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RESEARCH ARTICLE

Rapid growth of the Swainson's Hawk population in California since 2005

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ABSTRACT

By 1979 Swainson's Hawks (*Buteo swainsoni*) had declined to as low as 375 breeding pairs throughout their summer range in California. Shortly thereafter the species was listed as threatened in the state. To evaluate the hawk's population trend since then, we analyzed data from 1,038 locations surveyed throughout California in either 2005, 2006, 2016, or 2018. We estimated a total statewide population of 18,810 breeding pairs (95% CI: 11,353–37,228) in 2018, and found that alfalfa (*Medicago sativa*, lucerne) cultivation, agricultural crop diversity, and the occurrence of non-agricultural trees for nesting were positively associated with hawk density. We also concluded that California's Swainson's Hawk summering population grew rapidly between 2005 and 2018 at a rate of 13.9% per year (95% CI: 7.8–19.2%). Despite strong evidence that the species has rebounded overall in California, Swainson's Hawks remain largely extirpated from Southern California where they were historically common. Further, we note that the increase in Swainson's Hawks has been coincident with expanded orchard and vineyard cultivation which is not considered suitable for nesting. Therefore, we recommend more frequent, improved surveys to monitor the stability of the species' potential recovery and to better understand the causes. Our results are consistent with increasing raptor populations in North America and Europe that contrast with overall global declines especially in the tropics.

Keywords: agricultural crop diversity, *Buteo swainsoni*, detection probability, model-based inference, monitoring, threatened species

LAY SUMMARY

- Swainson's Hawk (*Buteo swainsoni*) is listed as a "threatened" species in California where its population dropped to as low as 375 breeding pairs in 1979.
- We surveyed for the species throughout its breeding range in California in 2005, 2006, 2016, and 2018.
- We found that the Swainson's Hawk population in California has increased rapidly at an average annual rate of 14% during this time period to over 18,000 pairs in 2018, but the causes for the increase remain unclear.
- Although raptor populations are declining globally, especially in the tropics, our findings are consistent with recent recoveries of raptor populations in North America and Europe.

Rápido crecimiento de la población de *Buteo swainsoni* en California desde 2005

RESUMEN

Para 1979, *Buteo swainsoni* se había reducido a un mínimo de 375 parejas reproductoras en todo su rango de verano en California. Poco tiempo después, la especie fue catalogada como amenazada en el estado. Para evaluar la tendencia poblacional de esta especie desde entonces, analizamos datos de 1038 lugares censados en California en 2005, 2006, 2016 o 2018. Estimamos una población estatal total de 18.810 parejas reproductoras (IC 95%: 11.353–37.228) en 2018, y encontramos que el cultivo de alfalfa (*Medicago sativa*), la diversidad de cultivos agrícolas y la presencia de árboles no forestados para anidar estuvieron positivamente asociados con la densidad de *B. swainsoni*. También concluimos que la población veraniega de California de *B. swainsoni* creció rápidamente entre 2005 y 2018 a una tasa del 13,9% por año (IC 95%: 7,8–19,2%). A pesar de la fuerte evidencia de que la especie se ha recuperado en general en California, *B. swainsoni*

sigue extirpado en gran medida del sur de California, donde históricamente era común. Además, observamos que el aumento de *B. swainsoni* ha coincidido con la ampliación de huertos y viñedos, que no se consideran adecuados para anidar. Por lo tanto, recomendamos censos más frecuentes y mejorados para monitorear la estabilidad de la recuperación potencial de la especie y para comprender mejor las causas. Nuestros resultados son consistentes con el aumento poblacional de las aves rapaces en América del Norte y Europa, que contrastan con las disminuciones globales generales, especialmente en los trópicos.

Palabras clave: Buteo swainsoni, diversidad de cultivos agrícolas, especies amenazadas, inferencia basada en modelos, probabilidad de detección, monitoreo

INTRODUCTION

Globally raptor populations (i.e. Strigiformes, Cathartiformes, Accipitriformes, Falconiformes) are declining at rates faster than other bird taxa and this trend is accentuated in tropical regions (McClure et al. 2018). In contrast, there is evidence that raptor populations have recently rebounded in parts of Europe and North America in part due to recovery efforts such as the banning of dichlorodiphenyltrichloroethane (DDT) and other pesticides, reintroductions, and habitat protection (Deinet et al. 2013; Rosenberg et al. 2019).

Swainson's Hawk (*Buteo swainsoni*) is a long-distance migratory raptor that breeds in temperate North America and winters from Mexico to Argentina (Brown and Amadon 1968; Airola et al. 2019). In California, they nest in valleys, lowlands, and foothills from sea level on the coast to 2,100 m elevation in the Sierra Nevada Mountains (Bloom 1980). On their breeding range the species prefers native grasslands, riparian forests, and diverse agricultural landscapes, avoids orchards and vineyards, and requires non-agricultural trees for nesting (Woodbridge 1991; Battistone et al. 2019). Early accounts and museum records suggest they were widely distributed and abundant in the state before the modern era (Sharp 1902), but declines were observed by the middle of the last century (Grinnell and Miller 1944). Swainson's Hawks were listed as threatened by the State of California in 1983 based on surveys conducted in 1979 which estimated a statewide population of as low as 375 breeding pairs, potentially representing a decline of over 90% with respect to conditions before European settlement (Bloom 1980). Museum records and review of historical accounts suggested a range contraction of similar magnitude (Bloom 1980).

