. Number of bird species recorded at the Voorhis Ecological Reserve and Bernard Field Station by month from February 2013 to February 2014: (a) total species richness; (b) richness of resident species; (c) species richness of winter visitors; (d) species richness of summer visitors; (e) richness of transient species. Symbols indicate group means; error bars are one standard error. There are no error bars for Bernard Field Station data because each point represents one instance of sampling.

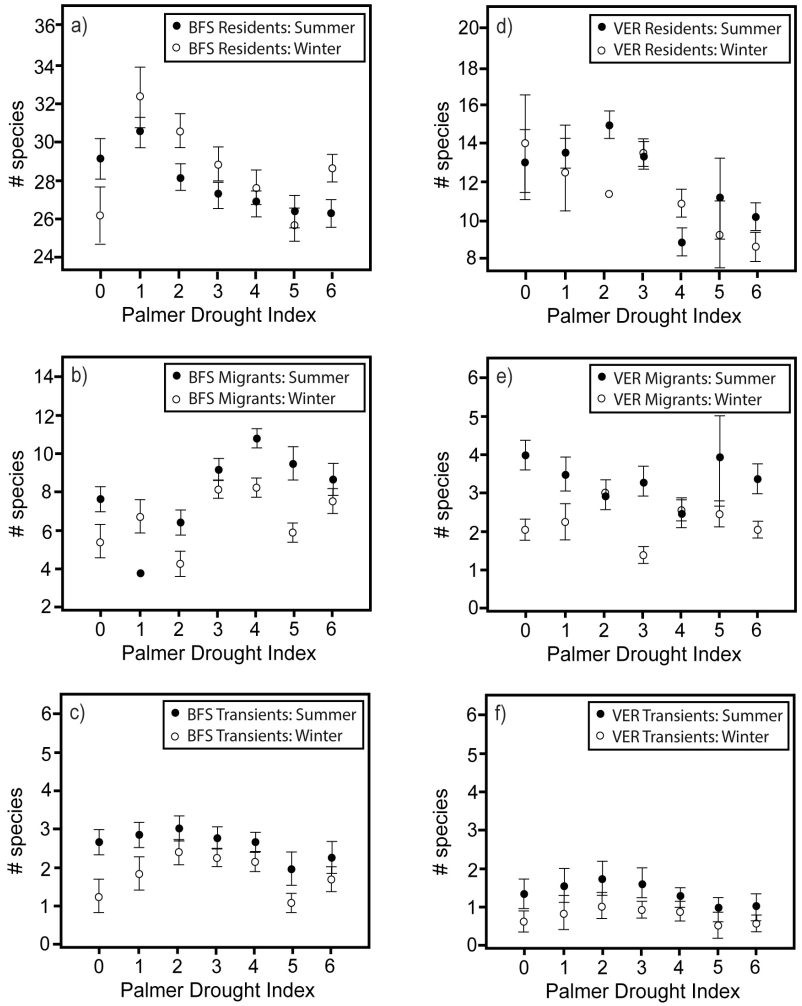


Figure 3. Bird species richness by drought index and season (a) for resident species from 2000 to 2014 at the Bernard Field Station (BFS), (b) for all migrant species from 2000 to 2014 in the Bernard Field Station, (c) for transient species from 1983 to 2003 at the Bernard Field Station, (d) for resident species from 1983 to 2003 at the Voorhis Ecological Reserve (VER), (e) for all migrant species from 1983 to 2003 at the Voorhis Ecological Reserve, and (f) for all transient species from 1983 to 2003 at the Voorhis Ecological Reserve. Palmer drought index scores of 4–6 indicate drought conditions. Symbols indicate group means; error bars are one standard error.

Table 1 Categorization of Status and Occurrence of Birds before or during Drought at the Bernard Field Station and Voorhis Ecological Reserve, Southern California, 1981–2014

