



Modeling the response of oak woodland birds to changing climate using 27 years of monitoring data

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Abstract: Using 27 years of point count data collected at the San Joaquin Experimental Range, Madera County, California, we modeled the importance of weather and climate variables on annual variability in the abundance of 35 bird species, to assess the potential responses of birds to changing environmental conditions. We used semi-parametric Poisson generalized additive models (GAM) with smoothing functions to explore relationships between bird abundance and the independent climatic and weather variables and to extract the best parametric polynomial model. We then selected among three parametric generalized linear mixed models (Poisson, quasi-Poisson, and negative binomial) on the basis of how well they explained the overdispersion of the counts. This approach also allowed us to estimate and control for variability among observers. Temperature variables were important in explaining variation in bird abundance. More species responded to cold than to hot temperatures: 18 were sensitive to cold, or were more abundant following warm winters or springs, whereas only 4 species were sensitive to heat. Because minimum temperatures are increasing faster than maximum temperatures, species sensitive to cold may benefit from warming. Abundance of Anna's Hummingbirds (*Calypte anna*), California Scrub-Jays (*Aphelocoma californica*), Oak Titmice (*Baeolophus inornatus*), and Bewick's Wrens (*Thryomanes bewickii*) decreased with warm temperatures, so an increase in mean temperatures is likely to affect these species negatively. One species, the Turkey Vulture (*Cathartes aura*), was more abundant after hot summers. Response to precipitation varied, with the number of species that increased in abundance with increasing precipitation being roughly equal to the number that decreased. El Niño Southern Oscillation (ENSO) events are predicted to increase in frequency and severity with climate change. The effects of ENSO vary geographically; for example, species that occur at lower elevations appear to respond differently from those that breed at higher elevations, where winter precipitation is dominated by snow rather than rain. In our low-elevation study area 12 species responded positively to warm, wet El Niño conditions; only 4 responded negatively. We found no clear pattern of response to long-term variation related to the Pacific Decadal Oscillation (PDO). We identified four species that decreased following drought years, but one of these, the Red-tailed Hawk (*Buteo jamaicensis*), was primarily responding (positively) to wet years. Abundance of Nuttall's Woodpeckers (*Picoides nuttallii*), Canyon Wrens (*Catherpes mexicanus*), and Lesser Goldfinches (*Spinus psaltria*) decreased with drought, so these species should be negatively affected by the increased frequency and severity of droughts projected with climate change. Oak woodland birds are closely tied to oaks and the acorns they produce, but questions about the ability of oaks to shift upward in elevation and latitude raise doubts about the ability of these bird species to adapt to climate change. Long-term monitoring data are useful for investigating and predicting avian responses to climate change. Understanding potential responses will help inform conservation decisions and planning for an uncertain future. We hope our predictions for how California oak woodland birds may respond to the changing climate will help prioritize future research and facilitate conservation.

Keywords: climate change, drought, El Niño, long-term data, monitoring, oak woodlands, precipitation, temperature

Supplemental Online Material for this paper (Appendices S1, S2, and S3) is available at www.wfopublications.org/Avifaunal_Change/Purcell-Mori_2/Purcell-Mori_2_SOM.pdf

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Global climate change will have dramatic impacts on ecosystems in the coming years. Projections from climate change models differ widely, but even the most benign predicted changes are sufficient to alter California's landscape significantly (Parmesan and Yohe 2003, Root et al. 2003, Dettinger 2005). Perhaps the biggest part of the problem with global climate change lies not simply in the changes *per se*, but in the rate of increase. The fossil record suggests that most species persisted through past cycles of climatic warming (Moritz and Agudo 2013), but the changes we are currently seeing and those projected by climate models are expected to occur at a rate and order of magnitude without precedent during at least the last 10,000 years (Root and Schneider 1993, IPCC 2001, Adger et al. 2003). The anticipated rates are widely acknowledged as too fast for evolutionary processes to keep pace (Davis and Shaw 2001, Jump and Peñuelas 2005).

Overwhelming evidence based on a review of key climate indicators confirms the world is warming (Arndt et al. 2010). Global average surface temperatures during the last three decades have been progressively warmer than during any preceding decade since 1850, with the 2000s (2000–2009) being the warmest decade in the instrumental record (Arndt et al. 2010). Results from global circulation models universally project increases in annual temperature for California, particularly in the summer months (Lenihan et al. 2003, Hayhoe et al. 2004, Dettinger 2005, Cayan et al. 2008). Heat waves are expected to increase in frequency and magnitude as well (Hayhoe et al. 2004, Kunkel et al. 2013).

There is much less certainty regarding trends in precipitation, which are complicated by interdecadal variability and years with extreme precipitation (Hayhoe et al. 2004). There is little consensus among modeled projections for California's precipitation over the next century. Results suggest relatively small changes in precipitation, but even small changes can be important (Hayhoe et al. 2004, Cayan et al. 2008). Three of four simulations done by Hayhoe et al. (2004) showed decreases in winter precipitation of 15–30%, with reductions centered in the Central Valley and along the north Pacific coast. The length, frequency, and severity of droughts are expected to increase (Hayhoe et al. 2004), and increased temperatures will contribute to this trend.

Cycles of El Niño–Southern Oscillation (ENSO) are associated with sea-surface temperature anomalies in the tropical Pacific Ocean and are a prominent feature of climate variability.

Global warming is expected to lead to increased frequency and severity of ENSO events (Kerr 1999, Cai et al. 2014, Widlansky et al. 2015), the effects of which vary geographically (Pavía and Badan 1998). In California, El Niño years generally entail above-normal precipitation, and La Niña years are generally associated with cold, dry conditions (Kiladis and Diaz 1989, Schonher and Nicholson 1989).

Unlike ENSO cycles, which typically recur every two to seven years (Kerr 1999), Pacific Decadal Oscillation (PDO) cycles last 20 to 30 years (Mantua and Hare 2002). Although many of the climate anomalies associated with the PDO are broadly similar to those associated with ENSO, they are generally not as extreme. The duration of the cycle is not well understood, nor are the mechanisms, but even in the absence of a theoretical understanding, climate anomalies that persist for one or more decades can affect ecosystems profoundly (Mantua and Hare 2002).

Oak woodlands represent some of the richest and most diverse ecosystems in California, providing habitat for over 330 species of birds, mammals, reptiles, and amphibians during some stage of their life cycle (Verner and Boss 1980, Block and Morrison 1990). For birds alone, they provide habitat for breeding, wintering, and migratory stopover of at least 147 species (Tietje et al. 2005). California's oak woodlands are threatened by residential and commercial development, woodcutting, conversion to agricultural uses including vineyards and orchards, invasive species, and introduced pathogens such as sudden oak death. California's oak woodlands have been reduced by nearly 50% from their original extent (Bolsinger 1988). Climate change, however, may pose an even greater threat to oak woodlands and the species that depend on them (Kueppers et al. 2005). The future of oak woodland communities depends not only on the persistence of oaks but also on understanding how associated wildlife responds to environmental change.

Understanding and predicting species' responses to the changing climate will help us plan for an uncertain future and will inform conservation decisions. Patterns of annual abundance may reveal responses to current and previous weather conditions, which can directly or indirectly influence the survival and productivity of wildlife. In this study, we used a long-term dataset from California oak woodlands to investigate the effects of weather and climate on bird abundance. We modeled the response in abundance of 35 breeding and migratory species to weather and climate

variables over a 27-year period. Specifically, we examined how variation in precipitation, temperature, ENSO, PDO, and drought (as assessed via the Palmer Drought-Severity Index [PDSI]) were associated with indices of abundance for these 35 species. Our objectives were to (1) examine relationships between bird abundance and seasonal weather patterns and longer-term climate cycles, (2) explore species-specific responses to climate change, and (3) use our results to predict how species in this ecosystem will respond to projected changes and to identify the species most vulnerable to global climate change.

METHODS

STUDY AREA

The San Joaquin Experimental Range (SJER) is located in the western foothills of the Sierra Nevada, in Madera County, California. Covering 1875 ha, it ranges in elevation from 215 to 520 m. The climate at SJER is Mediterranean with cool, wet winters and hot, dry summers. Most precipitation falls as rain, with snow unusual. Mean annual precipitation during the 27 years of this study (1986–2012) was 44 cm, although precipitation fluctuated markedly from year to year, with extremes of 22 and 80 cm. Eighty-six percent of precipitation fell from October through March.

Three tree species dominate the overstory: blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*). In some areas, the overstory is primarily blue oak, and the shrub and understory layer is meager or lacking. Annual grassland covers areas where both the overstory and understory are missing or not dense enough to shade out the grasses and forbs. SJER has been moderately grazed by cattle since about 1900, except for a 29-ha Research Natural Area, which has been ungrazed since 1934 and has a dense shrub layer. See Purcell and Mori (2018) for a more detailed description of the vegetation in the study area.

BIRD AND HABITAT DATA

We sampled 210 count stations, with 30 stations distributed along each of seven routes established throughout SJER. All stations were at least 200 m apart, whether along the same route or on different routes. From 1986 through 2012, counts were conducted from the last week of March through the end of April. Observers were assigned to routes randomly, such that only one observer sampled a given route each day; within a given year, all observers sampled all routes one time, except in

1986 and 1987, when observers counted each route twice (but still within the sampling period). From three to eight observers completed the set of surveys each year.

Each survey at a station consisted of a 5-minute, unlimited-distance point count by a single observer, who recorded all birds seen or heard. Protocols for the counts were standardized to control for sources of variability such as time of year, time of day, conditions related to a particular day, and observer variability. Efforts to reduce variability among observers included selecting the most proficient observers, pre-count training, and using the same observers over as many years as possible. Counting at the first station began 10 minutes after local sunrise and continued at subsequent stations at 10-minute intervals. Stations were sampled in the same sequence each time a route was sampled, further standardizing results. See Purcell and Mori (2018) for further details of the count methods.

We collected habitat data at each count station in 2001, quantifying variables unlikely to change markedly over time, including cover of the primary tree species (slow-growing, long-lived oaks, and pines), rock cover, and presence of water. Specifically, we estimated the percent cover of blue oak, interior live oak, foothill pine, shrubs (all species combined), and rock within 50 m of the station (Table 1). Water within the circular plot was recorded as none, standing or flowing water occasionally present, or usually present during the count period. We also recorded UTM coordinates at each station.

WEATHER DATA

Local weather data have been recorded at SJER since 1934. From 1934 through 1996, weather instruments were housed in a standard U.S. Weather Bureau shelter with a double roof, louvered sides, and a slotted bottom. Temperatures were recorded daily with a minimum/maximum thermometer. Precipitation was measured with a Universal Weighing-type Recording Rain Gauge until 1993, subsequently with a Fisher Porter rain gauge. In 1997, a digital weather station (Handar Model 555) that recorded average air temperature hourly was installed. In 2009, this was replaced with a digital weather station (Campbell Scientific CR1000) that recorded accumulated rain, average air temperature, relative humidity, average wind speed and direction, and maximum wind gust, with data recorded hourly and daily. Also installed was a TES25WS tipping-bucket rain gauge conforming to National Weather Service specifications.

TABLE 1. Description of weather, climate, and habitat variables.

