

## RESEARCH ARTICLE

**Protected areas safeguard landbird populations in central coastal California: Evidence from long-term population trends**

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**ABSTRACT**

Many bird populations have experienced population declines across North America over the past several decades. The establishment of protected areas has been used as a conservation action to maintain or help in the recovery of these populations; however, the effectiveness of protected areas in safeguarding bird populations within their borders from negative impacts to populations in surrounding unprotected areas has rarely been evaluated. Our study aimed to evaluate the effectiveness of protected areas in the San Francisco Bay Area of California for landbirds. We conducted point count surveys along riparian corridors in coastal Marin County in protected areas, predominately national parks, and estimated the population growth rates for 14 species over 23 years. We compared these growth rates to North American Breeding Bird Survey growth rate estimates from the Coastal California and the Northern Pacific Rainforest Bird Conservation Regions, which comprise larger, regional populations. A safeguarding effect was detected for 9 of the 14 species. We expected an effect on species strongly associated with riparian vegetation, which has incurred significant loss and degradation in the region; however, we instead observed benefits to general riparian users that were at least as great as the benefits to strong riparian specialists. We also expected that populations of resident species might benefit more than migrants; however, we found strong support for a safeguarding effect for both groups. Species with increasing growth rates in coastal Marin County protected areas in comparison to regionally stable or decreasing populations demonstrate the potential for protected areas to not only maintain populations despite declines outside their boundaries but also to help them recover from current and previous losses. Continuing long-term monitoring and associated full life cycle research will help identify if and when other drivers (e.g., climate change) may weaken these safeguarding effects, or when additional conservation and management is warranted.

*Keywords:* California, landbird, Marin, national park, Point Reyes, protected area, riparian, trend

**LAY SUMMARY**

- Designating protected areas has long been assumed to be an effective conservation tool and benefit bird populations within their borders, with very few studies evaluating this assumption.
- We tested the assumption by determining population trends for landbird species in protected areas in central coastal California using point count surveys and comparing our results to regional trends.
- Nine out of 14 species benefited from being inside protected areas with their population trends being more positive than the regional trends.
- Our study provides support for the effectiveness of designating protected areas as a conservation tool.
- We call for expanded long-term monitoring as well as exploration of reasons why the safeguarding effect was not universal and what actions are needed.

**Las áreas protegidas protegen poblaciones de aves terrestres en la costa central de California: Evidencia de tendencias poblacionales a largo plazo****RESUMEN**

Muchas poblaciones de aves han experimentado disminuciones poblacionales en América del Norte durante las últimas décadas. El establecimiento de áreas protegidas se ha utilizado como una acción de conservación para mantener o ayudar en la recuperación de estas poblaciones; sin embargo, rara vez se ha evaluado la efectividad de las áreas protegidas para proteger las poblaciones de aves dentro de sus fronteras de los impactos negativos en las poblaciones de las

áreas no protegidas circundantes. Nuestro estudio tuvo como objetivo evaluar la efectividad de las áreas protegidas para las aves terrestres del área de la Bahía de San Francisco en California. Realizamos censos en puntos de conteo a lo largo de corredores ribereños en las áreas protegidas costeras, predominantemente parques nacionales, del Condado de Marin, y estimamos las tasas de crecimiento de la población para 14 especies durante 23 años. Comparamos estas tasas de crecimiento con las estimaciones de la tasa de crecimiento de la Encuesta de Aves Reproductoras de América del Norte de las Regiones de Conservación de Aves del Bosque Lluvioso de la Costa de California y del Pacífico Norte, que comprenden poblaciones regionales más grandes. Se detectó un efecto de protección para 9 de 14 especies. Esperábamos un efecto sobre las especies fuertemente asociadas con la vegetación ribereña, que ha sufrido pérdidas y degradaciones significativas en la región; sin embargo, observamos en cambio beneficios para los usuarios de ribera generalistas que fueron al menos tan grandes como los beneficios para los especialistas de ribera. También esperábamos que las poblaciones de especies residentes se beneficiaran más que las migratorias; sin embargo, encontramos un fuerte apoyo para un efecto de protección de ambos grupos. Las especies con tasas de crecimiento en aumento en las áreas protegidas costeras del Condado de Marin, en comparación con las poblaciones regionalmente estables o en disminución, demuestran el potencial de las áreas protegidas no solo para mantener las poblaciones a pesar de las disminuciones fuera de sus límites, sino también para ayudarlas a recuperarse frente a las pérdidas actuales y pasadas. El seguimiento continuo a largo plazo y la investigación asociada del ciclo de vida completo ayudarán a identificar si otros factores (e.g., cambio climático) pueden debilitar estos efectos de protección, o cuándo se justifica una conservación y un manejo adicionales.

*Palabras clave:* área protegida, ave terrestre, California, Marin, parque nacional, Point Reyes, ribereño, tendencia

## INTRODUCTION

Despite decades of conservation attention, populations of many once-common bird species are in steep decline around the world (Reif 2013; Inger et al. 2015; Rosenberg et al. 2019), with consequences for their long-term sustainability as well as important ecosystem processes (Sekercioglu et al. 2004; Gaston and Fuller 2008). Concerns over these trends, and the ongoing pressures on bird populations from climate change and habitat loss, have resulted in calls for additional conservation actions to slow or reverse these trends. Proposed strategies include expanded/continued investment in permanent protected areas (Watson et al. 2014; Watson and Venter 2017). However, protected areas on their own may have limited efficacy for bird conservation, especially for migratory species; globally, protected areas are estimated to adequately cover all life cycle stages of 45% of nonmigratory bird species and only 9% of migratory bird species (Runge et al. 2015). Additionally, range shifts induced by climate change may further reduce habitat area or quality in these protected areas (Hannah et al. 2007; Hole et al. 2009). The primary tools to address these limitations and mitigate further bird population declines will likely include protecting new areas, enlarging existing protected areas, modifying natural resource management activities within protected areas, and collaborating with public and private landowners at the landscape scale.