		Bernard		Voorhis	
Species	Status	Pre-drought	Drought	Pre-drought	Drought
California Quail (*Callipepla californica*)	Resident	X	X	X	X
Rock Pigeon (*Columba livia*)	Resident	X	X	—	—
Band-tailed Pigeon (*Patagioenas fasciata*)	Resident	X	X	X	—
Eurasian Collared-Dove (*Streptopelia decaocto*)	Resident	X	—	—	—
Spotted Dove (*Streptopelia chinensis*)	Resident	—	—	X	—
Mourning Dove (*Zenaida macroura*)	Resident	X	X	X	X
Greater Roadrunner (*Geococcyx californianus*)	Resident	X	—	X	—
Common Poorwill (*Phalaenoptilus nuttallii*)	Transient	—	—	X	—
Vaux's Swift (*Chaetura vauxi*)	Transient	X	X	X	—
White-throated Swift (*Aeronautes saxatalis*)	Resident	X	X	X	—
Black-chinned Hummingbird (*Archilochus alexandri*)	Summer	X	X	X	X
Anna's Hummingbird (*Calypte anna*)	Resident	X	X	X	X
Costa's Hummingbird (*Calypte costae*)	Summer	X	X	X	X
Rufous Hummingbird (*Selasphorus rufus*)	Transient	X	X	X	—
Allen's Hummingbird (*Selasphorus sasin*)	Resident	X	X	X	X
Calliope Hummingbird (*Selasphorus calliope*)	Transient	X	—	—	—
Great Blue Heron (*Ardea herodias*)	Resident	X	—	—	X
Turkey Vulture (*Cathartes aura*)	Resident	X	X	X	X
White-tailed Kite (*Elanus leucurus*)	Resident	X	—	X	—
Northern Harrier (*Circus hudsonius*)	Resident	X	—	X	X
Sharp-shinned Hawk (*Accipiter striatus*)	Winter	X	X	X	X
Cooper's Hawk (*Accipiter cooperii*)	Resident	X	X	X	X
Red-shouldered Hawk (*Buteo lineatus*)	Resident	X	X	—	X
Swainson's Hawk (*Buteo swainsoni*)	Transient	X	—	—	—
Red-tailed Hawk (*Buteo jamaicensis*)	Resident	X	X	X	X

(*continued*)

		Bernard		Voorhis	
Species	Status	Pre-drought	Drought	Pre-drought	Drought
Golden Eagle (*Aquila chrysaetos*)	Transient	—	—	X	—
Barn Owl (*Tyto alba*)	Resident	X	—	—	—
Great Horned Owl (*Bubo virginianus*)	Resident	X	X	X	X
Acorn Woodpecker (*Melanerpes formicivorus*)	Resident	X	X	X	—
Red-breasted Sapsucker (*Sphyrapicus ruber*)	Winter	X	X	—	—
Nuttall's Woodpecker (*Dryobates nuttallii*)	Resident	X	X	X	X
Downy Woodpecker (*Dryobates pubescens*)	Resident	X	X	—	—
Northern Flicker (*Colaptes auratus*)	Resident	X	X	X	X
American Kestrel (*Falco sparverius*)	Resident	X	X	X	X
Merlin (*Falco columbarius*)	Winter	X	X	—	—
Prairie Falcon (*Falco mexicanus*)	Transient	—	—	X	—
Red-crowned Parrot (*Amazona viridigenalis*)	Resident	X	—	—	—
Olive-sided Flycatcher (*Contopus cooperi*)	Transient	X	X	—	—
Western Wood-Pewee (*Contopus sordidulus*)	Transient	X	—	X	—
Willow Flycatcher (*Empidonax traillii*)	Transient	X	X	—	—
Hammond's Flycatcher (*Empidonax hammondii*)	Transient	X	X	—	—
Gray Flycatcher (*Empidonax wrightii*)	Transient	X	—	X	—
Pacific-slope Flycatcher (*Empidonax difficilis*)	Summer	X	—	X	X
Black Phoebe (*Sayornis nigricans*)	Resident	X	X	X	X
Say's Phoebe (*Sayornis saya*)	Resident	X	X	X	X
Ash-throated Flycatcher (*Myiarchus cinerascens*)	Summer	X	X	X	X
Cassin's Kingbird (*Tyrannus vociferans*)	Resident	X	X	X	X
Western Kingbird (*Tyrannus verticalis*)	Summer	X	X	X	X
Loggerhead Shrike (*Lanius ludovicianus*)	Resident	X	—	X	X
Hutton's Vireo (*Vireo huttoni*)	Resident	X	X	—	—
Cassin's Vireo (*Vireo cassinii*)	Transient	X	X	—	X
Plumbeous Vireo (*Vireo plumbeus*)	Transient	—	—	X	—
Warbling Vireo (*Vireo gilvus*)	Transient	X	—	X	—

(*continued*)

Table 1 (*continued*).