The causes of Swainson's Hawk declines are complex and challenging to disentangle. Besides California, declines have been documented in southern Oregon (Littlefield et al. 1984; Janes 1987), western Nevada (Oakleaf 1975), and prairie and boreal regions of Canada (Kirk and Hyslop 1998). Habitat loss from urban encroachment (e.g., residential, industrial) and certain forms of agriculture were probable causes of the species' decline in some areas of California (Bloom 1980). Recent conservation concern for the species in the state has focused on urban and energy development and orchard and vineyard cultivation which are not considered suitable for nesting (CDFW 2016; Battistone et al. 2019; CDC 2019). Great Basin juniper invasions, thought to result from grazing and fire suppression (Burkhardt and Tisdale 1976), likely reduced nesting and foraging habitat in northeast California (Bloom 1980). Outside of California, agricultural intensification on both summer and winter grounds (e.g., Colorado and Argentina), including removal of nesting and roosting trees and destruction of riparian habitats, was identified as the leading cause of decline (Olendorff and Stoddart 1974; Sarasola and Negro 2006). Acute toxicity from insecticide poisoning killed tens of thousands of Swainson's Hawks in Argentina (Woodbridge et al. 1995; Goldstein et al. 1996). Reduced reproductive success via eggshell thinning due to organochlorine pesticides is a plausible but unproven hypothesis explaining the extirpation of Swainson's Hawks from Southern California where DDT use was widespread during the middle 20th century (Bloom 1980; Risebrough et al. 1989).

In contrast to the historical population decline in parts of western North America, several studies suggest that the Swainson's Hawk population in California may now be rebounding in some places. Gifford et al. (2012) showed an increase in population size for portions of the Central Valley, where most of the Swainson's Hawks occur, during 2003–2009. The Butte Valley population in Northeastern California has increased 4-fold over the past 40 years (Kane et al. 2020).

Robust population monitoring is important to track how populations expand, contract, or remain stable among different regions. Understanding how the ecology of Swainson's Hawk differs across their range is critical to effective conservation strategies. For example, genetic and migratory research indicates that the California population may be distinct from the rest of the breeding population in North America (Hull et al. 2008; Airola et al. 2019). It is also essential that analysis of survey data adequately controls for detectability that may vary by year and confound accurate identification of population trends (Wallace et al. 2016; Johnson et al. 2019). A variety of Swainson's Hawk surveys have occurred throughout California over the past two decades (Briggs et al. 2011; Estep and Dinsdale 2012; Gifford et al. 2012), but they were mostly localized

within specific areas of the state, or they were not focused on population estimation. To remedy the lack of robust, comprehensive population estimates, the California Department of Fish and Wildlife (CDFW) coordinated breeding surveys throughout much of the state during 2005 and 2006 (Battistone et al. 2019) and again in 2016 and 2018. Surveys from these four years included measures of detection probability that allow a robust comparison of abundances across years (Pollock et al. 2002).

Our objectives were to estimate the current size of the Swainson's Hawk population in California and to assess the rate of population growth since 2005. We used a robust analysis of the available CDFW survey data (2005, 2006, 2016, 2018) to evaluate how abundance varied spatially with habitat conditions and after adjusting for annual differences in detection probability. We considered implications for Swainson's Hawk conservation in California and for raptors globally.

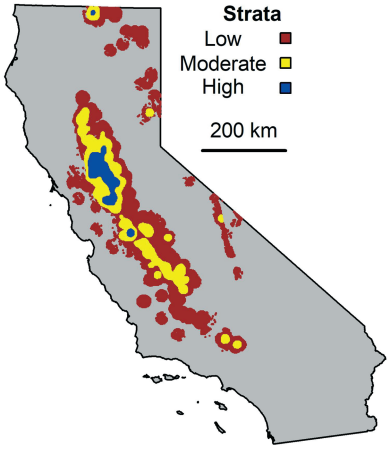

FIGURE 1. Study area representing the extent of Swainson's Hawk summer breeding range throughout California. We used kernel density analysis of past occurrences to delineate the strata shown here which we used to guide stratified sampling of surveys conducted in 2018. The strata were defined as low (<75th percentile kernel density of past occurrences), moderate (75th–95th percentile), and high (>95th percentile).