Variable	Description
Precipitation	
P_{ann}	Annual precipitation (May–April) of count year
P_{av2}	Running average of annual precipitation (May–April) for the 2 years preceding counts
P_{av3}	Running average of annual precipitation (May–April) for the 3 years preceding counts
P_{winter}	Average monthly precipitation (October–March) of the current year
$P_{\text{winter}_{-1}}$	Average monthly precipitation (October–March) of year – 1
Temperature	
T_{spring}	Average spring temperature (March–May) in year preceding counts
T_{summer}	Average summer temperature (June–August) in year preceding counts
T_{winter}	Average winter temperature (December–February) in count year
T_{min}	Minimum temperature in winter (October–March) preceding counts
T_{max}	Maximum temperature in year (May–April) preceding counts
$N_{\text{days} \geq 38^{\circ}}$	Number of days $\geq 38^{\circ}\text{C}$ in year (May–April) preceding counts
$N_{\text{days} \leq 0}$	Number of days $\leq 0^{\circ}\text{C}$ in year (May–April) preceding counts
Southern Oscillation Index (SOI)	
SOI_{ann}	SOI (May–April) of count year
$\text{SOI}_{\text{ann} - 1}$	SOI (May–April) of count year – 1
$\text{SOI}_{\text{winter}}$	SOI (October–March) of count year
$\text{SOI}_{\text{winter} - 1}$	SOI (October–March) of count year – 1
Pacific Decadal Oscillation (PDO)	
PDO	PDO (November–March) of count year
PDO_{-1}	PDO (November–March) of count year – 1
Palmer Drought-Severity Index (PDSI)	
PDSI_{ann}	Average annual PDSI of count year (May–April)
$\text{PDSI}_{\text{spring}}$	Average spring PDSI of count year (October–March)
Habitat variables	
$\text{PC}_{\text{BlueOak}}$	Percent cover of blue oak in 50-m-radius circle
$\text{PC}_{\text{LiveOak}}$	Percent cover of interior live oak in 50-m-radius circle
$\text{PC}_{\text{FoothillPine}}$	Percent cover of foothill pine in 50-m-radius circle
PC_{Shrub}	Percent cover of shrubs in 50-m-radius circle
PC_{Rock}	Percent cover of rock in 50-m-radius circle
Water	Presence of water (3 categories) in 50-m-radius circle: none; standing or flowing water occasionally present; water usually present during count period

In some cases, gaps in the weather data were filled from other sources. In a few cases, temperatures were taken from Onset StowAway or Hobo Temp data loggers in the weather shelter. In other cases, we used data from NOAA's National Climatic Data Center (www.ncdc.noaa.gov) from a nearby weather station (Friant Government Camp, USC00043261), calibrated for monthly differences in the two datasets.

We explored the effects of weather and climate on bird abundance, considering variables that from previous research we expected might influence abundance. We distinguished weather conditions, those that act over a short period of time, from climate, which involves long-term meteorological conditions. We defined the most appropriate weather year for this study as 1 May through 30 April, as it included the survey period (late March to 30 April) as well as the preceding months whose weather affected our counts.

Variation in precipitation and temperature can influence abundance directly if birds move in response to current conditions, or indirectly by influencing productivity and survival (e.g., DeSante and Geupel 1987, Hefflefinger et al. 1999, Chase et al. 2005, Holloran et al. 2005, Mattsson and Cooper 2009, Blomberg et al. 2012). We examined five precipitation and seven temperature variables (Table 1). Precipitation variables included total annual precipitation (May–April) of the count year, running averages of annual precipitation for both the two years and three years preceding the counts, and average monthly precipitation in the wet-season (October–March) for both the current year and for the preceding year. Temperature variables included the average spring temperature (March–May) in the year preceding the counts. For the effects of hot temperatures we considered average summer temperature (June–August), maximum temperature (May–April), and

the number of days with temperatures exceeding 38 °C in the year (May–April) preceding the counts. For cold, we examined average winter temperature (December–February), minimum winter temperature (October–March), and the number of days with minimum temperatures below freezing (0 °C) in the year preceding the counts.

We used the El Niño–Southern Oscillation Index (SOI; standardized indices from www.cpc.ncep.noaa.gov/data/indices/soi) and the PDO (jisao.washington.edu/pdo/PDO.latest) to assess longer-term climate variability. We averaged annual values of SOI (May–April) and winter values (October–March; *sensu* Marshall et al. 2011) because the effect of SOI is strongest during the wet season. For both of these variables we considered both the current year and the year preceding the counts for a total of four SOI variables (Table 1). Negative values of SOI (El Niño) are associated with warmer, wetter winters; positive values (La Niña) are associated with colder, drier winters. We averaged monthly PDO indices from November to March for the current year and one year preceding (*sensu* Ballard et al. 2003; Table 1). Negative values (cool phase) of the PDO index are associated with colder, later springs and below-average precipitation; positive values (warm phase) are associated with warmer, earlier springs and hot, dry summers.

We used the PDSI (based on California division 5 from www1.ncdc.noaa.gov/pub/data/cirs/) to assess response to drought. This index incorporates precipitation as well as temperature and also takes into account preceding conditions. We calculated two PDSI variables: mean monthly values across the year preceding the counts (May–April) and for the wet season (October–March; Table 1). Negative PDSI values represent dry conditions with high potential evaporation (i.e., high temperatures); positive values represent wet years.

STATISTICAL ANALYSIS

We initially considered for analysis the 41 bird species with at least five detections in each of the 27 years of the study (following Ballard et al. 2003). This criterion proved too lenient for adequate modeling of responses in some cases, however, so our final dataset comprised 35 species (see Table 2 for their scientific names). We dropped six species because (1) their abundance was too variable across years to model well (Northern Flicker, *Colaptes auratus*, and Black-throated Gray Warbler, *Setophaga nigrescens*), (2) their abundance was both low and variable across years (Cassin's Vireo, *Vireo cassinii*, American

Robin, *Turdus migratorius*, and Wilson's Warbler, *Cardellina pusilla*), or (3) observers were not able to count them accurately (Golden-crowned Sparrow, *Zonotrichia atricapilla*). Our final sample size for analysis included 27,510 point counts (27 years × 210 stations × observers).

The analysis involved three steps. In the initial stage, we examined species' responses to weather and climatic variables with a semi-parametric generalized additive model (GAM) with mean count as the dependent variable. We calculated mean count as the average count across observers for each count station and year, resulting in a sample size of 5670 mean counts per species. We considered the use of the average count valid because both count and mean count are measured at the same point in the same year; in addition, if an explanatory variable is important in explaining abundance, it should likewise be important in explaining average abundance. The spatial variables (UTM northing and easting), year, route, presence of water, and percent cover of rock were included in all models as fixed effects. For the habitat (vegetation), weather, and climate categories we selected one variable from each because of multicollinearity (Table 1; see Appendices S1 and S2 for correlation matrices).

As a first approach for selection of variables, we used the following semi-parametric regression model:

$$\text{Mean count} = f(\text{easting, northing}) + \text{route} + g(\text{year}) + \text{water} + v(\text{rock}) + w(\text{veg}) + \sum_i x_i(\text{weather/climate}) + \text{residual error},$$

where the dependent variable is count averaged across observers for each count station and year, and f , g , v , w , and x_i ($i = 1$ to 6) are smoothing (spline) functions of the covariates. On the basis of large-number theory (central limit theorem) we assumed an approximate normal distribution for the residual error. We constructed models by using all combinations of route, water, rock, and one variable from each group of weather/climate and vegetation variables. These groups included the three annual precipitation, two average precipitation, seven temperature, four SOI, two PDO, two PDSI, and four vegetation variables, resulting in a total of 2688 possible combinations (models). Our ability to fit the splines in each model with such a large number of possible variables was due to our large sample size. We used GAM routines in R to fit the smoothing functions and to obtain the graphs and the statistics for fit (mgcv-GAM, version 3.2.3, R Core Team 2015). We used Akaike's information criterion (AIC; Burnham

TABLE 2. The 35 bird species modeled with a semi-parametric Poisson regression (GAM), and the percent deviance explained by the full model and by partial deviance components for weather and climate variables (see Table 1), location variables (spatial component and route), and habitat variables (percent cover of blue oak, live oak, foothill pine, shrub, and rock, and the categorical variable for water). Partial deviance components for year and Julian date are not shown.

Species	Full model (%)	Weather/ climate (%)	Location (%)	Habitat (%)
California Quail <i>Callipepla californica</i>	19.10	1.76	9.27	0.32
Mourning Dove <i>Zenaida macroura</i>	14.52	0.89	9.71	0.73
Anna's Hummingbird <i>Calypte anna</i>	8.72	0.32	3.13	1.40
Turkey Vulture <i>Cathartes aura</i>	21.41	0.68	18.12	0.53
Red-tailed Hawk <i>Buteo jamaicensis</i>	14.18	1.07	11.17	0.22
Acorn Woodpecker <i>Melanerpes formicivorus</i>	20.72	3.75	5.51	0.79
Nuttall's Woodpecker <i>Picoides nuttallii</i>	5.50	0.94	1.46	0.28
American Kestrel <i>Falco sparverius</i>	7.61	0.93	2.82	0.78
Ash-throated Flycatcher <i>Myiarchus cinerascens</i>	51.02	2.79	1.47	0.20
Western Kingbird <i>Tyrannus verticalis</i>	28.15	1.09	9.77	4.47
Hutton's Vireo <i>Vireo huttoni</i>	18.58	0.61	8.91	1.95
California Scrub-Jay <i>Apelocoma californica</i>	8.28	2.31	1.39	0.33
Common Raven <i>Corvus corax</i>	21.27	0.52	3.86	0.41
Violet-green Swallow <i>Tachycineta thalassina</i>	14.47	0.82	9.66	0.73
Oak Titmouse <i>Baeolophus inornatus</i>	13.98	1.61	2.47	0.43
Bushtit <i>Psaltiriparus minimus</i>	6.44	2.30	1.03	1.07
White-breasted Nuthatch <i>Sitta carolinensis</i>	9.38	1.32	5.36	1.20
Canyon Wren <i>Catherpes mexicanus</i>	35.24	0.34	22.79	1.97
House Wren <i>Troglodytes aedon</i>	22.13	4.81	7.00	1.36
Bewick's Wren <i>Thryomanes bewickii</i>	20.25	1.63	5.98	2.28
Blue-gray Gnatcatcher <i>Polioptila caerulea</i>	10.37	1.64	4.03	0.97
Ruby-crowned Kinglet <i>Regulus calendula</i>	30.07	0.93	3.75	1.75
Western Bluebird <i>Sialia mexicana</i>	11.49	0.90	5.92	1.81
European Starling <i>Sturnus vulgaris</i>	20.80	0.68	9.18	3.83
House Finch <i>Haemorhous mexicanus</i>	14.19	1.68	2.83	0.79
Lesser Goldfinch <i>Spinus psaltria</i>	7.20	1.20	2.16	0.42
Orange-crowned Warbler <i>Oreothlypis celata</i>	12.03	2.72	3.29	0.70
Yellow-rumped Warbler <i>Setophaga coronata</i>	26.35	2.00	2.35	1.37
California Towhee <i>Melospiza crissalis</i>	8.75	0.03	2.26	1.78
Lark Sparrow <i>Chondestes grammacus</i>	13.69	1.11	5.87	2.96
White-crowned Sparrow <i>Zonotrichia leucophrys</i>	22.80	3.12	10.30	0.64
Dark-eyed Junco <i>Junco hyemalis</i>	29.55	2.90	1.83	0.68
Western Meadowlark <i>Sturnella neglecta</i>	50.00	0.62	38.55	2.87
Brown-headed Cowbird <i>Molothrus ater</i>	15.22	0.93	7.64	0.87
Bullock's Oriole <i>Icterus bullockii</i>	25.85	0.65	9.96	3.34

and Anderson 1998) and the percent deviance explained to select the 10 best models.

Second, we examined the effect of the explanatory variables in the top 10 models identified in step one on the true count (rather than the mean count). Because count was not averaged over observer, we were able to include an explanatory variable to examine the influence of sampling date on the counts. In this context, we use the term Julian date to denote ordinal day of year. We used semi-parametric spatial Poisson regression models from the family of generalized additive models (Hastie and Tibshirani 1990, Wood 2006) with nonparametric smoothing functions of the

covariates as an exploratory approach to determine the functional shapes of the explanatory variables. Assuming count to be Poisson-distributed, we modeled the expected count as follows:

$$\text{Expected(count)} = e^{\lambda\beta},$$

where

$$\lambda\beta = s(\text{easting, northing}) + \text{route} + t(\text{year}) + u(\text{Julian date}) + \text{water} + v(\text{rock}) + w(\text{veg}) + \sum_i x_i(\text{weather/climate}),$$

which is a linear combination of spline functions (s, t, u, v, w, x_i) of the continuous variables in the selected 10 models.

We used this approach for lack of prior knowledge of the functional shapes of relations between counts and explanatory variables, and to drop explanatory variables that appeared to have no relation to counts. Because many of the weather variables were correlated, we examined the 10 top models and removed variables that were correlated ($r^2 > 0.20$). To avoid overparameterization, we also removed variables with nonsignificant partial residuals, or those that minimally affected the deviance explained by the model (less than 0.05%; Arnold 2010). When two models were similar in deviance explained, but differed in ease of interpretation, we used the model that was more biologically interpretable. We again used R GAM for statistical computing and graphics to fit the smoothing functions for the Poisson-distributed counts (R Core Team 2015).