One of the common goals for designating reserves and protected areas is to maintain robust, self-sustaining animal populations by protecting and enhancing habitats that would otherwise likely be lost or degraded (Watson et al. 2014, 2016). While much conservation research has identified areas of high priority for multiple species (e.g., Moilanen 2007), and evaluated the coverage and

representation of species across networks of protected areas (e.g., Runge et al. 2015), evaluations of their effectiveness in reducing population declines are relatively uncommon and have shown mixed results (Gaston et al. 2008; Geldmann et al. 2013). Protected areas are assumed to safeguard animal populations within these areas from the negative effects of habitat loss and degradation on populations outside these areas. This assumption may not hold true if, for example, the area is not sufficiently secured and managed (Leverington et al. 2010), the area is not of the appropriate size for the species (Di Franco et al. 2018), the species of interest only spends part of its life cycle in the area (Humble et al. 2020), or climate change is having a strong influence on biotic or abiotic conditions in the area (Ferro et al. 2014). To make the most effective use of protected areas for animal conservation, long-term monitoring and research inside and outside of protected areas will be necessary to evaluate their performance in protecting populations.

In this study, we evaluated the effectiveness of protected areas in the San Francisco Bay region of California in supporting improved population trends relative to regional trends that include unprotected areas. Specifically, we analyzed data collected through a long-term monitoring program in riparian corridors throughout a network of predominantly national parks, as well as adjacent state and county parks. We compared local, long-term population growth rates to growth rates over the same time period estimated from the Breeding Bird Survey (BBS) dataset (Sauer et al. 2017) for the California portions of both the Coastal California Bird Conservation Region 32 (hereafter CA-32; NABCI 2020) and the Northern Pacific Rainforest Bird Conservation Region 5 (hereafter CA-5; NABCI 2020). Although the 2 Bird Conservation Regions (BCRs) include a mix of protected and unprotected areas, if protected

areas in the San Francisco Bay region are effectively safeguarding bird populations from effects of broader regional habitat loss and degradation, we would expect species to have higher population growth rates within the protected areas than the average population growth rate throughout the BCRs. In particular, we expected that year-round residents, whose full life cycle is spent within the protected areas, would be more likely to benefit from the protected areas than migratory species, which may spend half of the year or more outside the protected areas. Finally, because riparian vegetation outside of protected areas has been heavily degraded in California (RHJV 2004), we also expected that species strongly associated with riparian vegetation (riparian specialists) would be more likely to benefit from the protected areas than species with less restrictive habitat associations (riparian users).

## METHODS

### Monitoring Program

The US National Park Service's Inventory and Monitoring Program (hereafter I&M Program) developed a policy, in part, "to detect or predict changes that may require intervention, and to serve as reference points for more altered parts of the environment" (National Park Service 1992). The I&M Program grouped national park units into networks to facilitate cooperation on monitoring protocols, data comparability, and resource sharing. The monitoring programs are designed to be long-term and are focused on the important resources designated by each network, known as "vital signs." The San Francisco Bay Area Network designated riparian landbirds as one of its vital signs (Adams et al. 2006), and a monitoring plan was developed (Gardali et al. 2010, 2020). A critical step in evaluating the effectiveness of protected areas is developing and implementing monitoring plans to evaluate population trends in protected areas, and we recognize the development of the I&M Program in our methods to highlight its importance to our study.

### Study Area

Landbird surveys were conducted in the San Francisco Bay Area of California, predominantly in 2 national park units (Point Reyes National Seashore and in the Marin County portion of Golden Gate National Recreation Area), as well as in a portion of 1 California State Park (Mount Tamalpais State Park) and at 1 site managed by Marin County Parks (Bolin Lagoon Open Space Preserve) (Figure 1). The parks all provide a similarly high level of protection with prohibitions on most extractive activities (e.g., logging, mining, and hunting); in some areas, cattle grazing or silage production are allowed. The parks are open to public recreation with motorized access restricted to roads. All study sites are located within the western coastal portion

of Marin County, and we collectively refer to them as "Coastal Marin sites." The sites have a Mediterranean climate (Peel et al. 2007) marked by 2 distinct seasons, a wet and cool November to April, followed by a dry and warm May to October. Additionally, another monitoring effort elsewhere within the San Francisco Bay Area Network of parks was conducted at Pinnacles National Park during this period (Humble et al. 2017) and was considered for inclusion in this study; however, because we were unable to precisely estimate growth rates there due to fewer years of data available to date, it was eliminated from further inclusion and analysis (Supplementary Material Table S1).

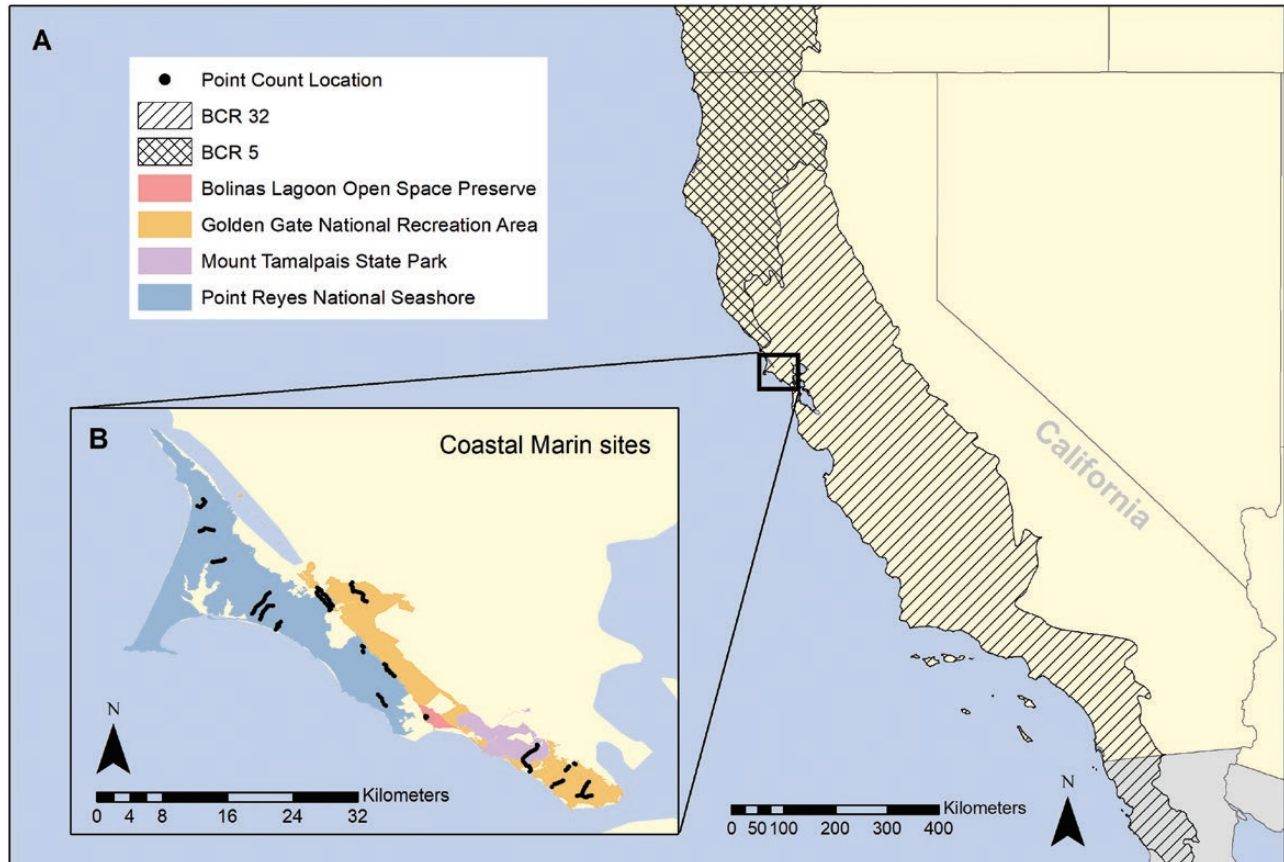
Bird surveys were conducted along riparian corridors, in part because of the high avian biodiversity and abundance in these areas. Due to the narrow extent of the riparian vegetation in some locations, surveys often included other adjacent habitats (such as coastal scrub and freshwater marsh). The riparian vegetation is dominated by arroyo willow (*Salix lasiolepis*) and often red alder (*Alnus rubra*), with an understory that frequently includes California blackberry (*Rubus ursinus*), stinging nettle (*Urtica dioica*), salmonberry (*Rubus spectabilis*), and California mugwort (*Artemisia douglasiana*), forming either a willow riparian scrub or an alder-willow riparian canopy forest (Shuford and Timossi 1989; Samuels et al. 2005).