METHODS

Study area and design

We used data from Swainson's Hawk surveys conducted in 2005, 2006, 2016, and 2018 that were distributed throughout potential breeding habitat within California. The geographical extent of the surveys was based on expert knowledge and occurrence data available at the time. Although intended to provide statewide population estimates, these surveys employed randomized stratified sampling with the objective of allocating greater sampling effort to higher density regions, with the result that the majority (91%) of surveys were concentrated in the Central Valley. Furthermore, the boundaries of the study areas and definitions of sampling strata varied by year. To address these complexities, we applied model-based inference (Gregoire 1998) in our integrated analysis of the survey data such that we extrapolated total population size across the state based on covariate associations from the modeling (Battistone et al. 2019; Furnas 2020).

We used the extent of the 2018 statewide surveys as the final study area for our modeling (Figure 1, 67,153 km^2). We delineated this area by collating a wide set of records of Swainson's Hawk breeding occurrences from California within the past 20 years. The principal data sources included survey detections from 2005, 2006 (Battistone et al. 2019), and 2016, the California Natural Diversity Database (CDFW 2018), the eBird database (Sullivan et al. 2009), and local survey results from the southern portion of the Central Valley (Estep and Dinsdale 2012; E. Tennant, personal communication), Antelope Valley and Tehachapi regions (P. Bloom personal communication), and Butte Valley in Northeast California (Vennum 2017). Observations of adult Swainson's Hawks from these datasets were flagged as possible breeding records only if they occurred between April and August, and if one or more of the following was noted: nest building, courtship, territorial behavior, copulation, mating, roosting, active nest, egg(s), nestling(s) (hatchlings/chicks), fledgling(s). Flagged records were further evaluated individually, based on all information available to confirm or reject the sighting as a breeding record for inclusion in the analysis. To remove potentially duplicative records of breeding territories from the merged dataset, clusters of breeding records located within 100 m of each other were consolidated to a single centroid, thereby creating a unified spatial data layer of breeding locations throughout the state of California from the past 20 years.

We created a coarse-scale species distribution map by first converting the breeding record point layer to a density raster layer using kernel density estimation in a geographical information system (Bailey and Gatrell 1995; bandwidth = 15 km, cell size = 200 m). Next, we divided raster cells into three strata based on the density value percentiles: low (<75th percentile), moderate (75–95th percentile), and high (>95th percentile). We further intersected this raster with 2.59-km^2 (i.e. 1 square mile) sampling quadrats from the U.S. Public Land Survey Sections land-mapping system (USGS 2004); these sections were the sampling units used in all surveys included in our analysis. Although we only used these strata to select survey locations in 2018, we also used them to delineate all of the survey data used in the population modeling. This sampling frame contained 25,932 sections (67.9% low-density stratum, 25.6% moderate-density stratum, 6.5% high-density stratum).

Bird surveys

The surveys from all years followed a generally similar bird survey protocol as described by Battistone et al. (2019). We chose the square Public Land Survey Sections as the survey units in part because they were often well-delineated by roads. In summary, each surveyor visited each of their assigned survey sections 1–3 times during March–July corresponding to the breeding season. They attempted to find all breeding pairs within their assigned sections. To count as a breeding pair, we required that surveyors observed both members of the pair in association with a nest or nesting area, or observed an adult or young in or near a nest. Some sections required multiple visits to search the entire area; in this case, subsequent visits were spaced several days to more than one month apart. Some sections only required one visit because they lacked suitable nest trees, or were already occupied by another species (e.g., a single nest tree in a section occupied by nesting Red-tailed Hawks [*Buteo jamaicensis*]). Surveyors customized the timing of their visits to match the varying phenology of different locations throughout the state. In some instances, initial visits were focused solely on finding old nests before trees fully leafed out. In 2016 and 2018, we replaced some of the initial on-the-ground assessment with office review such that some survey sections were never visited due to lack of suitable nesting trees visible in aerial imagery and assumed not to be suitable for nesting by Swainson's Hawks.

For sections where the species was detected, surveyors documented the total number of breeding pairs observed within each survey section. To count as a breeding pair, we required that surveyors observed both members of the pair in association with a nest or nesting area, observed an adult or young in or near a nest, or observed territorial behavior (e.g., nest defense behavior, copulation/courtship displays). During each visit, the surveyors drove all accessible roads, walked portions of the section, and sometimes used boats to enable scanning of all accessible and visible areas. To facilitate estimation of the detection probability, a subset of the survey sections from 2006, 2016, and 2018 were independently surveyed by a second surveyor who followed the same protocol. We took steps to ensure duplicate surveys were blind to each surveyors' results.

Estimation of population size and trend

Because only a fraction of sections (9.5%) could be independently surveyed by 2 observers due to limited surveyor resources, we chose not to use a hierarchical model to simultaneously estimate abundance while controlling for detectability. Instead, we estimated detection probability separately which we used to adjust our naïve estimate of abundance as follows: True abundance = Naïve abundance/detection probability. We used bootstrapping to ensure that overall uncertainty in our estimate of population size reflected uncertainties in both detectability and spatial variability in abundance.