Finally, we estimated the parametric functions (polynomial) of the selected explanatory variables from step two and evaluated their significance in the presence of other sources of variability. In this analysis we were able to include a random effect to account for overdispersion due to observer variability. We quantified variability among observers and the amount of unaccounted variability (overdispersion not accounted for by the Poisson distribution). To estimate these parameters (coefficients and variance components), we fit a parametric generalized linear mixed model, selecting among Poisson, quasi-Poisson, and negative binomial distributions (Joe and Zhu 2005) on the basis of how well each accounted for overdispersion (see Appendix S3 for a full description of the three models). Parametric functions selected were suggested by the smoothed partial residuals from the fitted GAMs, resulting in polynomials no higher than order 5.

For all three regression models we assumed that

$$\text{Expected}(\text{count}|\varepsilon) = e^{X\beta + \varepsilon},$$

where the dependent variable is count per station for a given observer, $X\beta$ is the selected linear combination of polynomials of the spatial and fixed effects of the selected independent variables, and ε is the random effect due to observers. For all three models, we assumed ε to have the standard normal distribution with variance = σ^2 . We assumed that $\text{count}|\varepsilon$ was Poisson-distributed with the expected mean given in the equation above. Selection of the proper statistical model depended on how well the variability due to observers (ε) and unexplained variability (θ and δ , dispersion parameters for the quasi-Poisson and negative binomial distributions, respectively) were estimated (see Appendix

S3), based on the criterion of the generalized chi-squared test for goodness of fit. We used the GLIMMIX procedure in SAS (SAS Institute 2012) to estimate the coefficients (β) of the parameters for fixed (polynomial) and random effects (σ^2 , θ , and δ).

RESULTS

The average number of birds detected per station per year from 1986 to 2012 is shown for each species in Table 3. The fits of the parametric generalized linear mixed models were good, with the ratio between the generalized chi-squared statistic and its degrees of freedom close to 1 (± 0.1). Results of models for the semi-parametric Poisson regression (GAM) and the parametric generalized linear mixed models were similar, indicating that the polynomial functions for the variables were a good approximation to those in the smoothed GAM analysis.

INFLUENCE OF COVARIATES ON THE COUNTS

Weather covariates did not explain a large percentage of variability in the yearly counts of birds at SJER (Table 2). The average reduction in deviance explained by weather variables was 1.47%, with a maximum of 4.81% for the House Wren and a minimum of 0.03% for the California Towhee. However, including weather and climate covariates did change the shape of the trend curve in some cases from that based on a simple model with no weather covariates, and adding the weather variables also reduced the trends' variability.

Location within the study area made the greatest contribution to the models' overall deviance and was the greatest source of deviance explained for 29 of the 35 species (Table 2). This result suggests that these species' abundance within SJER was not uniform, and that this variability was not otherwise accounted for by the habitat variables, which generally had low explanatory power (Table 2). Weather variables provided more explanatory power than any other class of variable for two species, the California Scrub-Jay and Bushtit (Table 2). Year was most important in explaining deviance for two species, the Common Raven and Yellow-rumped Warbler. Julian date was the most important source of variability for three species. Among these, the Ruby-crowned Kinglet and Dark-eyed Junco are winter residents that began to leave before the end of the count period, and the Ash-throated Flycatcher is a migratory species that arrived after the counts had begun.

The effect of observer variability ranged from

TABLE 3. Estimated percentage of variance components exceeding the Poisson variance in the mean count per species. Mean count is the average number of birds detected per station per year (1986–2012), estimated variance is the variance of the mean count calculated with the formulas in Appendix S3, total overdispersion % is the percentage of the variance exceeding the Poisson variance (the Poisson distribution assumes the variance is equal to the mean), observer overdispersion % is the percentage of the overdispersion variance due to observer per year, and extra overdispersion % is the percentage of the overdispersion variance due to extra variability from unknown sources. The percentages of the variance components were calculated using the estimated covariance parameters yielded by SAS proc GLIMMIX for the model that best fit the data (see Appendix S3 for the formulas for the variance components due to overdispersion).

Species	Model ^a	Mean count	Estimated variance	Total overdispersion %	Observer overdispersion %	Extra overdispersion %
California Quail	MNB	1.42	1.83	25.3	11.5	13.7
Mourning Dove	MSP	1.01	1.05	5.8	5.8	0.0
Anna's Hummingbird	MSP	0.19	0.20	5.3	5.3	0.0
Turkey Vulture	MQP	0.37	1.12	68.1	5.9	62.2
Red-tailed Hawk	MNB	0.38	0.47	20.9	4.5	16.4
Acorn Woodpecker	MSP	3.16	3.80	19.3	19.3	0.0
Nuttall's Woodpecker	MSP	0.26	0.26	5.0	5.0	0.0
American Kestrel	MSP	0.05	0.05	4.9	4.9	0.0
Ash-throated Flycatcher	MSP	0.84	0.88	7.8	7.8	0.0
Western Kingbird	MQP	0.34	0.50	35.7	6.6	29.2
Hutton's Vireo	MSP	0.04	0.04	10.1	10.1	0.0
California Scrub-Jay	MSP	1.04	1.12	10.4	10.4	0.0
Common Raven	MNB	0.62	0.77	20.5	4.2	16.3
Violet-green Swallow	MNB	0.98	2.29	59.0	11.0	48.0
Oak Titmouse	MSP	1.92	2.03	6.9	6.9	0.0
Bushtit	MQP	0.44	0.63	32.8	9.5	23.3
White-breasted Nuthatch	MSP	0.80	0.84	7.2	7.2	0.0
Canyon Wren	MQP	0.08	0.08	3.7	3.0	0.7
House Wren	MSP	0.40	0.45	21.2	21.2	0.0
Bewick's Wren	MSP	0.52	0.55	11.4	11.4	0.0
Blue-gray Gnatcatcher	MSP	0.05	0.05	8.7	8.7	0.0
Ruby-crowned Kinglet	MSP	0.29	0.30	9.0	9.0	0.0
Western Bluebird	MQP	0.28	0.41	33.6	5.7	27.9
European Starling	MNB	1.00	1.91	49.4	10.9	38.5
House Finch	MNB	0.73	0.95	26.4	10.3	16.1
Lesser Goldfinch	MSP	0.65	0.70	12.9	12.9	0.0
Orange-crowned Warbler	MSP	0.13	0.14	14.7	14.7	0.0
Yellow-rumped Warbler	MNB	1.35	2.71	53.0	19.5	33.5
California Towhee	MSP	0.37	0.39	8.0	8.0	0.0
Lark Sparrow	MNB	0.10	0.13	26.6	11.1	15.5
White-crowned Sparrow	MNB	0.84	2.19	66.2	28.4	37.8
Dark-eyed Junco	MNB	0.31	0.57	53.7	22.5	31.2
Western Meadowlark	MQP	0.23	0.23	4.2	3.7	0.5
Brown-headed Cowbird	MQP	0.27	0.40	38.3	11.8	26.5
Bullock's Oriole	MSP	0.22	0.22	7.4	7.4	0.0

^aMNB, mixed negative binomial; MSP, mixed standard Poisson; MQP, mixed quasi-Poisson.

accounting for 3.0% of the variance for the Canyon Wren to 28.4% for the White-crowned Sparrow (Table 3). Observers likely recorded Canyon Wrens accurately because of the species' low density and loud, very distinctive song. The White-crowned Sparrow and other flocking species such as the Dark-eyed Junco are difficult to count accurately, often remaining hidden and undercounted in vegetation.

YEAR-ROUND RESIDENTS

California Quail

California Quail were less abundant following years of above-average rainfall and years with more days below freezing (Appendix 1). They were more abundant in locations with blue oaks and where some water was present, and they avoided rocky areas.

Mourning Dove

Mourning Doves were more abundant in drought years, in years with above-average winter rainfall in the year preceding the count year, and during the warm phase of the PDO (Appendix 1). They were also more abundant in areas with less cover of rock and foothill pine, and where water was present.

Anna's Hummingbird

The full model had low explanatory power, and weather variables were not strong predictors of abundance (Table 2). Results suggested that Anna's Hummingbirds increased with increasing average precipitation during the previous two years and decreased after years with more days above 38 °C (Appendix 1). Anna's Hummingbirds were more abundant in areas with more rock and water and intermediate amounts of shrub cover.

Turkey Vulture

Turkey Vultures increased with increasing summer temperatures and were more abundant following El Niño years (Appendix 1). Location accounted for the greatest amount of variation in this species (Table 2). Turkey Vultures were not found near water and tended to avoid areas with interior live oak.

Red-tailed Hawk

Counts of the Red-tailed Hawk were consistent, with low variability due to observers (Table 3). Location was again the greatest source of variability for this raptor. This species was more abundant following warm winters, El Niño winters, and wet years (Appendix 1). It was more abundant in areas with rock and where some water was present.

Acorn Woodpecker

This cooperative breeder was conspicuous and vocal, and was the species most commonly detected at SJER (Table 3). Counts varied substantially among observers (Table 3), likely because the birds were abundant and occurred in groups that were difficult to count. Weather variables were fairly important in explaining variation in the Acorn Woodpecker's abundance (Table 2). The species increased with increasing precipitation in the year of the counts, in La Niña years, during drought years, and during the warm phase of the PDO (Appendix 1). It was also more abundant in areas with less rock cover, some water, and somewhat greater cover of blue oaks.

Nuttall's Woodpecker

Counts of this species were consistent among observers (Table 3). The full model explained the least amount of overall deviance among all species modeled, although weather variables still explained close to average amounts of deviation (Table 2). Nuttall's Woodpeckers were more abundant in years with above-average precipitation in the year preceding the count year and less abundant in drought years (Appendix 1). They were less abundant in areas with rock, more abundant where there was some water, and tended to occur with blue oak.

American Kestrel

Observer variability was low for this species (Table 3). The full model had low explanatory power, although weather variables were relatively important (Table 2). Kestrels were more abundant in years with lower-than-average rainfall, following warmer-than-average winters, and during the cool phase of the PDO (Appendix 1). They avoided areas with dense cover of interior live oak and water, preferring more open areas.

Hutton's Vireo

While the full model had average explanatory power, weather variables explained only a small portion of the deviance, with location variables most important (Table 2). Results suggest that Hutton's Vireos were more abundant in years with below average precipitation and after years with cooler springs (Appendix 1). They avoided rocky areas and tended to occur near water.

California Scrub-Jay

Weather variables were important in explaining variation in California Scrub-Jay numbers (Table 2). Scrub-jays were less abundant after winters with higher-than-average precipitation, after years with high summer temperatures, and in wetter-than-normal years (Appendix 1). They were also more abundant in areas with less rock cover, more shrub cover, and some water.

Common Raven

Observer variability in counts of the Common Raven was low (Table 3). Year effects explained more variability than any other category; the species is increasing in abundance (see Purcell and Mori 2018). Ravens were more abundant after years with higher-than-average rainfall, after years with warmer springs, and during the warm phase of the PDO (Appendix 1). Ravens were less abundant in areas where water was present and in areas with dense cover of blue oak.

Oak Titmouse

The response of the Oak Titmouse to maximum temperatures was nonlinear, the species reaching its greatest abundance with maximums near 41 °C, with abundance declining at both lower and higher values. Titmice were more abundant during the cool phase of the PDO (Appendix 1). They avoided areas with low cover of blue oaks and rocky areas.

Bushtit

Although the full model had low explanatory power, weather variables were the most important source of deviance explained, whereas year, location, and date explained the smallest amount of variation of any species (Table 2). Bushtits decreased following several years of below-average precipitation and in dry La Niña years; not surprisingly, this tiny passerine was sensitive to low minimum temperatures (Appendix 1). Bushtits were also more abundant in areas with greater cover of live oak.

White-breasted Nuthatch

This cavity-nesting species was more abundant following several years of higher-than-average precipitation, in La Niña years, and during the warm phase of the PDO (Appendix 1). Nuthatches also avoided areas with greater cover of rock and shrubs and were more common in areas where water was occasionally present.

Canyon Wren

Canyon Wrens were easily detected, and observer variability was the lowest of any species (Table 3). While the full model was fairly robust, weather and climate variables were not strong predictors of Canyon Wren abundance (Table 2). Canyon Wrens were more abundant following two years of above-average precipitation and were less abundant in drought years (Appendix 1). Location was very important in explaining abundance of Canyon Wrens, as were habitat variables (Table 2). This species was more abundant in areas with more cover of rock and live oak, and in areas that lacked water.