### Site Selection

Study sites consisted of a total of 186 bird survey points (point count stations) organized into 15 transects (Supplementary Material Table S1). The initial rationale for establishing each of these transects varied and occurred prior to the implementation of the I&M Program. These transects generally were located in relatively accessible riparian corridors that could accommodate multiple point count stations at least 200 m apart and were selected for continued long-term monitoring as part of one or more larger regional efforts, including the I&M Program. Collectively, these transects cover a majority of the riparian vegetation in each of the national parks in Marin County. Additionally, a few riparian point count stations in Mount Tamalpais State Park and Bolinas Lagoon Open Space Preserve—other public lands that are contiguous or adjacent to these national parks—were also selected for inclusion in this I&M Program because of their comparable monitoring history and importance in the region. Further site selection details can be found in the Riparian Landbird Monitoring Protocol for Golden Gate National Recreation Area and Point Reyes National Seashore (Gardali et al. 2020).

### Data Collection

To assess landbird-community composition and species abundance, and their changes over time in riparian corridors, we conducted point count surveys using standard



**FIGURE 1.** (A) Borders of Coastal California Bird Conservation Region (BCR) (32) and Pacific Northwest Rainforest BCR (5) within California, USA. (B) Point count locations and boundaries of protected areas for Coastal Marin sites used in this study.

protocols (Ralph et al. 1995; Gardali et al. 2020), from 1997 through 2019. The general monitoring regime since the implementation of the initial monitoring protocols (Gardali et al. 2010) is to monitor point count transects every third year, with a subset of core transects (6 of 15) monitored every year (Supplementary Material Table S1).

Briefly, the point count survey method entails repeated visits to the same point count station, where an experienced observer records the species and distance (placing them into distance bins, e.g., 0–10 m, 10–20 m, 20–30 m, 30–50 m, 50–100 m) of each individual bird detected (visually and aurally) over an interval of 5 min (Ralph et al. 1995). In general, 2 surveys were conducted at each point count station during the peak of breeding season, currently defined as between 1 May and 30 June at Coastal Marin sites (Gardali et al. 2020). Protocols for the seasonal timing and number of visits differed slightly prior to 2011 and the establishment of the current protocols developed for the San Francisco Bay Area Network I&M Program (Gardali et al. 2020); for this analysis, we excluded surveys outside the current definition for the peak of the breeding season. Consequently, the number of visits included in this analysis per point count station per year ranged from 1 to 3. To

minimize bias due to variation in detection probability with distance and by species, and because the distance bins used changed over the years prior to the finalization of the protocols, we included in our analysis only birds detected within 50 m of each point count station.

### Data Analysis

We selected a subset of candidate passerine and near-passerine species (Table 1) to consider for analysis of population trends based on their conservation status and sample size in our study. To create a list of possible species to include, we first considered species with special conservation status (i.e. a California Bird Species of Special Concern; Shuford and Gardali 2008), those that serve as regional focal species from the California Partners in Flight habitat conservation plans for riparian, oak woodland, and coastal scrub and chaparral (CalPIF 2002, 2004; RHJV 2004), or those on the national Partners in Flight Watch List (Panjabi et al. 2019). Additionally, because it is also important to evaluate the trends for common species, we also considered species that were very abundant in our dataset but were not already included in the above. From this list of candidate species, we excluded species for which the point

**TABLE 1.** Focal species selected for analysis at Coastal Marin sites, and their species codes and conservation status, grouped by migratory status and habitat association. Species grouped under riparian specialists predominantly breed regionally in riparian habitat, but not exclusively; riparian users are species that breed predominantly outside of riparian habitat. Migratory status is simplified such that species that are predominantly resident but may have some migratory individuals within the population are generally considered resident for purpose of this analysis. For conservation status: California Partners in Flight (CalPIF) habitat conservation plan focal species, including Oak-CalPIF = oak woodland focal species (CalPIF 2002), Riparian-CalPIF = riparian focal species (RHJV 2004), and Scrub-CalPIF = scrub focal species (CalPIF 2004); CA-BSSC = CA Bird Species of Special Concern (Shuford and Gardali 2008); and national Partners in Flight (PIF) Watch List (Panjabi et al. 2019).