To estimate detection probability, we used *N*-mixture modeling of the independent survey results from both surveyors (Royle 2004; Battistone et al. 2019). We assumed that the latent abundance state followed a negative binomial distribution. Due to limited sample size of the replicated surveys, we did not include any spatial covariates in these analyses; however, we did model detection differences among years which we treated as a categorical variable. This was necessary because surveys from the earlier era (e.g., 2005–2006) were generally characterized by a higher level of surveyor skill than during 2016–2018. As we were unable to empirically estimate detection probability in 2005, we assumed it to be the same as what we estimated for 2006. We justify this decision in part because most of the surveyors were the same for both years. We fit the model using the *pcount* function in the *unmarked* package (Fiske and Chandler 2011) for the R programming language.

To estimate abundance over all samples (not just duplicated surveys) we fitted generalized linear models (GLM) with a log-link assuming a negative binomial distribution for the response variable (observed count of breeding pairs per section). To evaluate interannual changes in abundance, we included survey year as a categorical variable with 2005 set as the baseline. We also analyzed spatial covariates that might explain spatial variation in density, including most of the covariates from earlier analysis of the 2005–2006 data (Battistone et al. 2019). Previous research has indicated that agricultural crop diversity (Babcock 1995, Estep and Dinsdale 2012), alfalfa (*Medicago sativa*, lucerne) cultivation (Smallwood 1995; Swolgaard et al. 2008; Cahill 2014), and remnant areas of natural habitats (Smallwood 1995; Estep and Dinsdale 2012) are positively associated with Swainson's Hawk abundance, and that orchards and vineyards are negatively associated (Swolgaard et al. 2008; Cahill 2014). We also included the density strata described earlier. Lastly, we included the occurrence of potential nests trees which is a limiting factor for breeding (Woodbridge 1991).

We used the CropScape database to sum the total number of agricultural crop types in each section during each survey year (Han et al. 2012). As these data were unavailable before 2007, and to de-emphasize the short-term effects of year-to-year variation in agricultural practices, we averaged section-level crop counts from 2007 and 2008 to represent conditions in 2005–2006. Similarly, we averaged crop data from 2016 and 2018 to represent conditions for both those years. We used the same approach to calculate the proportions of alfalfa, orchards/vineyards, and the total area of natural habitats (e.g., grasslands, shrublands, riparian forests, wetlands) in each section. We used the 2015 FVEG layer of land use land cover to identify whether sections did or did not contain any non-agricultural, tree-dominated 30-m pixels (CAL FIRE 2015). We considered

this metric a proxy for the occurrence of a potential nest tree. We normalized all spatial covariates except the categorical sampling strata and nest tree covariate. Sampling strata were modeled as two indicator variables for moderate and high presumed density assuming low density as the baseline.

We adopted an information-theoretic approach to model selection and inference using the small sample size correction for AIC (AIC_c, Burnham and Anderson 2002). To limit model combinations to a tractable quantity, we first evaluated univariate models including the seven abundance covariate groups (e.g., year, crop diversity, alfalfa, orchards/vineyards, native vegetation, nest tree, sampling strata), and also evaluated several potential interactions (e.g., crop diversity*year, crop diversity*native vegetation, nest tree*year). We evaluated base models with respect to the null model of constant abundance unaffected by covariates. For all covariates and interactions with >90% model weight compared to the null model, we fit all combinations of models that included those remaining covariates. We used model selection criteria to either identify a top model or average across the set of top competing models (Burnham and Anderson 2002).

We used the model results to extrapolate predicted abundances over the entire study area (Gregoire 1998; Battistone et al. 2019). We obtained an estimate of population size by year by summing all the predicted section-level abundances from the entire study area. We calculated a 95% confidence interval (CI) for our final estimate of population size by means of parametric bootstrapping that combined uncertainties about the abundance and detection probability components of the modeling (50,000 resamples; Efron 1982; Battistone et al. 2019). In each resampling iteration, we estimated the true population size for each year by dividing a bootstrapped naïve estimate from the abundance modeling by a bootstrapped estimate of detection probability for that year.

As we fitted our abundance models using a categorical variable on survey year, we could not directly calculate the annual rate of population growth. We note that, similar to economic models, ecological population models typically assume either exponential or logistic growth (Sinclair et al. 2006). Further, the log link used in our abundance modeling implicitly assumed an exponential rate of change in the response variable of counts with respect to covariates. Therefore, we fitted log normal models within the bootstrapping procedure of annual total populations sizes to additionally estimate the rate of exponential growth and its uncertainty. This allowed us to estimate the average annual rate of growth and its 95% confidence interval. We provide all data used in modeling, the R code showing detailed specification of the models, and full model results as an online supplement (see Supplementary Material Data S1 and Furnas et al. 2022).

Validation of population estimates

We evaluated model fit by means of a parametric bootstrap goodness-of-fit test using the chi-squared test statistic (Kery and Royle 2016, Section 7.5.4). For each test, the null hypothesis was that the chi-squared statistic for observed survey detection data under the fitted model was equal to chi-squared for data generated by the model. We estimated the probability (*P*-value) of the observed statistic under the null hypothesis by comparing it to the distribution of the statistic for 1,000 parametric bootstrap datasets. We assumed good model fit if we could not reject this null hypothesis for a one-sided test (i.e. P-value ≥ 0.05). We evaluated goodness-of-fit separately for our detection probability model and our top abundance GLM.