Bewick's Wren

Bewick's Wrens responded nonlinearly to average spring temperature, reaching their highest abundance when spring temperatures averaged approximately 15 °C, and decreasing at both lower and higher mean spring temperatures. They were more abundant in La Niña years, and were less abundant during the warm phase of the PDO

(Appendix 1). Bewick's Wrens were more abundant in areas with more foothill pines and some water.

Western Bluebird

Bluebirds were more abundant in years with below-average winter precipitation, following winters with fewer days below freezing, and during the cool phase of the PDO (Appendix 1). They avoided areas with rocks and shrubs.

European Starling

Starlings were more abundant after years with higher-than-average precipitation, after warmer springs, and in El Niño years (Appendix 1). They were more abundant in areas with water and avoided areas with rocks and shrubs.

House Finch

House Finches were more abundant in years with below-average rainfall, following winters with fewer days below freezing, and during the cool phase of the PDO (Appendix 1). They were less abundant in La Niña years. They were also less abundant in areas with greater cover of rock and shrubs and more abundant in areas with some water.

Lesser Goldfinch

The full model had low explanatory power; however, climate and location variables were the most informative (Table 2). Lesser Goldfinches were more abundant in wet years, in El Niño years, and during the cool phase of the PDO (Appendix 1). Goldfinches were also more abundant in areas with more cover of rock and pines.

California Towhee

The full model had weak explanatory power, and weather variables did not appear important in explaining variability in towhee counts; abundance was better explained by location within the study area (Table 2). Results suggested that California Towhees increased following several years with higher-than-average precipitation and were more abundant in areas with rocks and shrubs (Appendix 1).

Lark Sparrow

Lark Sparrows were more abundant following winters with fewer days below freezing and in drought years (Appendix 1). Habitat variables were relatively important in explaining variability in abundance (Table 2); Lark Sparrows were less abundant in areas with greater cover of rock and shrubs.

Western Meadowlark

There was little variation among observers in counts of the Western Meadowlark (Table 3). The full model explained 50% of the deviance, the second highest of all species, and most of the deviance (39%), the highest of any species, was explained by location (Table 2). The explanatory power of weather and climate variables was comparatively small. Meadowlarks were less abundant after years with cool springs and after two years of higher-than-average precipitation (Appendix 1). They were less abundant in areas with water and foothill pines, and more abundant in areas with rock cover.

BREEDING SUMMER RESIDENTS

Ash-throated Flycatcher

The full model explained 51% of the deviance, the highest of all species. Julian date was the most important source of variability in abundance of this migrant, which arrived after the counts had begun. Nevertheless, weather and climate variables explained an above-average portion of the deviance (Table 2). Ash-throated Flycatchers were more abundant following warm springs in the year preceding the count, following El Niño years, in drought years, and during the warm phase of the PDO (Appendix 2). They avoided areas with dense shrub cover and tended to avoid water.

Western Kingbird

Western Kingbirds decreased in years following two years of higher-than-average precipitation, in wetter-than-average years, and during the warm phase of the PDO (Appendix 2). They reached their highest abundance in years with warm spring temperatures. Habitat variables explained more variability in abundance for this species than for any other (Table 2). Kingbirds were more abundant in areas with water and less abundant in areas with rock and foothill pines.

Violet-green Swallow

Violet-green Swallows were more abundant following warm winters and one year after El Niño events; they were less abundant in wet years (Appendix 2). Location accounted for the greatest amount of variation in this aerial forager (Table 2). Swallows avoided water and areas with greater cover of pines.

House Wren

Counts of the House Wren differed greatly

among observers (Table 3). Weather variables explained more variability in House Wren abundance than for any other species (Table 2). House Wrens were more abundant following three years of higher-than-average precipitation and in years with warmer winters, and were less abundant one year after a La Niña year (Appendix 2). House Wrens were more abundant in areas with water and with greater cover of rock and shrubs.

Blue-gray Gnatcatcher

The full model for the Blue-gray Gnatcatcher was not particularly robust, but weather variables explained a greater-than-average amount of variation in the species' abundance (Table 2). Gnatcatchers were more abundant in years with higher-than-average precipitation in the preceding year, in years with fewer days below freezing, in El Niño years, and during the warm phase of the PDO (Appendix 2). Gnatcatchers were also more abundant in areas with more rock and pines.

Brown-headed Cowbird

Brown-headed Cowbirds were less abundant following winters with greater-than-average precipitation and in years with low minimum temperatures, and were more abundant in drought years (Appendix 2). Habitat variables explained roughly half of the deviance (Table 2); cowbirds were more abundant in areas with water and with greater cover of rock and blue oak.

Bullock's Oriole

Bullock's Orioles were less abundant following winters with more days below freezing and in La Niña years (Appendix 2). Habitat variables explained a greater-than-average proportion of deviance; orioles were less abundant in areas with greater cover of rock and pines and more abundant where water was present.

WINTER RESIDENTS AND SPRING/FALL MIGRANTS

Ruby-crowned Kinglet

The full model for the Ruby-crowned Kinglet had good explanatory power (Table 2), although Julian date explained most of the variability, with detections declining later in the count period. This migrant was less abundant following three years with higher-than-average levels of precipitation and during the warm phase of the PDO (Appendix 3). It was more abundant in areas with live oak and avoided areas with rock.

Orange-crowned Warbler

Variability among observers in counts of this winter resident was fairly high (Table 3). This warbler's song is often confused with that of the Dark-eyed Junco, so variation in detections among observers may represent, in part, errors in identification. The full model explained a higher-than-average amount of variability, and weather variables and location were fairly important in explaining variation in abundance (Table 2). Orange-crowned Warblers were more abundant following two years with higher-than-average precipitation, during colder springs, and during the cold phase of the PDO (Appendix 3). They were more abundant in areas with shrubs and water, and avoided rocky areas.

Yellow-rumped Warbler

Observer variability in counts of the Yellow-rumped Warbler was likewise high (Table 3). Weather and climate variables contributed relatively high explanatory power for this species (Table 2). It was more abundant following years with higher-than-average precipitation and one year after El Niño years (Appendix 3). This winter resident's response to average spring temperatures in the year preceding the counts was nonlinear, increasing up to approximately 13 °C, and decreasing at higher mean temperatures (Appendix 3). This species avoided areas with rocks and shrubs.

White-crowned Sparrow

As noted above, White-crowned Sparrows are difficult to count accurately, and this was reflected in high observer variability (Table 3). Weather variables and location were both important in explaining variability in abundance (Table 2). White-crowned Sparrows were less abundant following years with cold springs and more abundant in El Niño years (Appendix 3). They were more abundant in areas with shrubs and avoided areas with rock cover.

Dark-eyed Junco

Counts of this sparrow also had high variability attributable to differences among observers (Table 3). The full model for the Dark-eyed Junco was relatively strong, and weather variables explained above-average variability (Table 2); however, Julian date explained the most variability, with numbers falling through the count period as migrants departed. Juncos were more abundant in years with higher-than-average precipitation in the year

preceding the count year, in La Niña years, and during the cool phase of the PDO (Appendix 3). They were more abundant in areas with water and less abundant with increasing cover of rock and shrubs.

SUMMARY OF TEMPERATURE EFFECTS

Of the 26 species with temperature variables in their final models, 4 were sensitive to heat. California Scrub-Jays decreased following years with high summer temperatures and Anna's Hummingbirds decreased as the number of days with temperatures exceeding 38 °C during the preceding year increased. The Oak Titmouse and Bewick's Wren showed nonlinear responses to temperature, suggesting threshold effects for these two species. Titmice increased in abundance until annual maximum temperatures reached about 41 °C and then decreased at higher maximum temperatures. Bewick's Wrens increased in abundance as average spring temperatures increased until approximately 15 °C but declined at higher average temperatures. Conversely, Turkey Vultures attained their highest abundance following hot summers.

Eighteen species were sensitive to cold. Eight decreased with low minimum temperatures or many days of below-freezing temperatures. The abundance of six species increased following a warm spring the year preceding the count, and four increased following a warm winter. Abundance of two species, the Hutton's Vireo and the Orange-crowned Warbler, increased in abundance following a cold spring in the year before the count. The Yellow-rumped Warbler's response to average spring temperatures was nonlinear, with abundance peaking at approximately 13 °C.

SUMMARY OF EFFECTS OF PRECIPITATION

The responses of species to precipitation varied, with the number of species increasing with precipitation nearly equal to those whose relationship with precipitation was the inverse. Of the 24 species with precipitation variables in their final models, 13 increased with increasing rainfall and 11 decreased with increasing precipitation.

SUMMARY OF EFFECTS OF ENSO

More species responded positively to warm, wet El Niño years than to cold, dry La Niña years. Of the 16 species with ENSO variables included in their final models, 12 were more abundant following El Niño years and 4 were more abundant following La Niña years.

SUMMARY OF PDO EFFECTS

We found no clear pattern of response to the PDO. Of 16 species with PDO variables in their final models, 8 were more abundant during the cycle's warm phase (positive values of the index), and 8 were more abundant during the cool phase (negative values of the index).

SUMMARY OF RESPONSE TO DROUGHT (PDSI)

Of the 12 species with PDSI variables in their final models, 8 showed a positive response to drought. The response of the California Scrub-Jay, however, was driven by a negative response to wet years rather than a positive response to dry years, when its abundance did not stray far from the null line (Appendix 1). Four species decreased in drought years, although one of these, the Red-tailed Hawk, appeared to be primarily responding (positively) to wet years rather than to drought (Appendix 1). Species sensitive to drought included the Nuttall's Woodpecker, Canyon Wren, and Lesser Goldfinch.

DISCUSSION

Over the 27 years of this study, we observed substantial variation in weather and climate conditions. Mean precipitation varied from 22 to 80 cm annually, mean summer temperatures varied from 24 to 27 °C, and mean winter temperatures varied from 6 to 10 °C, with maximum lows and highs of -12 °C and 45 °C, respectively. This variability exceeds the magnitude of projected mean changes from future climate scenarios and thus provides variability sufficient for modeling the responses of individual species to future conditions.

We found that temperature variables are important in explaining variability in bird abundance. The Anna's Hummingbird, California Scrub-Jay, Oak Titmouse, and Bewick's Wren decreased with warmer temperatures, and we expect these species may be negatively affected by warming resulting from climate change. Our regression analyses do not reveal the reasons behind responses; however, research on hummingbirds may provide clues to their response to warming temperatures. Anna's Hummingbirds are potentially sensitive to warming temperatures, as hovering is an energetically expensive behavior requiring heat to be shunted from the body (Powers et al. 2015), and torpor, which reduces energy expenditure in cold temperatures, saves less energy when nighttime temperatures are warmer (A. Shankar pers. comm.). Chase et al. (2005) found that warm summers depressed productivity of Song Sparrows

(*Melospiza melodia*) in coastal California. Sanz et al. (2003) found that increases in spring temperatures associated with climate change negatively affected some components of fitness of the Pied Flycatcher (*Ficedula hypoleuca*). In contrast, in our study area Turkey Vultures attained their highest abundance following hot summers. This species is an aerial forager and expends less energy at high temperatures, which are associated with the availability of thermal updrafts used in foraging (Dodge et al. 2014).

Many more species, however, were sensitive to cold temperatures. Numerous studies have found negative effects of cold temperatures on survival and productivity. For example, Winkler et al. (2013) found that cold temperatures had a significant negative effect on the productivity of Tree Swallow (*Tachycineta bicolor*) nests. Dybala et al. (2013) found that survival of adult Song Sparrows increased with warmer winter temperatures. Gullet et al. (2014) found that survival of Long-tailed Tits (*Aegithalos caudatus*) was greatest following warm springs and suggested that this species will increase as climates warm. Insectivores are expected to be more affected by cold weather, as such conditions kill active insects (Holmes and Sherry 1988), whereas bark gleaners and seed eaters can still forage successfully in cold temperatures. Of the 18 species that we found to be sensitive to cold, 12 were primarily insectivores, 4 were primarily seed eaters, 1 specialized on small mammals, 1 was an omnivore, and none was a bark gleaner (Ehrlich et al. 1988). Similarly, Ballard et al. (2003) found that rates of prey capture by four insectivores were reduced in years with more days below freezing. Species negatively affected by cold could thus benefit from global warming. Additionally, because minimum temperatures are increasing at about twice the rate of maximum temperatures (IPCC 2001), species negatively affected by cold average temperatures and extreme lows are most likely to experience advantages from warming.