| Species                               | Scientific name                  | Species code | Conservation status          |
|---------------------------------------|----------------------------------|--------------|------------------------------|
| <b>Migratory riparian specialists</b> |                                  |              |                              |
| Black-headed Grosbeak                 | <i>Pheucticus melanocephalus</i> | BHGR         | Riparian-CalPIF              |
| Swainson's Thrush                     | <i>Catharus ustulatus</i>        | SWTH         | Riparian-CalPIF              |
| Warbling Vireo                        | <i>Vireo gilvus</i>              | WAVI         | Riparian-CalPIF              |
| Wilson's Warbler                      | <i>Cardellina pusilla</i>        | WIWA         | Riparian-CalPIF              |
| <b>Resident riparian specialists</b>  |                                  |              |                              |
| Common Yellowthroat <sup>a</sup>      | <i>Geothlypis trichas</i>        | COYE         | Riparian-CalPIF              |
| Nuttall's Woodpecker                  | <i>Dryobates nuttallii</i>       | NUWO         | Oak-CalPIFF                  |
| Song Sparrow                          | <i>Melodia melospiza</i>         | SOSP         | Riparian-CalPIF              |
| <b>Migratory riparian users</b>       |                                  |              |                              |
| Orange-crowned Warbler                | <i>Leiothlypis celata</i>        | OCWA         | None                         |
| Olive-sided Flycatcher                | <i>Contopus cooperi</i>          | OSFL         | CA-BSSC, PIF Watch List      |
| <b>Resident riparian users</b>        |                                  |              |                              |
| Bewick's Wren                         | <i>Thryomanes bewickii</i>       | BEWR         | None                         |
| California Scrub-Jay                  | <i>Aphelocoma californica</i>    | CASJ         | Oak-CalPIF                   |
| Chestnut-backed Chickadee             | <i>Poecile rufescens</i>         | CBCH         | None                         |
| Spotted Towhee                        | <i>Pipilo maculatus</i>          | SPTO         | None                         |
| Wrentit                               | <i>Chamaea fasciata</i>          | WREN         | Scrub-CalPIF, PIF Watch List |

<sup>a</sup>We have classified Common Yellowthroat as a year-round resident species because some, if not all, Common Yellowthroats are present year-round locally, though the species is migratory across parts of its range (Guzy and Ritchison 2020).

count method may be less accurate for estimating population trends (e.g., flocking species, swallows, and hummingbirds), and species with few detections in our dataset. A total of 14 species met our criteria for analysis (Table 1).

To estimate the long-term population growth rates of each species, we adapted the hierarchical Bayesian model for the analysis of North American BBS data described by Sauer and Link (2011), to accommodate the repeated visits to point count stations in each year and facilitate comparison of our point count data to BBS analysis results. As in the Sauer and Link (2011) model, the change in the population size of each bird species across all our Coastal Marin sites is modeled as a Poisson regression. The mean count of birds on a survey ( $\lambda_{ijt}$ ) in transect  $i$ , point count station  $j$ , year  $t$  is a function of explanatory variables:

$$\log(\lambda_{ijt}) = \beta_0 + \beta_1 (t - t^*) + \omega_i + \delta_j + \gamma_t \quad (1)$$

where  $\beta_0$  and  $\beta_1$  are the intercept and slope,  $t^*$  is the baseline year, and  $\omega_i$ ,  $\delta_j$ , and  $\gamma_t$  represent additional random effects of transect, point count stations, and year, respectively. We treated these random effects as mean-zero normal random variables with constant variances  $\sigma_\omega^2$ ,  $\sigma_\delta^2$ , and  $\sigma_\gamma^2$ , respectively. We assigned the slope and intercept variables vague normal prior distributions (mean 0, variance  $10^3$ ), and we assigned the variances vague uniform prior distributions (ranging 0 to 10).

### Comparison to Regional Growth Rates

We evaluated our results in the context of larger-scale population growth rates for each species throughout the California portions of BCR 32 (CA-32) and BCR 5 (CA-5). All our survey points are contained within BCR 32 (Figure 1), but because our study area lies near the northern edge of BCR 32 and just south of the southern limit of BCR 5, we compared our population growth rates to those from both BCRs. For each species in our analysis, we first used the R package *bbsBayes* (Edwards and Smith 2020) to obtain and analyze BBS data over the same set of study years (1997–2019; Pardieck et al. 2020). To estimate population growth rates, stratified by the intersection of BCRs and US state boundaries, we fit the “slope” model implemented in *bbsBayes*, which is a hierarchical Bayesian model comparable to that of Sauer and Link (2011) and our model described above, which includes a parameter “beta” for the slope of the population growth rate that is equivalent to  $\beta_1$  in Equation (1).

We then quantitatively compared species-specific population growth rates from our Coastal Marin sites to the population growth rates from the California portion of each BCR, while accounting for the uncertainty in each of the growth rate estimates. We adapted a method described by Smith et al. (2014) in which the difference between pairs of estimates is estimated using a Bayesian model that is analogous to a weighted paired  $t$ -test, taking into account

the variance and sample size for each estimate. In this comparison model, the estimated population growth rates ( $\hat{\beta}_{sd}$ ) for each species  $s$  from dataset  $d$  is assumed to come from a normal distribution with mean and variance equal to the true growth rate ( $\beta_{sd}$ ) and true variance ( $\sigma_{sd}^2$ ). The true variance is estimated from the estimated variance ( $\hat{\sigma}_{sd}^2$ ) using a chi-squared distribution with  $n$  degrees of freedom:

$$\frac{n\hat{\sigma}_{sd}^2}{\sigma_{sd}^2} \sim \chi_n^2 \quad (2)$$

where  $n$  is the number of BBS survey routes or Coastal Marin transects included in the analysis. We assigned the true growth rates ( $\beta_{sd}$ ) vague normal prior distributions (mean 0, variance  $10^6$ ), and assigned the true variances ( $\sigma_{sd}^2$ ) vague gamma prior distributions (shape 0.001, rate 0.001).