Species	Status	Bernard		Voorhis	
		Pre-drought	Drought	Pre-drought	Drought
Bell's Vireo (*Vireo bellii*)	Summer	X	—	—	—
California Scrub-Jay (*Aphelocoma californica*)	Resident	X	X	X	X
American Crow (*Corvus brachyrhynchos*)	Resident	X	X	X	X
Common Raven (*Corvus corax*)	Resident	X	X	X	X
Tree Swallow (*Tachycineta bicolor*)	Transient	X	—	—	—
Violet-green Swallow (*Tachycineta thalassina*)	Transient	X	X	X	—
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	Summer	X	X	X	X
Cliff Swallow (*Petrochelidon pyrrhonota*)	Summer	X	X	X	X
Barn Swallow (*Hirundo rustica*)	Summer	X	X	—	—
Mountain Chickadee (*Poecile gambeli*)	Transient	X	X	X	X
Oak Titmouse (*Baeolophus inornatus*)	Resident	X	X	X	—
Bushtit (*Psaltriparus minimus*)	Resident	X	X	X	X
White-breasted Nuthatch (*Sitta carolinensis*)	Transient	X	X	—	—
Rock Wren (*Salpinctes obsoletus*)	Resident	X	—	X	—
House Wren (*Troglodytes aedon*)	Resident	X	X	X	X
Bewick's Wren (*Thryomanes bewickii*)	Resident	X	X	X	X
Cactus Wren (*Campylorhynchus brunneicapillus*)	Resident	X	—	X	X
Blue-gray Gnatcatcher (*Polioptila caerulea*)	Resident	X	X	X	X
California Gnatcatcher (*Polioptila californica*)	Resident	—	—	X	X
Ruby-crowned Kinglet (*Regulus calendula*)	Winter	X	X	X	X
Wrentit (*Chamaea fasciata*)	Resident	X	X	X	X
Western Bluebird (*Sialia mexicana*)	Resident	X	X	X	X
Swainson's Thrush (*Catharus ustulatus*)	Transient	X	—	X	X
Hermit Thrush (*Catharus guttatus*)	Winter	X	X	X	X
American Robin (*Turdus migratorius*)	Resident	X	X	X	X
California Thrasher (*Toxostoma redivivum*)	Resident	X	X	X	X
Northern Mockingbird (*Mimus polyglottos*)	Resident	X	X	X	X

(*continued*)

		Bernard		Voorhis	
Species	Status	Pre-drought	Drought	Pre-drought	Drought
European Starling (*Sturnus vulgaris*)	Resident	X	X	X	—
Cedar Waxwing (*Bombycilla cedrorum*)	Winter	X	X	X	—
Phainopepla (*Phainopepla nitens*)	Summer	X	X	X	X
Northern Red Bishop (*Euplectes franciscanus*)	Resident	X	—	—	—
Scaly-breasted Munia (*Lonchura punctulata*)	Resident	X	—	—	—
House Sparrow (*Passer domesticus*)	Resident	X	X	X	—
House Finch (*Haemorhous mexicanus*)	Resident	X	X	X	X
Purple Finch (*Haemorhous purpureus*)	Winter	X	X	X	—
Pine Siskin (*Spinus pinus*)	Winter	X	X	—	—
Lesser Goldfinch (*Spinus psaltria*)	Resident	X	X	X	X
Lawrence's Goldfinch (*Spinus lawrencei*)	Transient	X	X	X	—
American Goldfinch (*Spinus tristis*)	Resident	X	X	X	X
Spotted Towhee (*Pipilo maculatus*)	Resident	X	X	X	X
Rufous-crowned Sparrow (*Aimophila ruficeps*)	Resident	—	—	X	X
California Towhee (*Melozone crissalis*)	Resident	X	X	X	X
Chipping Sparrow (*Spizella passerina*)	Winter	X	X	X	X
Brewer's Sparrow (*Spizella breweri*)	Transient	X	X	—	—
Lark Sparrow (*Chondestes grammacus*)	Resident	X	X	X	—
Bell's Sparrow (*Artemisiospiza belli*)	Resident	—	—	X	—
Savannah Sparrow (*Passerculus sandwichensis*)	Transient	X	X	X	—
Fox Sparrow (*Passerella iliaca*)	Winter	X	X	X	—
Song Sparrow (*Melospiza melodia*)	Resident	X	X	X	X
Lincoln's Sparrow (*Melospiza lincolnii*)	Winter	X	X	X	—
White-throated Sparrow (*Zonotrichia albicollis*)	Winter	X	X	—	—
White-crowned Sparrow (*Zonotrichia leucophrys*)	Winter	X	X	X	X
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	Winter	X	X	X	X

(*continued*)

Table 1 (*continued*).