To further assess performance of the model-based population estimates we used classic, stratified sampling equations to alternatively estimate population sizes (Cochran 1977). We divided these design-based estimates by our model-based estimate of detection probability, and used the delta method to represent overall uncertainty from sampling design and detection probability sources (Link and Nichols 1994). To evaluate how well the model-based approach extrapolated density throughout the study area, we computed the proportion of the total California population found in the Central Valley and Butte Valley (i.e. Northeastern California) regions vs. other parts of the state.

RESULTS

Bird surveys

We surveyed a total of 1,038 sections including 235 (23%) in the low-density stratum, 530 (51%) in the moderate-density stratum, and 273 (26%) in the high-density stratum. We detected a total of 268 breeding pairs including 22 (8%) in the low-density stratum, 121 (45%) in the moderate-density stratum, and 125 (47%) in the high-density stratum (Table 1). Only one of those detections (e.g., Owens Valley in 2018) was greater than 30 km outside of the Central Valley or outside of the Butte Valley in Northeastern California (Figure 2).

Population and trend estimates

We estimated detection probabilities of 0.70 (standard error [SE] = 0.20) per territory if occupied in 2006, 0.42 (SE = 0.11) in 2016, and 0.36 (SE = 0.09) in 2018. During initial model selection we found evidence of abundance associations with the following covariates: year, crop diversity, alfalfa, nest tree, sampling strata, the year-crop diversity interaction, and the crop diversity-native vegetation interaction. Upon full model selection, a single model containing the year-crop diversity interaction and the alfalfa, nest tree, and sampling stratum covariates comprised >90% of all model weights. Consequently, we adopted this

TABLE 1. Summary statistics of California-wide surveys for Swainson's Hawks.

Year	Survey effort and summary results	Sampling stratum[a]			
		Low	Moderate	High	Total
2005	Survey sections	90	147	89	326
	Sections with detections	1	35	41	77
	Total count of breeding pairs	1	46	58	105
	Average count/section	0.01	0.31	0.65	0.32
2006	Survey sections	85	217	115	417
	Sections with detections	14	33	51	98
	Total count of breeding pairs	16	38	71	125
	Average count/section	0.19	0.18	0.62	0.30
2016	Survey sections	16	71	46	133
	Sections with detections	2	25	22	49
	Total count of breeding pairs	3	40	40	83
	Average count/section	0.19	0.56	0.87	0.62
2018	Survey sections	44	95	23	162
	Sections with detections	5	28	11	44
	Total count of breeding pairs	6	39	18	63
	Average count/section	0.14	0.41	0.78	0.40

[a] Survey effort was stratified by a priori determinations of presumed density. We used the 2018 strata here and in our integrated analysis of data from all years (see Figure 1).

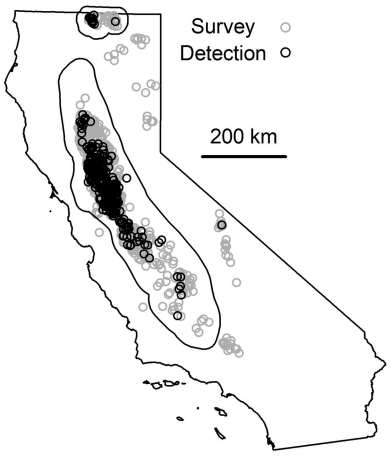

FIGURE 2. Visual representation of results from California-wide surveys of Swainson's Hawk conducted during 2005, 2006, 2016, and 2018. All but one of detections were within 30 km of the Central Valley (larger polygon) or within the Butte Valley (smaller polygon).

single model as our final model for use in population estimation. (Table 2).

We estimated that there were 18,810 (95% CI: 11,353–37,228) breeding pairs of Swainson's Hawks throughout California in 2018. The distribution was 22% in the high-density stratum, 39% in the moderate-density stratum, and 39% in the low-density stratum (Figure 3). The statistical distribution of densities was right-skewed (e.g., estimated density <15 pairs per 100 km^2 for 30% of the study area vs. >50 pairs per 100 km^2 for 13% of area or >100 pairs per 100 km^2 for 3% of area, Figure 4). We estimated an average annual exponential population growth of 13.9% (95% CI: 7.8–19.2%) during 2005–2018 (Figure 5).

Validation

We confirmed good model fit for the *N*-mixture model (P = 0.49) and our top GLM (P = 0.30). Additionally, our design-based population estimates for 2018 closely matched those based on covariate modeling (Figure 6). For the model-based estimates we found that 85.7% of the population was predicted within 30 km of the Central Valley, 3.7% was predicted within the Butte Valley, and the remaining 10.6% was predicted to occur elsewhere in California.