Within the model, we simultaneously estimated the species-specific differences in true growth rates between Coastal Marin sites and each of the BCRs ( $d_s$ ) as:

$$d_s = \beta_{s,CM} - \beta_{s,BCR} \quad (3)$$

such that positive differences indicate that the growth rate from the Coastal Marin sites is higher than the growth rate for the BCR. We also estimated the average of these species-specific differences ( $d_g$ ) for groups of species ( $g$ ) that included either all species, or subsets of only year-round residents, migratory species, riparian specialists, or riparian users:

$$d_g = \frac{\sum_1^{S_g} d_s}{S_g} \quad (4)$$

where  $S_g$  is the total number of species in each group  $g$ . While grouping species in other ways (e.g., body mass, diet, phylogenetic relationships) might provide additional insights, we chose these groups because of the habitat focus of the monitoring (riparian) and the potentially large difference in the effect of only protecting areas for part of a species annual lifecycle (migratory status).

### Model Fitting and Interpretation

For all models described above, we conducted the Markov Chain Monte Carlo analyses in the program JAGS via the R packages *rjags* and *bbsBayes* (Plummer 2003, 2018; Edwards and Smith 2020). We ran 3 chains for each analysis, and evaluated convergence using the Gelman–Rubin diagnostic (Gelman and Rubin 1992;  $\hat{r} < 1.05$ ). Where necessary, we extended models until chains sufficiently converged and produced at least 1,000 effective samples for the target parameters: slope parameters  $\beta_1$  (Equation 1) and *beta* (BBS “slope” model), and species- and group-specific differences in slope  $d_s$  (Equation 3) and  $d_g$  (Equation 4).

From the posterior distributions of each target parameter, we extracted the median and 95% highest posterior density interval (HPDI), as well as the probability that the parameter was greater than or less than zero. We interpreted parameters with  $\geq 95\%$  probability of being greater than or less than zero as indicating strong support for a difference from zero (i.e. either an increasing or declining population trend, or a difference in population trends between Coastal Marin sites and one of the BCRs). For slope parameters, we also evaluated the precision of each of our estimates using the half-width of the 95% HPDI (Sauer and Link 2011). We then converted all slope parameter statistics (medians, lower and upper HPDI limits, and precision values) to units of average annual growth rate (%) as  $e^x$ . As in Sauer and Link (2011), we considered an estimate to be imprecise if the half-width exceeded 3% per year, meaning a 3% per year change would not be detected.

### RESULTS

At Coastal Marin sites, we surveyed 186 point count locations across 15 transects between 1997 and 2019 with individual locations each surveyed for 5–23 years, not necessarily consecutively (Supplementary Material Table S1). We found that 4 species had stable population sizes, 4 species were declining, and 6 species were increasing (Table 2). All but 2 of the species’ growth rate estimates had a precision between 1% and 3%, indicating that our analysis would be able to detect a long-term growth rate larger than +3% or –3% for these 12 species (and for some would detect even smaller rates). Nuttall’s Woodpecker (*Dryobates nuttallii*) and Olive-sided Flycatcher (*Contopus cooperi*) had precision estimates between 5% and 7%; while their growth rate estimates are very imprecise, their posterior distributions indicated >95% probability of increasing and declining trends, respectively. When considering species by habitat association and migratory status, we again found a mix of increasing, stable, and declining population growth rates among the 7 riparian specialist species and 7 riparian user species, as well as among the 8-year-round resident species and 6 migratory species (Table 2).

Population growth rate estimates derived from the BBS data for CA-32 and CA-5 showed population trends that were either declining or stable for all 14 species (Table 2). The precision estimates for all of these growth rates were  $\leq 3\%$  except 2 species in just one of the BCRs, indicating sufficient precision to detect an increase or decrease for most species (Sauer and Link 2011). There were similarly mixed results by habitat association and migratory status, with declining and stable population trends within each group. The estimated differences in species-specific growth rates between Coastal Marin sites and each of the BCRs were positive (indicating growth at Coastal Marin

**TABLE 2.** Annual growth rate estimates (% change per year) and upper and lower limits of the 95% HPDI limits for each species included in our analysis for Coastal Marin sites, compared to estimates from the California portions of Bird Conservation Region (BCR) 32 (CA-32) and BCR 5 (CA-5) derived from BBS data. Trend estimates with >95% probability of being greater or less than zero are in bold, with declining trends also italicized). Precision estimates (calculated as the half-width of the 95% HPDI) show the smallest long-term growth rate the model should be able to detect. Species are grouped by migratory status and habitat association, as shown in Table 1.

| Species                               | Coastal Marin sites                |               |  | CA-32 (BBS)                        |               |  | CA-5 (BBS)                         |               |  |
|---------------------------------------|------------------------------------|---------------|--|------------------------------------|---------------|--|------------------------------------|---------------|--|
|                                       | Annual growth rate (%)<br>(95% CI) | Precision (%) |  | Annual growth rate (%)<br>(95% CI) | Precision (%) |  | Annual growth rate (%)<br>(95% CI) | Precision (%) |  |
| <b>Migratory riparian specialists</b> |                                    |               |  |                                    |               |  |                                    |               |  |
| Black-headed Grosbeak                 | <b>-2.15</b> (-3.86, -0.33)        | 1.82          |  | <b>-2.32</b> (-3.29, -1.41)        | 0.97          |  | 1.05 (-0.07, 2.29)                 | 1.17          |  |
| Swainson's Thrush                     | <b>1.91</b> (0.28, 3.53)           | 1.61          |  | <b>-1.70</b> (-3.33, -0.17)        | 1.63          |  | -0.41 (-1.97, 1.09)                | 1.55          |  |
| Warbling Vireo                        | 1.18 (-0.62, 2.99)                 | 1.80          |  | -0.07 (-1.23, 1.21)                | 1.23          |  | <b>-2.49</b> (-3.69, -1.30)        | 1.23          |  |
| Wilson's Warbler                      | <b>1.62</b> (0.54, 2.74)           | 1.09          |  | 0.61 (-1.16, 2.51)                 | 1.84          |  | <b>-2.03</b> (-3.59, -0.42)        | 1.63          |  |
| <b>Resident riparian specialists</b>  |                                    |               |  |                                    |               |  |                                    |               |  |
| Common Yellowthroat                   | <b>-1.35</b> (-2.55, -0.13)        | 1.24          |  | <b>-2.01</b> (-3.84, -0.39)        | 1.78          |  | -1.24 (-4.62, 1.83)                | 3.32          |  |
| Nuttall's Woodpecker                  | <b>7.49</b> (1.75, 14.33)          | 6.01          |  | -0.07 (-1.20, 1.12)                | 1.17          |  | -0.35 (-3.70, 3.27)                | 3.56          |  |
| Song Sparrow                          | <b>-2.07</b> (-3.14, -0.98)        | 1.11          |  | <b>-1.98</b> (-3.00, -1.01)        | 1.02          |  | <b>-1.34</b> (-2.58, -0.17)        | 1.23          |  |
| <b>Migratory riparian users</b>       |                                    |               |  |                                    |               |  |                                    |               |  |
| Orange-crowned Warbler                | <b>1.80</b> (0.58, 3.12)           | 1.25          |  | <b>-2.42</b> (-3.74, -1.10)        | 1.36          |  | 0.47 (-1.09, 1.96)                 | 1.53          |  |
| Olive-sided Flycatcher                | <b>-10.46</b> (-15.13, -5.89)      | 5.30          |  | <b>-2.16</b> (-4.01, -0.29)        | 1.92          |  | -1.06 (-3.24, 1.00)                | 2.17          |  |
| <b>Resident riparian users</b>        |                                    |               |  |                                    |               |  |                                    |               |  |
| Bewick's Wren                         | 1.23 (-1.63, 4.10)                 | 2.87          |  | -1.09 (-2.54, 0.37)                | 1.48          |  | <b>-3.75</b> (-6.04, -1.68)        | 2.30          |  |
| California Scrub-Jay                  | -1.86 (-4.26, 0.46)                | 2.40          |  | <b>-2.08</b> (-2.82, -1.28)        | 0.79          |  | 0.30 (-0.79, 1.37)                 | 1.08          |  |
| Chestnut-backed Chickadee             | <b>1.41</b> (0.07, 2.75)           | 1.33          |  | -1.38 (-2.78, 0.33)                | 1.59          |  | <b>-2.46</b> (-4.12, -0.95)        | 1.64          |  |
| Spotted Towhee                        | 2.55 (-0.49, 5.56)                 | 2.99          |  | <b>-1.95</b> (-2.78, -1.21)        | 0.80          |  | <b>-1.82</b> (-2.73, -0.83)        | 0.97          |  |
| Wrentit                               | <b>2.35</b> (0.37, 4.46)           | 2.02          |  | -0.34 (-1.26, 0.54)                | 0.91          |  | <b>-2.44</b> (-3.63, -1.27)        | 1.22          |  |