Species	Status	Bernard		Voorhis	
		Pre-drought	Drought	Pre-drought	Drought
Dark-eyed Junco (*Junco hyemalis*)	Winter	X	X	X	X
Yellow-breasted Chat (*Icteria virens*)	Summer	X	X	—	—
Western Meadowlark (*Sturnella neglecta*)	Resident	X	X	X	X
Hooded Oriole (*Icterus cucullatus*)	Summer	X	X	X	X
Bullock's Oriole (*Icterus bullockii*)	Summer	X	X	X	X
Red-winged Blackbird (*Agelaius phoeniceus*)	Resident	X	X	X	—
Brown-headed Cowbird (*Molothrus ater*)	Resident	X	X	X	X
Brewer's Blackbird (*Euphagus cyanocephalus*)	Resident	X	—	—	—
Great-tailed Grackle (*Quiscalus mexicanus*)	Resident	X	—	—	—
Orange-crowned Warbler (*Oreothlypis celata*)	Resident	X	X	X	—
Nashville Warbler (*Oreothlypis ruficapilla*)	Transient	X	X	—	—
MacGillivray's Warbler (*Geothlypis tolmiei*)	Transient	X	—	X	—
Common Yellowthroat (*Geothlypis trichas*)	Resident	X	X	—	—
Yellow Warbler (*Setophaga petechia*)	Summer	X	—	X	X
Yellow-rumped Warbler (*Setophaga coronata*)	Winter	X	X	X	X
Black-throated Gray Warbler (*Setophaga nigrescens*)	Transient	X	X	—	—
Townsend's Warbler (*Setophaga townsendi*)	Transient	X	—	X	—
Hermit Warbler (*Setophaga occidentalis*)	Transient	X	—	—	—
Wilson's Warbler (*Cardellina pusilla*)	Transient	X	X	X	X
Summer Tanager (*Piranga rubra*)	Transient	X	—	—	—
Western Tanager (*Piranga ludoviciana*)	Transient	X	X	X	X
Black-headed Grosbeak (*Pheucticus melanocephalus*)	Summer	X	X	X	X
Blue Grosbeak (*Passerina caerulea*)	Summer	—	X	—	—
Lazuli Bunting (*Passerina amoena*)	Summer	X	—	X	—

Table 2 *F* Statistics from Generalized Linear Mixed Models of Bird Species Richness from 1983 to 2003 at the Voorhis Ecological Reserve and from 2000 to 2014 at the Bernard Field Station, Los Angeles County, California[a]

Response variable and site	Drought level	Season	Drought level × season
Degrees of freedom	6	1	6
Total richness			
Voorhis	1.346	5.322*	0.847
Bernard[b]	2.004	0.387	1.742
Richness of residents			
Voorhis	2.418*	0.124	1.468
Bernard	2.455*	9.125**	1.869
Richness of migrants			
Voorhis[b]	1.707	18.231***	0.477
Bernard[b]	2.055	10.865**	1.466
Richness of transients			
Voorhis	2.111	0.542	1.009
Bernard	1.057	0.238	0.955

[a]Levels of significance: $^{*}P < 0.05$, $^{**}P < 0.01$; $^{***}P < 0.001$; error df were 98 for the Voorhis Ecological Reserve and 121 for the Bernard Field Station.

[b]Data were log-transformed to improve normality.

DISCUSSION

At the Bernard Field Station, where during the drought the total number of species and the numbers of migrant species and of transients were greater than at the Voorhis Reserve, birds had access to a reliable water source. Drought may alter bird communities by depressing the availability of resources, and the effect of drought varies in different communities. Various studies have shown the negative effect drought has on bird occurrence (Faaborg 1982, Herremans 2004, Stracey 2010, Bennett et al. 2014). In a study based on Breeding Bird Survey data from the central U.S., Albright et al. (2010) found the most negative effects of drought in more arid regions, with species migrating to the tropics affected the most. They suggested that the decline of migrants during drought was due to migrants having the option to pass over unfavorable sites and select better locations, although this might vary with the availability and distance of such better habitat, the pull of site fidelity, which is often strong in long-distance migrants (Berthold 2001), and other factors. Both resident and migrant birds vary in how they react to changes in the environment. Some species are readily able to occupy new habitat under adverse conditions, while others are more heavily driven by site fidelity and return to the same locations year to year (Sedgwick 2004, Winter and Hargrove 2004, Barr et al. 2015). Albright et al. (2010) claimed that resident species in semiarid regions were affected less drastically, possibly because they are adapted to the environmental stresses characteristic of their habitats. Our results did not support these patterns.