We found the effects of precipitation on bird abundance to be diverse. Even with the uncertainty regarding predictions for California's future precipitation patterns, the species-specific responses revealed by our models are still informative and may suggest mechanisms of response to variation in precipitation on which future research should focus. For example, Dybala et al. (2013) attributed the positive response of juvenile Song Sparrows to precipitation to increased food availability in wet years.

ENSO affects the abundance and demographic rates of diverse animal taxa (Hall et al. 1988, Lima

et al. 1999, Sillett et al. 2000), and the effects vary geographically. As a result, we expect the effects on wildlife to vary by locality and region. In California, the effects of El Niño include not only above-normal rainfall at lower elevations (Pavía and Badan 1998) but unusually high snowfall in the Sierra Nevada, snow that persists well into the breeding season. Species breeding at low elevations in California have shown increased productivity following El Niño years (Hall et al. 1988, Morrison and Bolger 2002). This is consistent with our results showing three times as many species responding positively to El Niño than to La Niña years at our low-elevation site. In contrast, birds breeding at higher elevations in the Sierra Nevada have been affected negatively by El Niño events (Beedy 1982, Granholm 1982, Raphael and White 1984, Hejl and Beedy 1986, Hejl et al. 1988, DeSante 1990). Taken together, results suggest that responses of species breeding at lower elevations differ from those that typically breed at high elevations.

ENSO may affect nest predation (Morrison and Bolger 2002), survival and recruitment (Hejl et al. 1988), overwinter mortality of sedentary species (Beedy 1982, Raphael and White 1984), and immigration and emigration (DeSante 1990). At higher elevations, breeding birds are likely to move downslope in response to harsh conditions (Hejl et al. 1988). The mechanism most often cited for the effects of ENSO on populations is its influence on food availability (Hall et al. 1988, Sillett et al. 2000), although harsh conditions at higher elevations may also directly cause mortality and nest failure (KLP unpubl. data). Migrants may also be negatively affected by ENSO-related weather patterns on their wintering grounds (Hall et al. 1988).

We found no clear pattern of response to PDO. PDO cycles last about 20–30 years, although neither the duration of cycles nor their causes are well understood (Chao et al. 2000, Mantua and Hare 2002). In contrast to our results, Ballard et al. (2003) found the warm phase of the PDO in central coastal California to be generally favorable for birds, an outcome they ascribed to longer breeding seasons and milder winters and springs for winter residents. Little research has been done on effects of the PDO on birds in general, however, with most work to date examining responses of seabirds (e.g., Vandenbosch 2000, Sydeman et al. 2001).

Our models predict that three species will be adversely affected by drought. While our study period included several drought periods, it

included only the first year of the recent four-year drought California experienced between 2012 and 2015. This was the most severe drought known in California in hundreds of years (Griffin and Anchukaitis 2014), especially in California's southern Central Valley (Williams et al. 2015). Had we been able to examine bird response to this extreme drought, we may well have found additional drought-sensitive species. Drought can have pronounced effects on birds, especially in arid environments (Rotenberry et al. 1995), resulting in significant declines in abundance (Blake et al. 1992, George et al. 1992, Aldridge et al. 2008; but see Dinsmore 2008). Effects are expected to be indirect, acting primarily through reduction of food resources.

The most strongly documented responses of species to climate change have been distributional shifts in range that allow species to track their climatic niche and shifts in vegetation phenology (Parmesan and Yohe 2003, Chen et al. 2011, Moritz and Agudo 2013). Studies have shown shifts in geographic range limits, predominantly to higher latitudes and higher elevations for terrestrial species, but not in all cases (Chen et al. 2011, Tingley et al. 2012). In regions of gentle terrain, such as our study area, species must move greater distances to track climate changes than in areas with steeper topography.

Although current climate models predict broad patterns of change related to temperature, precipitation, and longer-term climate cycles, the California landscape is complex, and global circulation models do not currently support climate projections downscaled for specific locations (Cayan et al. 2008). To improve predictions of how species will respond to climate change, we need finer projections of local and regional climatic conditions (Wiens and Bachelet 2009). More importantly, however, we need to understand how vegetation will change, as climate change is expected to lead directly to changes in the distribution of plants and associated biotic communities. Because many animal species are associated with specific characteristics of vegetation, the distribution of animals is expected to change as vegetation shifts. But animal species may lag behind if vegetation changes fail to track changing climatic conditions over appropriate time scales (Sekercioglu et al. 2008, Corlett and Westcott 2013). Many of the bird species we considered are closely tied to oaks and the acorns they produce, and will likely track the future distribution of oaks (Verner and Boss 1980).

Climate change threatens to reduce the range

of the blue oak significantly over the next several decades. Vegetation modeling for the California foothills suggest replacement of oak woodlands by non-native grasslands (Lenihan et al. 2003, 2008). Using a fine-resolution regional climate model, Kueppers et al. (2005) projected the area suitable for the blue oak would shrink to 59% of its current potential range during this century. Their results cast doubt on the expectation of simple upward elevational shifts in the distributions of oak species. Results indicate contraction of the blue oak from much of its current range, with 39% of its future range in new areas, mostly to the north, from 2080 through 2099 (Kueppers et al. 2005). Lenihan et al. (2008) modeled the response of vegetation to climate-change scenarios and obtained results consistent with those of Kueppers et al. (2005). They predicted expansion of grasslands at the expense of woodlands, including blue oak woodlands such as those we studied. Projected net losses of woodland averaged 29% across the nine climate scenarios examined.

Predictions of the ecological consequences of climate change will be improved by an increased understanding of how species are affected by variation in weather and climate. Predictions are strengthened when a broad suite of weather and climate variables are considered, as we have done here (Ballard et al. 2003, Weatherhead 2005, Tingley et al. 2012, Dybala et al. 2013, Gullett et al. 2014). Correlations among weather variables can be high, but the use of sophisticated statistical approaches can help identify the strongest contributing factors if the goal is a predictive model rather than simply the significance of individual variables. Examining relationships between climate and individual species at specific locations is especially important, as responses are variable both among species and within a species at different locations.

Even given the uncertainty in climate change projections, over the next 25 years we are likely to see significant changes that will affect California's biotic diversity (Dettinger 2005). Climate change is already affecting living systems (Parmesan and Yohe 2003), but predicting exactly how plants and wildlife will respond remains challenging. Recognizing the climate signals among the multitude of other stressors such as land-use change, habitat alteration, habitat fragmentation, and normal variation in population dynamics associated with resource abundance and density dependence may be problematic. Stralberg et al. (2015) suggested that climate-change signals in projections of abundance are greater than the noise generated by uncertainty due to the combination of

sampling error, selection of variables, and choice of global climate model.

Given projections of likely changes in climate and global cycles, we have provided some indications of how bird species might respond locally to changing climatic conditions. Monitoring is essential to identifying relationships between climate and abundance, to provide early warnings of negative effects of climatic change, and to identify thresholds of response (Dybala et al. 2013). Long-term monitoring such as ours can provide information on potential population changes that may result from climatic change. Understanding how the abundance of different species is related to weather and climatic variables at different time scales, as well as to specific habitat characteristics, can serve as an initial conservation tool and may suggest actions to help mitigate potential negative consequences associated with climate change. At least two decades of data are needed to assess the effects of decadal climate cycles, and longer-term data are better. Our hope is that our efforts will be used to prioritize future research, identify where limited conservation resources will be most effective, and help facilitate conservation strategies that are resilient to climate change.

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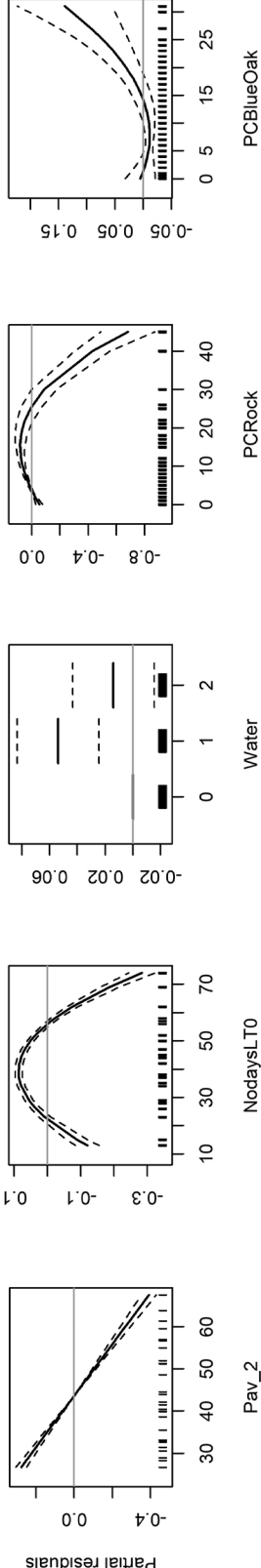
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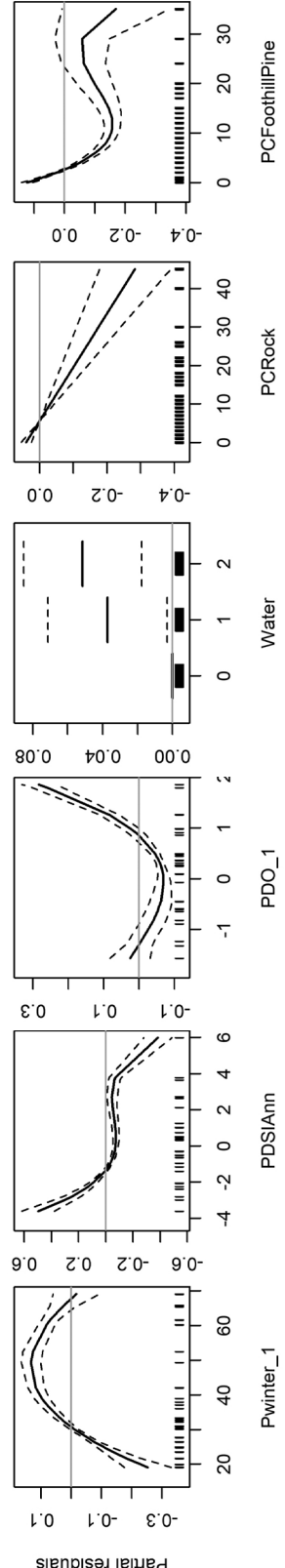
APPENDIX 1. Response in abundance of 23 species of birds resident year round at the San Joaquin Experimental Range (SJER), California, to weather/climate and habitat variables, fitted with semi-parametric Poisson regression (GAM; solid black line) plus 95% confidence intervals (dashed lines). The variables location (eastings/northing and route), Julian date, and year were included in all models (but were dropped when non-significant) and are not shown here (see Purcell and Mori [2018] for year effects). The mean

of the partial residuals for abundance is shown by the horizontal gray line at zero on the y-axis. Values above zero on the y-axis represent higher-than-average abundance; values below zero represent lower-than-average abundance. Tick marks on the x-axis indicate the number of observations. Confidence in the relationship is highest where tick marks are densest. Relationships where tick marks are sparse are less reliable. See Table 1 for names of variables and Table 2 for scientific names of species.