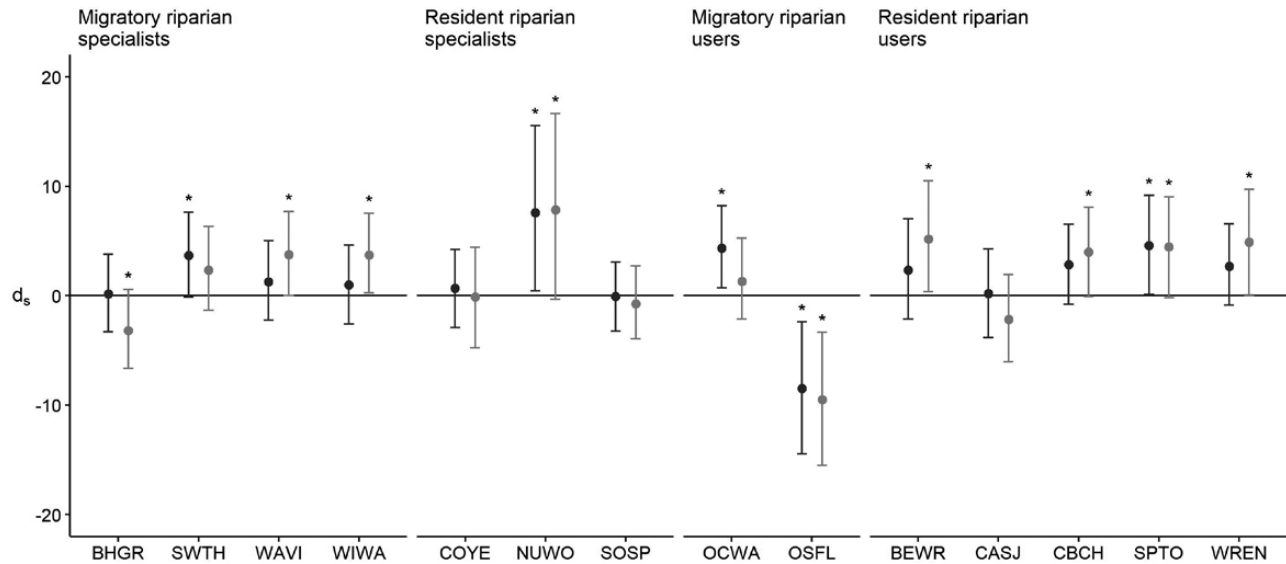
sites) for 4 of the 14 species in comparison to CA-32 and 7 in comparison with CA-5 (Figure 2). Most of the remaining species had no detectable difference in growth rate, indicating similar patterns of growth rates between Coastal Marin sites and the BCRs (9 in comparison to CA-32, 5 in comparison to CA-5). There was only 1 species that had a negative difference in comparison to both BCRs (Olive-sided Flycatcher), and 1 species with a negative difference in comparison to CA-5 (Black-headed Grosbeak [*Phaeucticus melanocephalus*]), indicating lower growth rates at Coastal Marin sites. In total, there were 9 species in which the growth rates were higher at Coastal Marin sites than in one (Bewick's Wren [*Thryomanes bewickii*], Orange-crowned Warbler [*Leiothlypis celata*], Swainson's Thrush [*Catharus ustulatus*], Warbling Vireo [*Vireo gilvus*], Wilson's Warbler [*Cardellina pusilla*], Chestnut-backed Chickadee [*Poecile rufescens*], Wrentit [*Chamaea fasciata*]) or both BCRs (Nuttall's Woodpecker, Spotted Towhee [*Pipilo maculatus*]). The 3 remaining species had similar growth rates between Coastal Marin sites and both BCRs (California Scrub-Jay [*Aphelocoma californica*], Common Yellowthroat [*Geothlypis trichas*], Song Sparrow [*Melodia melospiza*]; Figure 2).