DISCUSSION

We found strong evidence of rapid population growth of Swainson's Hawks in California between 2005 and 2018. Our results (e.g., 95% CI: 8–19% per year) are comparable to rapid growth rates documented for Osprey (*Pandion haliaetus*) in Chesapeake Bay (8.1%, 95% CI: 4.1–12.2, 1973–1995, Watts and Paxton 2007) and for Bald Eagle (*Haliaeetus leucocephalus*) in Chesapeake Bay (9.6%, 95% CI: 8.9–10.3, 1977–2001, Watts et al. 2008) and in Central California (14.2%, 95% CI: 12.5–15.9, 1993–2012, Sorenson et al. 2017) after the banning of DDT. Our estimated growth rate, however, was larger than an independent estimation of the rate of annual increase (6.6%, 95% CI: 4.9–8.4) from the Northern American Breeding Bird Survey (BBS) in California for the same timespan (https://www.mbr-pwrc.usgs.gov/bbs/trend/tf19.shtml, Link and Sauer 2002). Comparison of the BBS results among regions shows that the population growth in California has been much faster than throughout the species entire breeding range in North America (1.2% per year, 95% CI: 0.9–1.5). This difference is consistent with recovery from a historical

TABLE 2. Final model of covariates explaining variation in Swainson's Hawk abundance throughout California during 2005–2018. We fit a negative binomial model on counts of observed breeding pairs. Total estimates of abundances were subsequently computed after correcting for detection probabilities that varied by year.

Covariate	Parameter estimate	Standard error
Intercept	−2.565	0.246
Moderate stratum[a]	0.737	0.220
High stratum[a]	1.271	0.224
Year 2006[b]	−0.317	0.234
Year 2016[b]	0.625	0.278
Year 2018[b]	0.664	0.243
Crop diversity[c]	0.778	0.197
Year 2006*crop diversity[d]	0.239	0.285
Year 2016*crop diversity[d]	−0.348	0.253
Year 20018*crop diversity[d]	−0.574	0.239
Alfalfa[c]	0.184	0.039
Nest tree[e]	0.253	0.057
Dispersion[f]	3.67	1.66

[a] Categorical variable assuming the low sampling stratum parameterized as baseline.
[b] Categorical variable assuming 2005 as baseline.
[c] Standardized covariates.
[d] Model interaction terms.
[e] Dichotomous variable indicates occurrence of any potential nest trees.
[f] Measure of dispersion in a negative binomial model of counts. Values > 1 represent over-dispersion in comparison to a Poisson distribution.

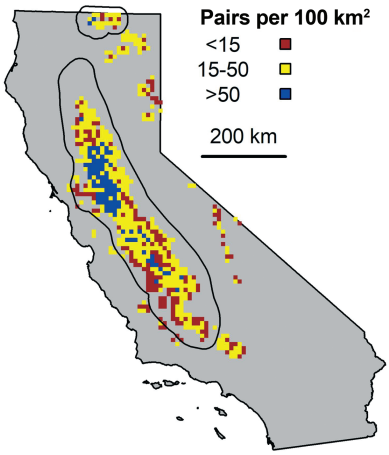

FIGURE 3. Spatial variation in predicted Swainson's Hawk breeding pair density throughout California based on modeling of survey data collected in 2005, 2006, 2016, and 2018. We predicted that 89% of the population in 2018 occurred within 30 km of the Central Valley (larger polygon) or within the Butte Valley (smaller polygon).

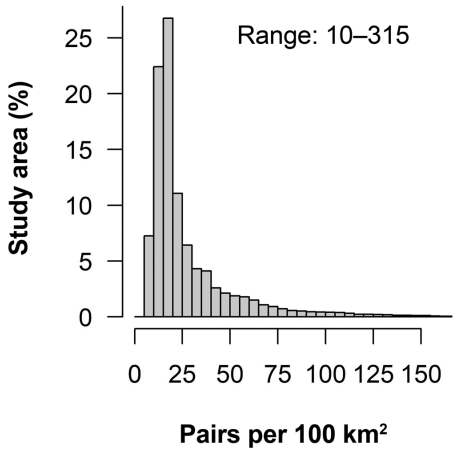

FIGURE 4. Model-predicted Swainson's Hawk densities throughout the California breeding range study area in 2018.

decline that was more severe in California than elsewhere (White 1994; Sarasola et al. 2008).

In 1979, when the California population was as low as 375 pairs, Bloom (1980) also estimated the historical population in California before European settlement and the effects of 20th century agricultural intensification and urbanization. Based on measurements of density in remnant high-quality habitats, and extrapolation of the past extent of habitat throughout California, he estimated a historical baseline of 4,284–17,136 breeding pairs. Our current population estimate from 2018 of 18,810 (95% CI: 11,353–37,228) is within the range of that historical baseline. This comparison provides some limited evidence that the Swainson's Hawk population in California may have regained a historical level, but we caution that Bloom's analysis was not statistically quantitative and the true historical population could have been much higher. Despite the apparent, rapid recent increase in density, one third of the species range in California in our analysis was characterized by densities <15 pairs per 100 km² in 2018 (Figure 4). We also caution that our model-based mapping of density throughout the state likely overestimated in some