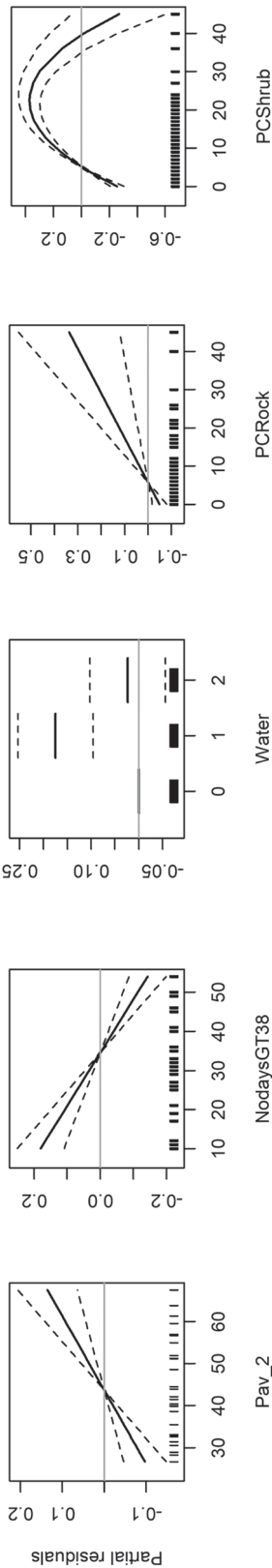
California Quail



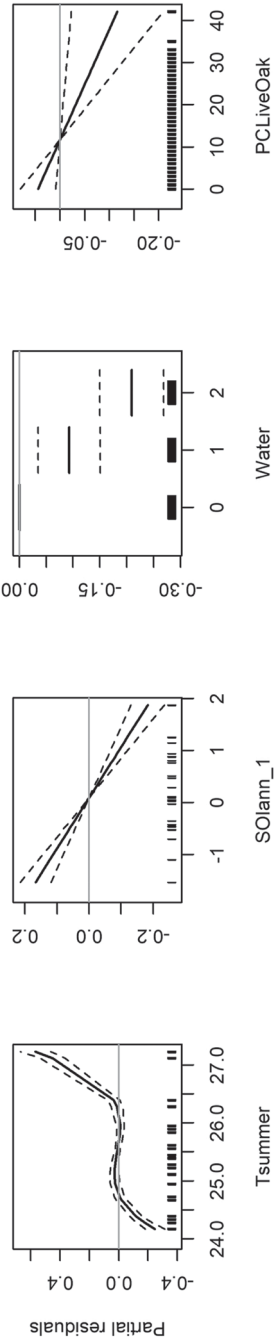
Mourning Dove



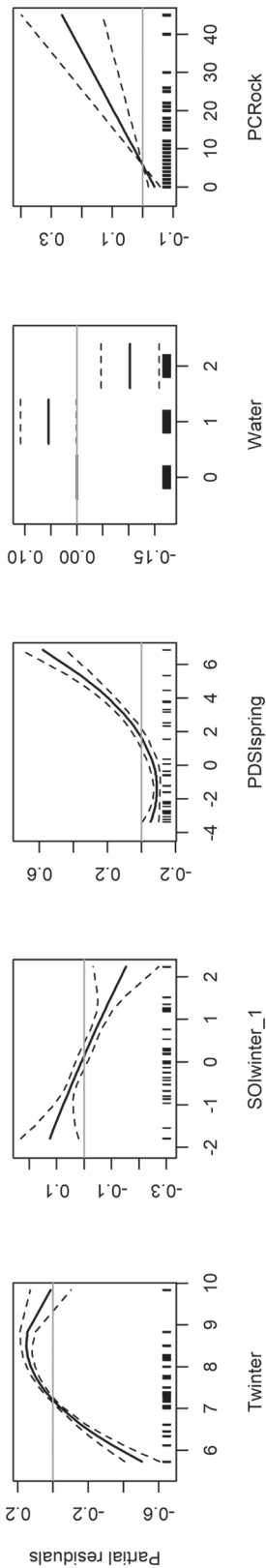
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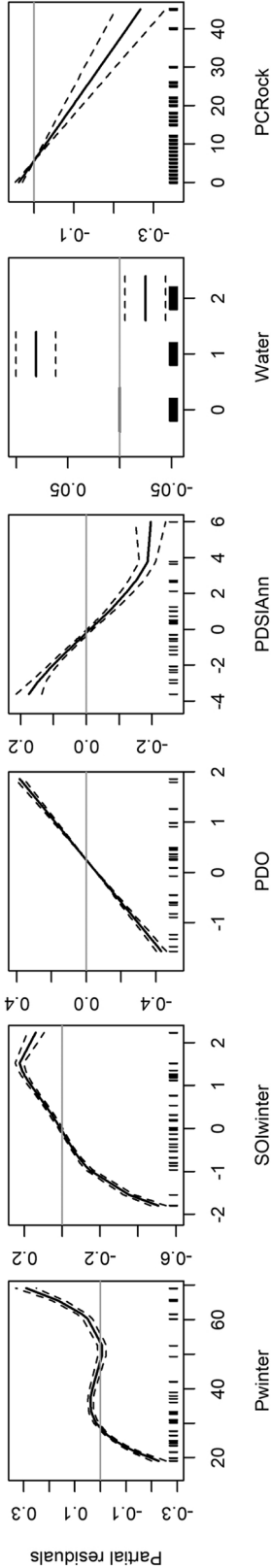
Turkey Vulture