When we grouped species together to estimate the overall average difference in growth rates, we excluded

Nuttall's Woodpecker and Olive-sided Flycatcher because detections of these species in the Coastal Marin sites were rare relative to the other species (prevalence <2% of all point count station visits across all years), such that small changes in their abundance resulted in relatively large growth rate estimates. Excluding them ensured these species would not have excessive influence on the estimated average difference across species in each group. For all the remaining species combined, the average difference in growth rates was positive between Coastal Marin sites and each BCR, indicating the Coastal Marin sites had higher growth rates on average than either of the BCRs (Figure 3). For most breakdowns, by habitat association and migratory status groups, we found >90% probability that the Coastal Marin sites had higher growth rates on average than either of the BCRs; this general pattern still held but was slightly lower for riparian associates in CA-5 (88% probability).

## DISCUSSION

Our evaluation of long-term landbird population growth rates provides evidence for a positive benefit of protected areas overall, even though the pattern did not hold for



**FIGURE 2.** Estimated differences in species-specific annual growth rates ( $d_s$ ; Equation 3) between Coastal Marin sites and the California portions of Bird Conservation Region (BCR) 32 (dark gray) and BCR 5 (light gray). Error bars represent the 95% HPDIs for these estimated differences, after accounting for the estimated variance and sample size of each of the individual growth rate estimates. Differences with  $\geq 95\%$  probability of being greater than or less than zero are marked with an asterisk (\*), indicating strong support for a non-zero difference. Positive differences indicate that growth rates were higher at Coastal Marin sites than in the BCR. Species are grouped by habitat association and migratory status. Full species names associated with the codes can be found in Table 1.

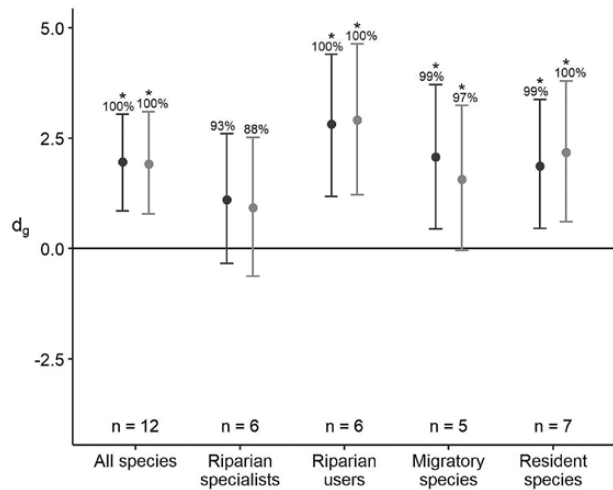
all species. For protected areas in the Coastal Marin region, 9 of the 14 species had local population growth rates that were better than expected from average growth rates throughout one or both CA-32 and CA-5. All of these 9 species had increasing growth rates or stable populations at Coastal Marin sites while the populations in the 2 BCRs were stable or declining (respectively). Therefore, these species were all maintaining or increasing local populations rather than just declining at a lower rate. Although maintaining a stable regional population is generally desirable, the extensive loss and degradation of habitat in California, especially riparian vegetation, has likely already depressed these populations regionally (RHJV 2004). Our finding that some species have increasing growth rates in Coastal Marin protected areas in comparison to regionally stable bird populations, shows the potential for protected areas to not only maintain populations, but also to help them recover from previous losses.

We did not find that the protected areas were effectively safeguarding all of our study species, however, with 3 species showing similar rates as the 2 BCRs and 2 species (Black-headed Grosbeak and Olive-sided Flycatcher) with lower growth rates at Coastal Marin sites than in one or both BCRs. These species provide further evidence that protected areas are not necessarily sufficient conservation measures that can maintain or increase bird populations over other unique factors affecting individual species. We chose to then investigate 2 factors, habitat association and migratory status, to shed light on

the causes for the varied growth rates across our study species.

When grouping the species by habitat association, we found that riparian users (as distinct from riparian specialists) had higher long-term growth rates on average at Coastal Marin sites than in either CA-32 or CA-5 with  $>95\%$  probability of a difference greater than zero. The parks within our study protect habitats besides riparian, and even though our surveys were riparian focused, they included portions of those other habitats in some situations. As a result, our surveys included not only individuals that were primarily or occasionally using riparian habitat, but in some cases, individuals that were only using adjacent habitats. The positive population growth rates we detected for riparian users might indicate not only the effects of conserving riparian vegetation but conserving other habitats within the protected areas as well. Long-term growth rates for riparian specialist species at Coastal Marin sites were also higher on average than in either BCR, but the support was less compelling, with 88–93% probability of a difference greater than zero. However, our prediction for stronger safeguarding effects of riparian specialists than riparian users was not supported overall. However, the positive benefits on 3 riparian specialists (Swainson's Thrush, Warbling Vireo, and Wilson's Warbler) are encouraging given how much riparian vegetation has been lost throughout California, with only 2–15% of its historic extent remaining; the existing riparian vegetation covers a mere 0.5% of the total area of all land-cover





**FIGURE 3.** Group-specific differences in growth rates ( $d_g$ ; Equation 4) between Coastal Marin sites and the California portions of Bird Conservation Region (BCR) 32 (dark gray) and BCR 5 (light gray), by habitat association and migratory status, as well as overall species in the study (excluding Olive-sided Flycatcher and Nuttall's Woodpecker; see text in Results for details). Number of species within each group is listed below each graph. Error bars represent the 95% HPDIs for these average estimated differences, after accounting for the estimated variance and sample size of each of the individual growth rate estimates. Positive differences indicate that growth rates were higher at Coastal Marin sites than in the BCR. Also shown are the probabilities that the difference is greater than zero; those with  $\geq 95\%$  probability of being greater than or less than zero are marked with an asterisk (\*), indicating strong support that growth rates were on average higher at Coastal Marin sites than in the BCR for that group of species.

types in the state but plays an important role in ecosystem functions across landscapes (RHJV 2004).

When grouping the species by migratory status, we found that both migratory and resident species have higher long-term growth rates on average at Coastal Marin sites than in either BCR with  $>95\%$  probability. We had predicted that resident species would see a greater benefit than migratory species, given Neotropical migrants spend only the breeding season in Coastal California and thus the protected status of their breeding grounds is only a portion of what affects their populations; however, our results provide evidence that both groups benefitted. Although conservation efforts in geographies throughout their full life cycle must also be considered (Martin et al. 2007; Marra et al. 2015), our results illustrate the potential contributions of protected areas for conservation of migrant populations. Further study of variation in demographic parameters (e.g., productivity, survival, immigration, and emigration) within and beyond protected areas would help illuminate the causes of differences in population trends and the vulnerabilities of migrants to environmental change across multiple geographies throughout their annual life cycle.