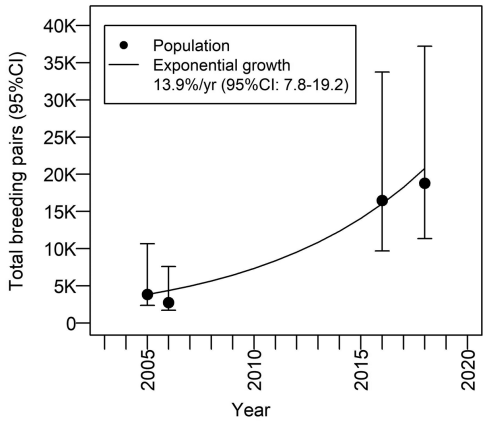

FIGURE 5. Modeling of survey results suggests rapid growth of the Swainson's Hawk population in California between 2005 and 2018. Confidence intervals on annual population estimates were computed via bootstrapping such that they reflect total uncertainty from both detection probability and spatial covariate modeling.

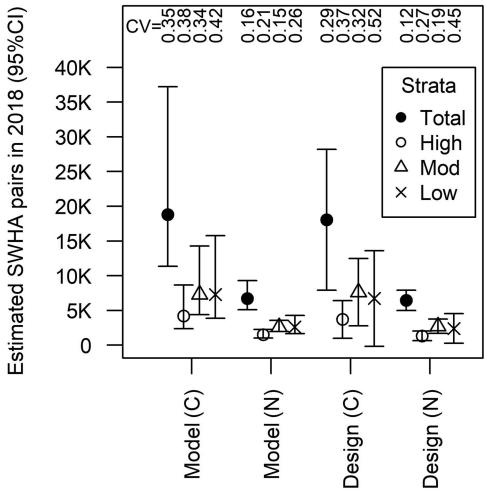

FIGURE 6. Congruence of model- and design-based estimates of Swainson's Hawk breeding population size in California during 2018. The model and design-based estimates are provided after (C) and before (N-naïve) correcting for detection probabilities. We also include coefficients of variation (CV) for estimates.

places (e.g., 13% of area was predicted to support >50 pairs per 100 km^2 to as high as 315 pairs per 100 km^2). In contrast, the highest densities reported by others in California have been <40 pairs per 100 km^2 (Bechard et al. 2020). We note that we expect that this artifact of our modeling extrapolation method did not likely bias our estimate of total statewide population size which was comparable to our design-based estimate.

It is not certain why Swainson's Hawks have rebounded in California and whether the species will increase further. Progress with riparian restoration efforts in the Central Valley may be one reason, as these riparian restorations have been associated with increased populations of other avian species (Dybala et al. 2018; Pandolfino and Handel 2018). Our finding that abundance was correlated with agricultural crop diversity and alfalfa cultivation may indicate that Swainson's Hawks have successfully adjusted to the use of managed landscapes which might have an artificially elevated carrying capacity. The diversity and spatiotemporal patterning of California agriculture may provide Swainson's Hawk greater access to rodent prey in areas of lower vegetation cover (Bechard 1982). Irrigated alfalfa fields are an important foraging resource to Swainson's Hawks, because this crop supports high small mammal and insect abundances which become easy prey during periodic harvests (Smallwood 1995). Although the total area of alfalfa cultivation in California has remained relatively constant since 1980, crop yields have increased over the same time period in response to the growing needs of the state's dairy industry (Putnam et al. 2007).

Winter range conditions may be equally important to the conservation and sustained recovery of Swainson's Hawks in California. The population summering in California that uses the Central Valley is genetically distinct from hawks summering throughout other parts of North America (Hull et al. 2008). This may partially be the result of different migratory pathways (Airola et al. 2019). The California population appears to display a lot of variation in where it winters (Sarasola et al. 2008), including more northerly locations in Western Mexico and Central America where they may have benefited from conversion of less suitable natural areas (e.g., woodland and desert) to agriculture that provides improved habitat conditions (Airola et al. 2019). A shorter migratory pathway may also afford demographic advantages including increased survival during transit and a longer, more-flexible reproductive phenology (Heath et al. 2012; Klaassen et al. 2014).

We found no evidence of rapid recolonization of coastal Southern California. Our scoping analysis to delineate a statewide study area identified no areas of potentially active breeding range in the region. Since 2018 we are aware of only one breeding pair at Seal Beach in Orange County (P. H. Bloom, personal communication). Nevertheless, the South Coast region likely supported a large Swainson's Hawk population prior to European settlement (Willett 1912; Chambers 1936). Even though much of Southern California is now heavily urbanized, we note that large areas of potentially suitable breeding and foraging habitat remain (e.g., 500 km^2 at Camp Pendleton military base between Los Angeles and San Diego). The last known nesting attempt by Swainson's Hawks in San Diego County (then Rancho Santa Margarita) was in 1933 from an egg set collected on what is today Camp Pendleton (WFVZ 2020).