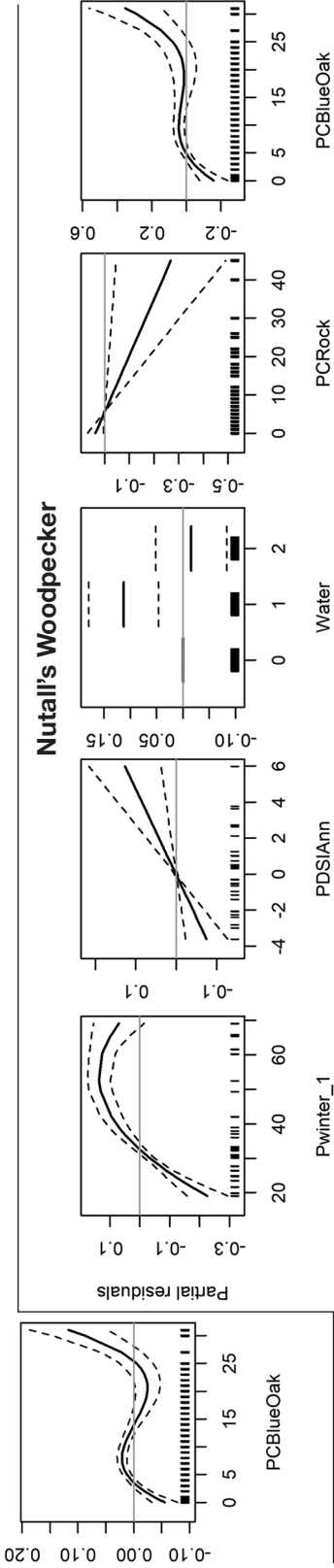
Red-tailed Hawk



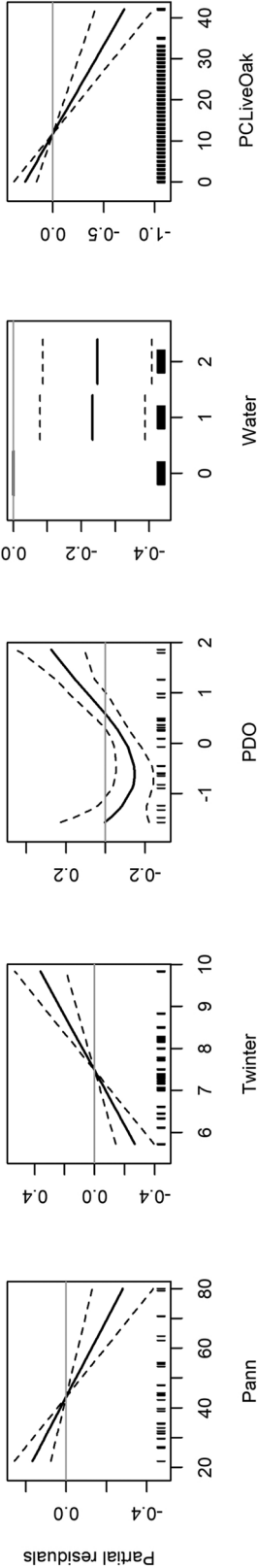
Acorn Woodpecker

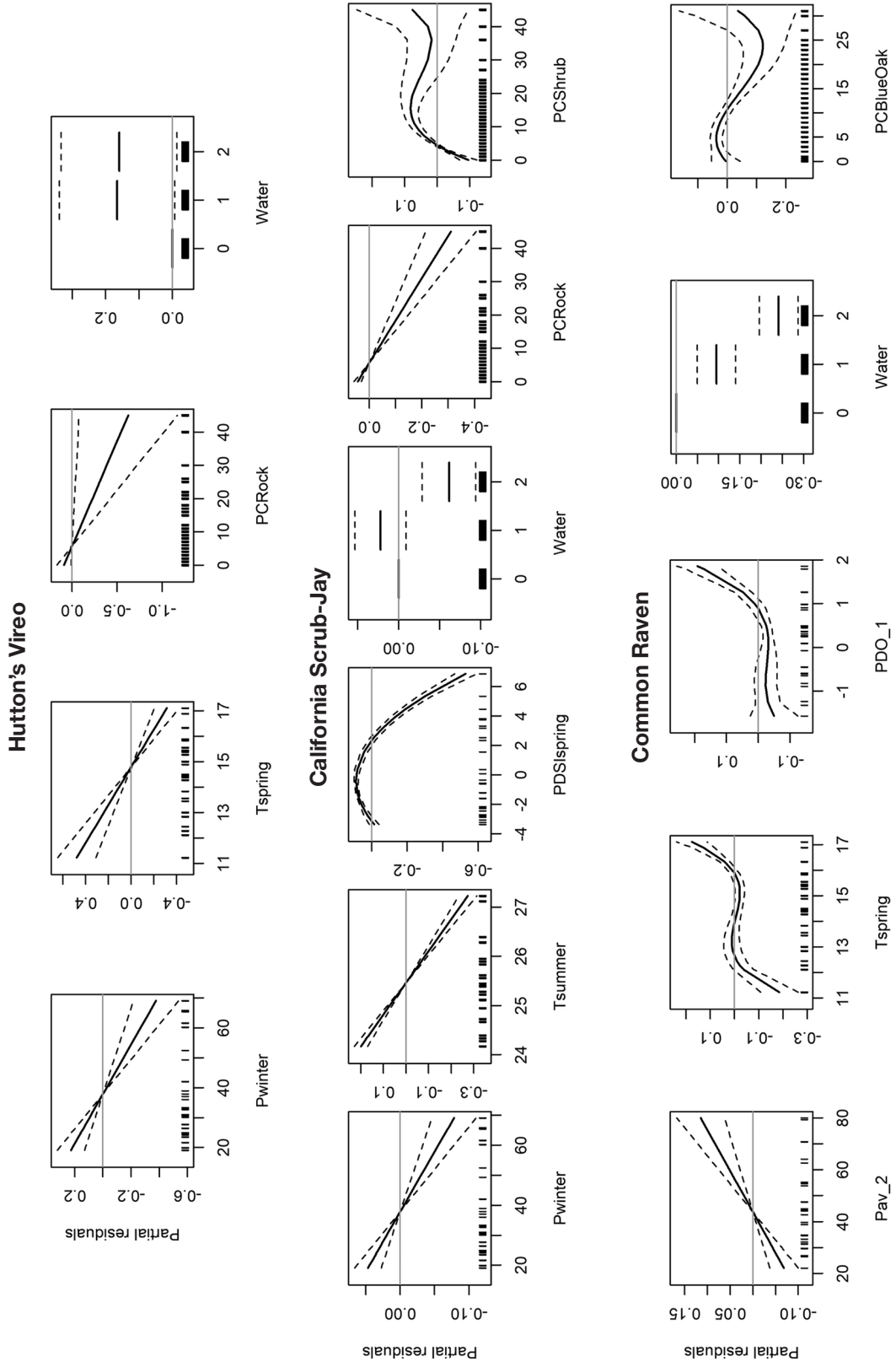


Nuttall's Woodpecker

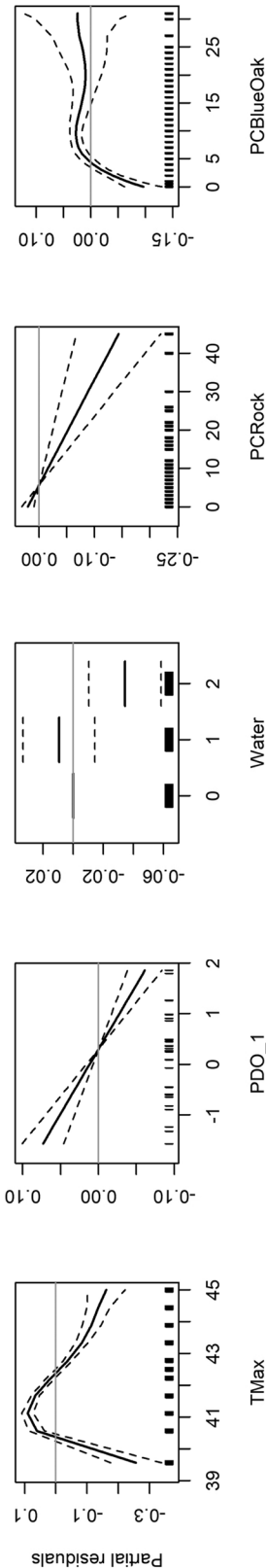


American Kestrel

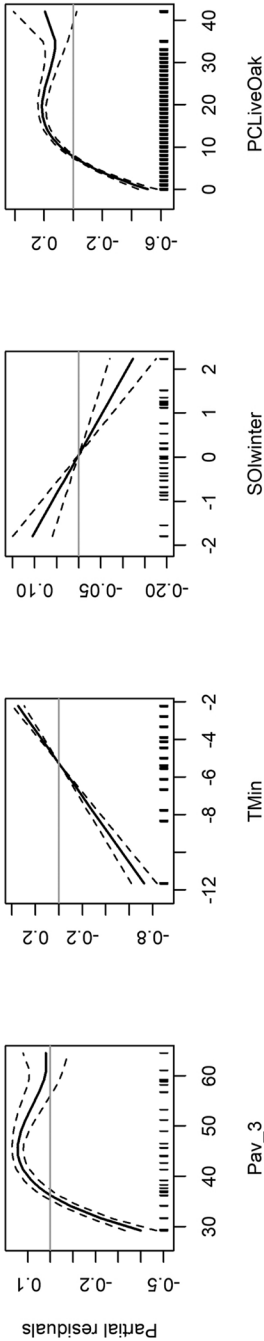




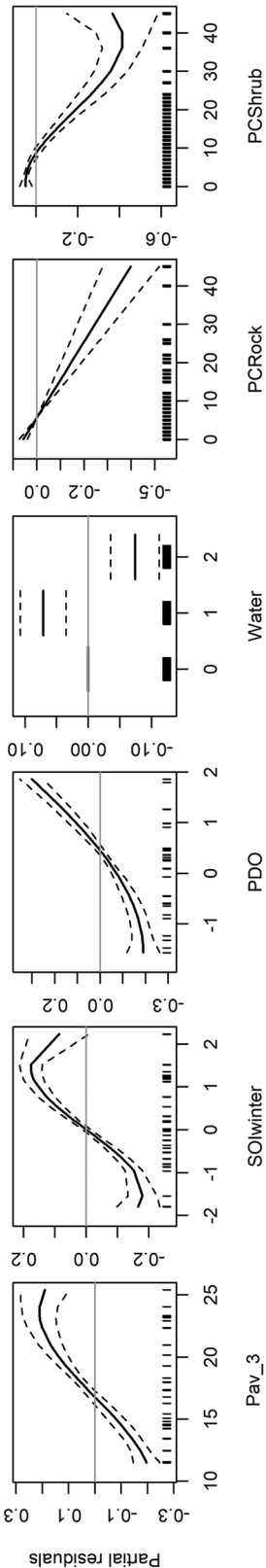
Oak Titmouse

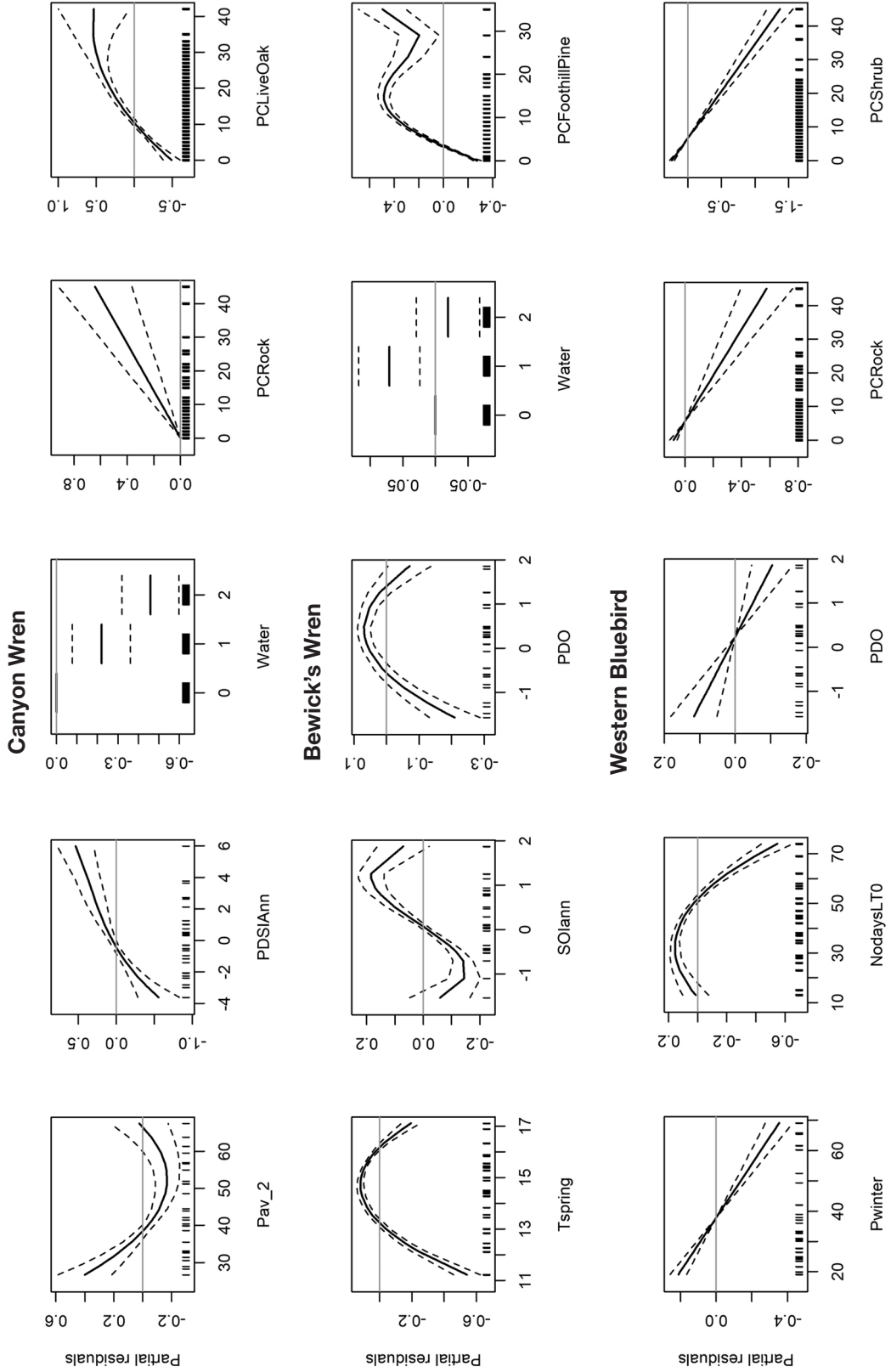


Bushtit

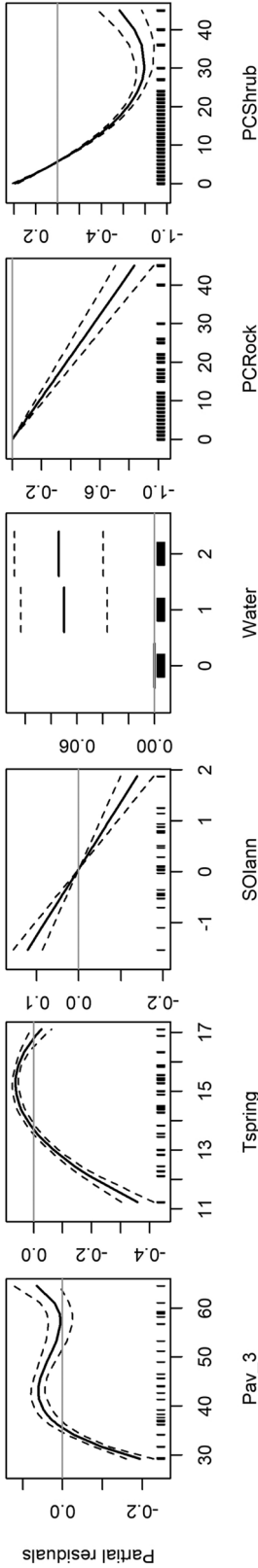


White-breasted Nuthatch

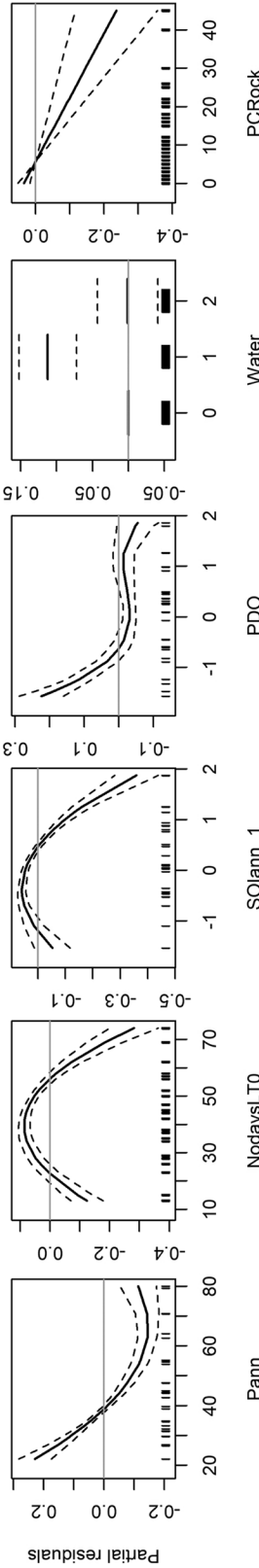




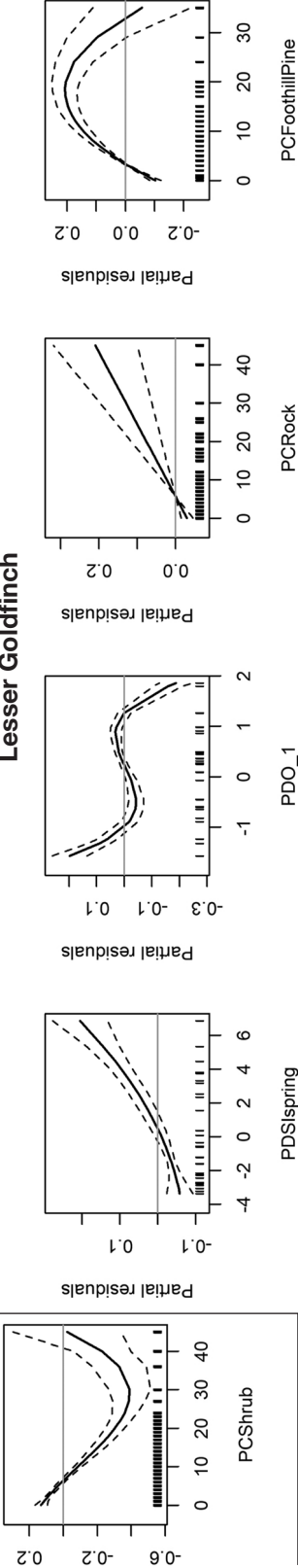