The growth rate differences between Coastal Marin sites and the BCRs for Nuttall's Woodpecker and Olive-sided Flycatcher were particularly large, though they were derived from small sample sizes resulting in low precision. Despite the low precision, we found strong evidence for a difference in growth rates between the Coastal Marin sites and both BCRs for each of these species. Nuttall's Woodpecker was previously rare to absent from the Coastal Marin sites (Shuford 1993) but has since been increasing throughout this region, as shown in this study. The cause for this expansion in range warrants further investigation, and suggests broader factors are likely playing a role in this long-term increasing trend. Olive-sided Flycatcher was included as one of our focal species because of its conservation status (a California Bird Species of Special Concern and on the Partners in Flight Watch List; Shuford and Gardali 2008; Widdowson 2008; Panjabi et al. 2019) and region-wide population declines (Shuford and Gardali 2008), despite the fact that our riparian-focused surveys do not encompass their preferred habitat (Altman and Sallabanks 2020). The greater declines at Coastal Marin sites than in the BCRs may be more a reflection of the regional variability of the widespread declines across its range, rather than the lack of effectiveness of the protected areas, and in contrast, there is evidence of an increasing population in protected upland habitats further inland in Marin County (Cormier et al. 2020).

The California portions of the 2 BCRs span a range of habitat types and land managers covering much of California, which could influence the interpretation of our results. Even though our surveys do include some upland habitat, including adjacent to the sometimes narrow riparian corridors, our study nevertheless focused on riparian vegetation, while the BCRs also include scrub, chaparral, conifer forest, grassland, and agricultural habitats, among others, with riparian habitat making up a small portion of the BCRs. Therefore, our results may speak more to the effectiveness of protected status in riparian and surrounding vegetation than in all of the habitat types contained within the studied protected areas. It is possible that for some species, population growth rates in either BCR may be driven by changes in habitats other than the riparian that was the focus of our study, which could confound our interpretation. All the focal species breed in riparian vegetation in our study sites whether or not their preferred breeding habitat is riparian, so although we were not surveying the core habitat of all the focal species, we believe our data provide a useful and accurate index of the growth rates for all the species evaluated in this study. Additionally, our results may also indicate a positive effect of riparian habitat for the riparian users that nest not only in riparian vegetation but near and outside the riparian in our dry summer climate.

Because the Coastal Marin sites are in the northwestern corner of BCR 32, we considered that the apparent effect of protected areas could instead be reflecting local variation in population trends within the BCR. To address this concern and provide more context to our results, we also included analysis of population trends within BCR 5, located just to the north of the Coastal Marin sites and with similar vegetation and climate. With the comparisons of Coastal Marin sites and both BCRs showing benefits of the protected areas, we have more confidence that our comparisons with BCR 32 do not simply represent a north–south difference in trends. Also of consideration is that the BBS surveys occurred on both protected and unprotected areas throughout the BCRs. With our results showing a generally positive benefit to populations in Coastal Marin, even though the comparison is not strictly between protected and unprotected areas, we suspect that the magnitude of the effect of protection would be greater if unprotected and protected areas were more directly compared.

Point Reyes National Seashore, Golden Gate National Recreation Area, Mount Tamalpais State Park, and Bolinas Lagoon Open Space Preserve all provide a high degree of protection to the flora and fauna within their boundaries in terms of direct human impacts. Most natural resource extraction activities (e.g., logging or mining) or hunting are prohibited in these parks, and they actively manage their lands for sensitive species and ecological function (e.g., minimize disturbance, habitat restoration). The bulk of these areas have been under protection for at least 40 years and most of them border other protected areas, including agricultural easements on private lands. The results of our study suggest that increasing the area of land under similar protections and management, whether through government land acquisition or incentive programs for private landowners, would lead to more positive landbird population trends region wide. However, we strongly suggest that conservation and management actions should not be limited to creating and maintaining protected areas, as actions both within and outside of protected areas, at landscape scales, are needed to sustain populations of all species (Wiens and Gardai 2013). With the continent-wide declines in bird populations (Rosenberg et al. 2019) and the current and future impacts of climate change on ecosystems and birds (Seavy et al. 2018), it is more important than ever to identify and implement effective conservation actions at multiple scales, with deep collaborations, and in consideration of multiple benefits (Gardali et al. 2021).

Without the foresight of the managers of these protected areas and the founders of the BBS and local long-term monitoring efforts, as well as the collaborative partnerships involved, we would not have been able to evaluate the effectiveness of these protected areas for landbirds and to identify long-term patterns in these bird populations. Such

monitoring programs need to be robust and involve a commitment of long duration in order to generate the power to estimate trends with reliable precision. For example, we were unable to estimate trends using data collected from Pinnacles National Park (the other park within the San Francisco Bay Area Network with a long-term riparian bird monitoring program; Humple et al. 2017), where bird surveys have been conducted intermittently since 2001, due at least in part to the limited number of years of surveys, resulting in low precision for estimates of annual growth rates. However, additional years of data collection will enhance our ability to evaluate this park's effectiveness in providing a safeguarding effect for birds; comparing our differential abilities to estimate growth rates precisely to date among these parks demonstrates the value of growing a long-term dataset. Additionally, long-term monitoring efforts within protected areas are often focused on gathering data to inform management decisions to maintain populations of flora or fauna within the area, sometimes only for sensitive species, which as our results show may have lower trend precision estimates due to their sample size than more common species. We recommend that funders and managers of protected areas also monitor common species as well as sensitive species, and that they look for opportunities to collect data that can be compared to regional population data so that they can evaluate the effectiveness of their protected area.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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**Ethics statement:** All surveys were conducted with permission from the land managers through a series of collection permits, cooperative agreements, or written authorizations across the study period. Only passive methods were used; no birds were handled or harassed as part of the component of this study summarized herein.

**Author contributions:** Conceived the idea, design, experiment: M.D.D., K.E.D., D.L.H., and T.G. Collected data: M.D.D., D.L.H., and T.G. Wrote the paper: M.D.D., K.E.D., D.L.H., and T.G. Analyzed data: M.D.D. and K.E.D.

**Data depository:** Analyses reported in this article can be reproduced using the data provided by [Dettling et al. \(2021\)](#).

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