Despite an overall increasing summer range population of the Swainson's Hawks in California, we recommend

caution with respect to conservation planning for the species in the state. The stability of the recovery remains unclear. For example, increasing population trends of the species in other areas of North America have switched direction over time in some places (Kirk and Hyslop 1998; Hoffman and Smith 2003). In California, orchard cultivation has expanded by >100% since 2000 (Chen et al. 2019), and these tree crops are low-quality foraging and nesting habitat for breeding Swainson's Hawks (Swolgaard et al. 2008; Battistone et al. 2019). It is unclear why hawk populations have increased so dramatically in the Central Valley where most of the orchard expansion has also occurred. We also remain concerned about urban and energy development, diminishing grasslands, pesticide poisoning, water availability, and climate change (CDFW 2016). For example, as climate changes, farmers may shift crops which could alter habitat conditions for hawks. Additionally, recent solar energy and nut orchard installations in the Antelope Valley of the west Mojave Desert may limit further potential expansion of Southern California breeding territories via removal of nest trees and foraging habitat. For these reasons, we recommend expanded, more frequent monitoring (e.g., every 5 years) of Swainson's Hawks throughout California.

We note that the precision of our estimates of detection probability was low, and we were unable to include spatial covariates to address expected heterogeneity in detection probability. Unfortunately, we could find only a few published examples of detection probability for quadrat surveys of raptors. Johnson et al. (2019) reported a range (0.44–0.79) of detection probabilities for 7-km^2-quadrat nest searches of Ferruginous hawks (*Buteo regalis*) that is comparable to our estimates, but the searches they reported used aircraft whereas ours were ground-based. Królikowska et al. (2018) reported an estimated detection probability of 0.55 (95% CI: 0.44–0.66) for ground-based searches of breeding Montagu's Harriers (*Circus pygargus*) within 100-km^2 quadrats. We attribute the high coefficient of variation (CV = 0.35) of our 2018 population estimate to our limited ability to model heterogeneity in detection probability (i.e. CV = 0.16 before including detection probability; Figure 6). Therefore, future surveys must allocate more effort to survey replication necessary to estimate detectability of quadrat searches (Pollock et al. 2002; Kery and Royle 2016). The problem of imperfect detectability could be further mitigated by recruiting more expert surveyors and devoting more resources to training novice surveyors.

Recent Swainson's Hawk survey efforts in California have prioritized stratified sampling to maximize sampling efficiency (Gifford et al. 2012; Battistone et al. 2019). Although this approach may work well for optimizing sampling efficiency for a classic design-based estimate (Cochran 1977), our model-based analysis was limited by the availability of survey data outside of the Central Valley. For example, a mere 5% of our surveys occurred >30 km beyond the Central Valley or within the Butte Valley, and we only detected one breeding pair in those other areas of the state which summed to 19% of the study area. In spite of this sampling limitation, we note that our modeling predicted that 10.6% of the total state population occurred in these outlying areas due to similar habitats conditions identified as predictive from regression. Therefore, it is possible (but not certain) that although our design- and model-based statewide population estimates were concordant with each other, they both may have overestimated by as much as 10% i.e. (assuming few or no hawks outside of the Central Valley and Butte Valley). A caveat on this caution is that the magnitude of the potential bias is appreciably smaller than the width of the confidence interval of the population estimate. For these reasons, we recommend that future monitoring include greater sampling effort in lower density regions outside of the Central Valley for facilitating improved model-based analyses and greater inference about range expansion. An integration of the data from our surveys with various sources of citizen science surveys (e.g., BBS, eBird, iNaturalist) could further strengthen inferences for identifying spatial patterns and temporal trends. (Pacifici et al. 2017).

Our results are relevant to global conservation of raptors. First, there is great need for improved monitoring of raptor populations, especially in the tropics where data collection has been sparse (Buechley et al. 2019). Our observations about sampling design and analytical methods are likely applicable to raptor monitoring efforts outside of California. Second, raptor populations are declining worldwide (McClure et al. 2018; Cruz et al. 2021). Although there may be reasons (Cruz et al. 2021) partially explaining why these declines have been more severe in the tropics, there is also increasing evidence that species in North America and Europe have rebounded in response to conservation actions including habitat restoration and the banning of DDT (Deinet et al. 2013; Rosenberg et al. 2019). This suggests that conservation efforts in other regions of the world have a similar potential to reverse the global decline of raptors.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: We used non-invasive, visual search surveys.

Author contributions: B.J.F., C.L.B., and D.H.W. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). C.L.B., D.H.W., E.N.T., R.M.O., M.J.K., and P.H.B. performed the experiments (collected data, conducted the research). B.J.F., D.H.W., E.N.T., R.M.O., M.J.K., P.H.B., and C.L.B. wrote the paper (or substantially edited the paper). B.J.F., D.H.W., E.N.T., R.M.O., M.J.K., P.H.B., and C.L.B. developed or designed methods. B.J.F. and M.J.K. analyzed the data.

Data deposits: Analyses reported in this article can be reproduced using the data provided by Furnas et al. (2022). A readme file is provided in the Supplementary Material that explains how to run the code.

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