During drought, we observed lower richness of resident species at both of our study sites. There are several possible explanations for this. It is possible that higher temperatures and less precipitation during drought

lead to a reduction in available resources, making productivity and survival more difficult (Bolger et al. 2005). Birds may also move to other parts of the landscape where water is artificially supplemented, although this may not be likely in the region we studied, as urbanized habitat is a barrier to dispersal of many resident birds of coastal sage scrub (Bolger et al. 1991). For species that are more dispersive or migratory, however, some examples of movement in response to drought are known in southern California. The two largest invasions of the White-breasted Nuthatch (*Sitta carolinensis*) in San Diego County outside of a its breeding range occurred in 1961 and 2002, after the two of the driest years in that county's history (Unitt 2004). Migrating Lazuli Buntings (*Passerina amoena*), normally scarce in urban areas of coastal southern California, were common in the city of San Diego in spring 2006, after the very dry winter of 2005-06 (P. Unitt pers. comm.)

In the absence of suitable refugia, resident species may succumb because of increased mortality and/or reduced reproductive output over several years (Craig and Chapman 2003). During extended droughts, clutches of birds with access to supplemental water may not decline as steeply (Hudgens et al. 2009). Even at the Bernard Field Station, however, with its supplemental water source, the number of resident species declined somewhat during the drought, although the decline was greater at the Voorhis Reserve, which lacks supplemental water. Thus, the presence of supplemental water may help alleviate drought stress in resident birds (Crooks et al. 2004). Reductions in reproductive output and increased mortality during drought may also be due to a reduced food supply for birds (Bolger et al. 2005).

Reduced detectability is another possible explanation for the reduction in number of resident species during drought: as birds reduce reproductive behavior, they may become more cryptic and difficult to detect (Bolger et al. 2005). With the data available, we are not able to determine whether declines in species richness are due to decreased detectability, decreased abundance, or true presence or absence. Investigation of the exact mechanisms causing such reductions remains a subject for future study.

Decreased reproductive output during a drought presents another factor affecting population persistence. Extended droughts that depress reproductive output in several consecutive years may lead to population declines and push small isolated populations over the brink of extirpation. For example, coastal southern California was in either a "severe" or "extreme" drought from June 2012 to January 2017 (Palmer 1965, NOAA 2017). Drought and heat stress intensified by climate change contribute to the decline and extirpation of species (Cahill et al. 2012), as exemplified by a 16-year study of the Burrowing Owl (*Athene cunicularia*) near Albuquerque, New Mexico, which found a correlation between drought and delayed breeding, decreased mass of both adults and young, and a 98% decline of the population (Cruz-McDonnell and Wolf 2015).

The number of species of migrants at the Voorhis Reserve in drought and nondrought periods did not differ significantly, and at the Bernard Field Station the richness of migrant species increased during drought, possibly because of the availability of supplemental water. Regardless of the presence of drought, species richness of migrants was much higher at the Bernard Field Station (7.7 species per survey) than at the Voorhis Reserve (1.6

species per survey). We suggest these results could illustrate an influence of supplemental water, which may provide migrants refugia from drought.

The effects of climate change on southern California landscapes are leading to profound changes in native communities. Intensified drought means that resident bird species will need to either acclimate to these conditions or disperse to areas with more favorable habitat. Restoration and management, such as providing supplemental water, may be an important consideration for maintaining the diversity of bird species in some regions. Our study provides analyses of long-term data that demonstrate how bird communities respond to a changing environment over time.

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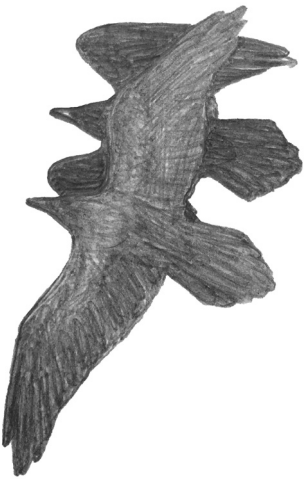

Common Ravens

Sketch by Teodelina Martelli