European Starling

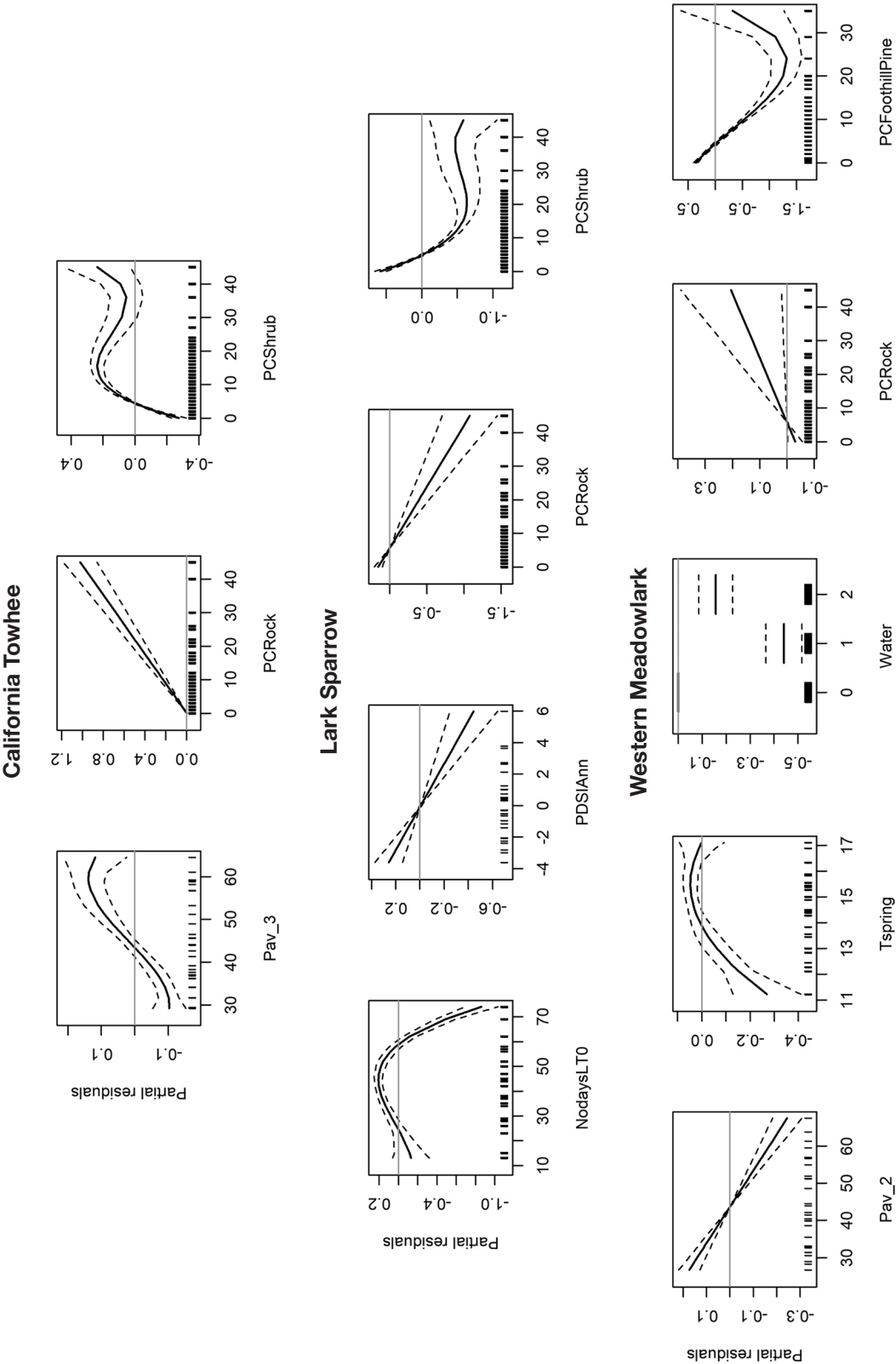


House Finch

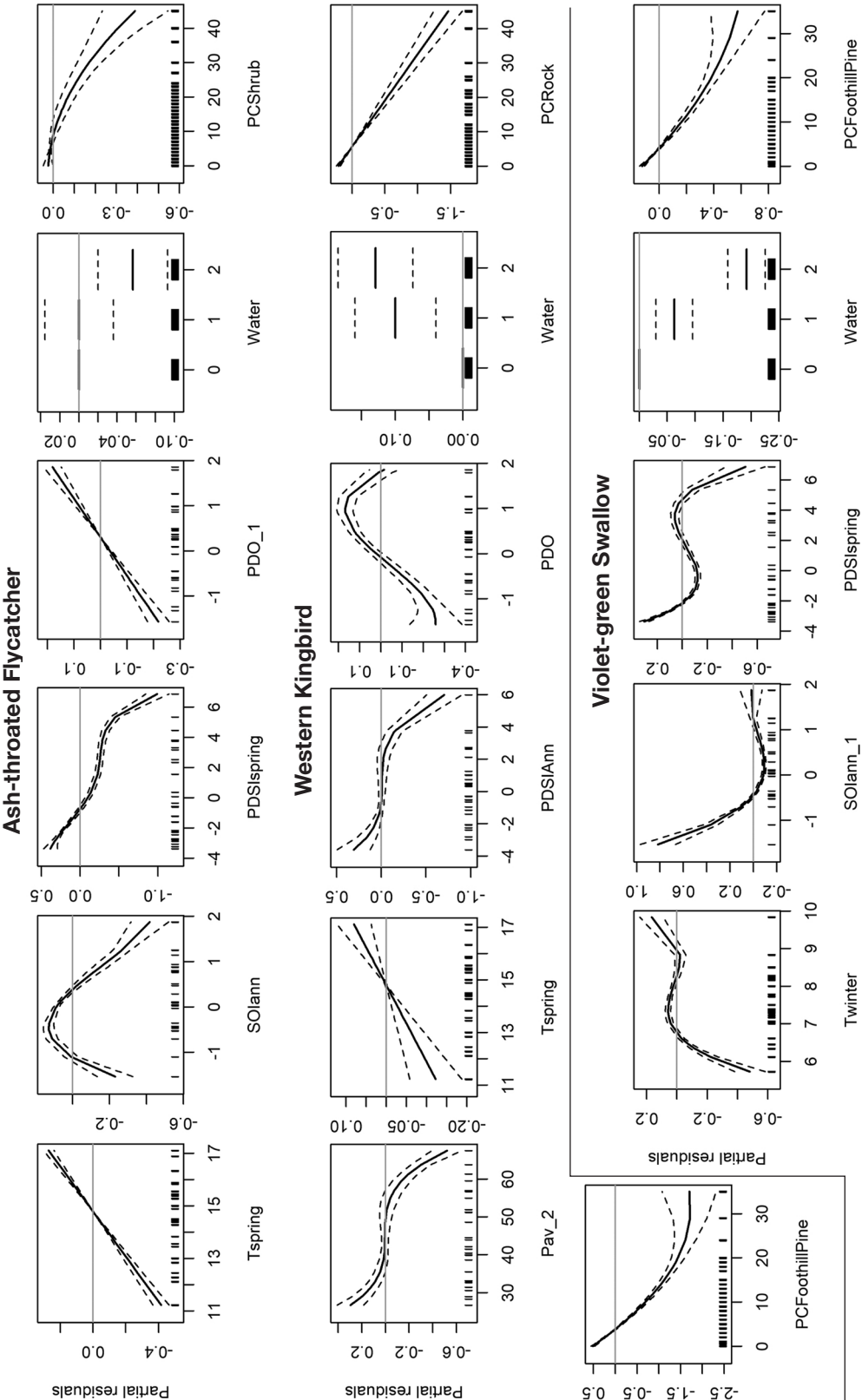


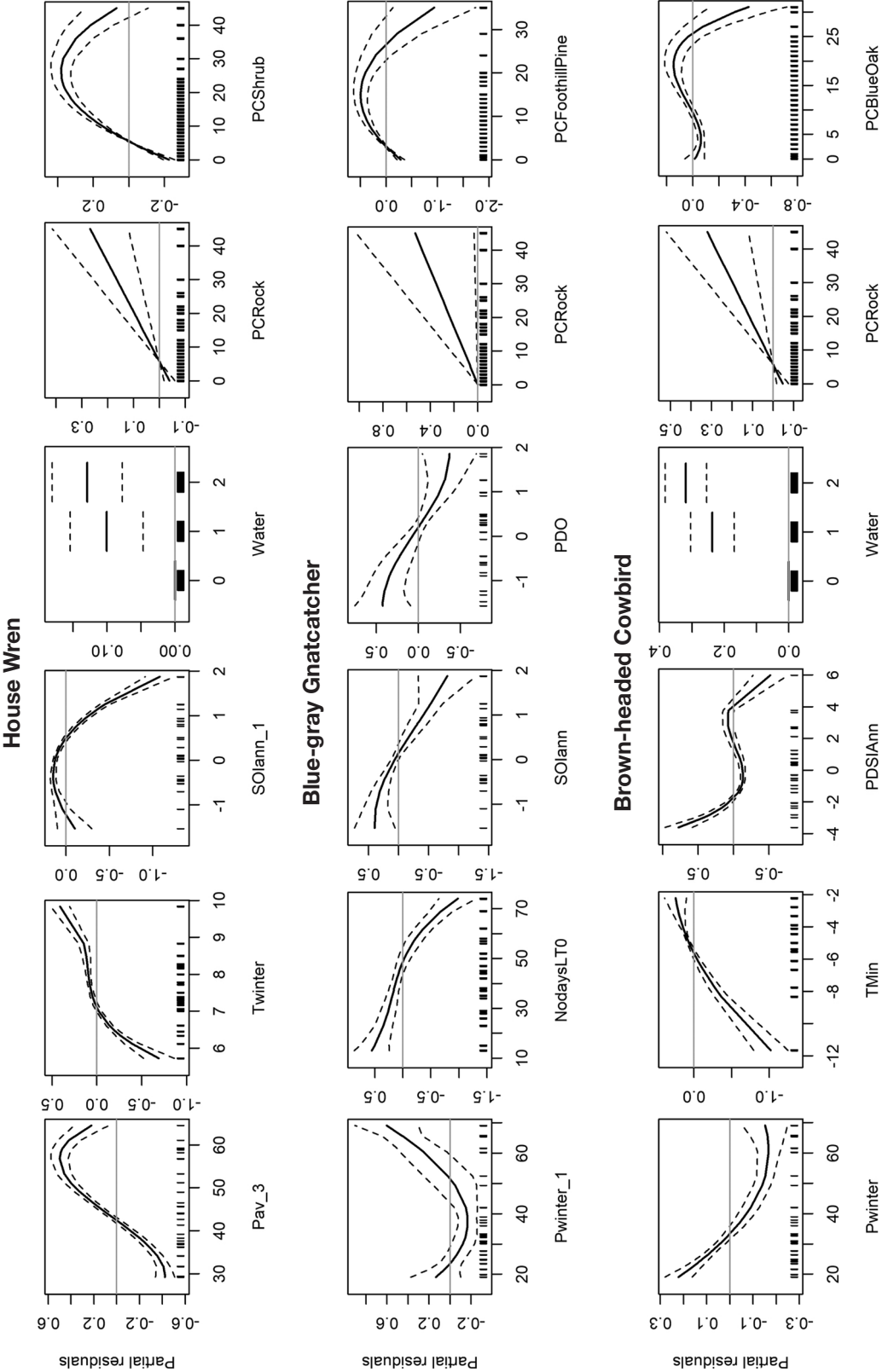
Lesser Goldfinch

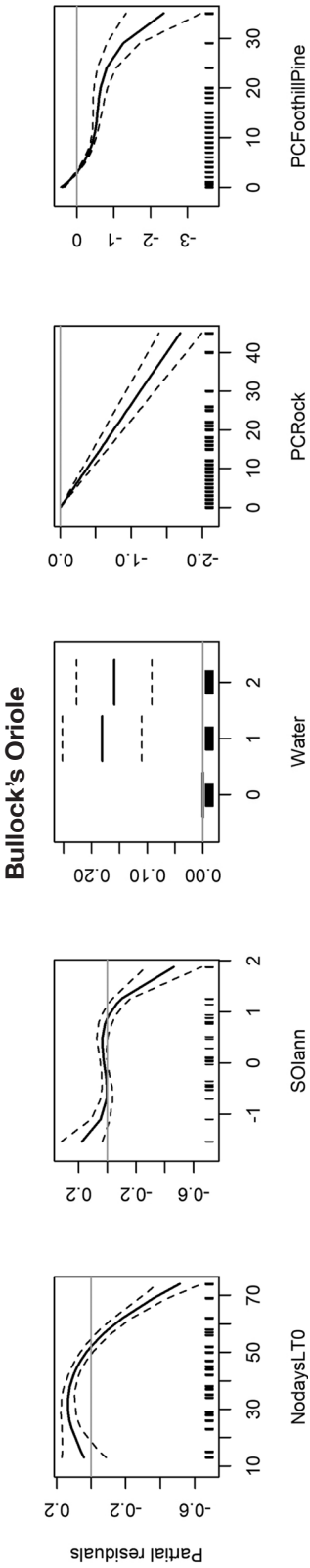




APPENDIX 2. Response of seven breeding summer residents at SJER to weather/climate and habitat variables. See Appendix 1 for details.







APPENDIX 3. Response of five winter residents and spring/fall migrants at SJER to weather/climate and habitat variables. See Appendix 1 for details.

