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RESEARCH

Status and Trends of Breeding Ardeidae in the San Francisco Bay Region

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ABSTRACT

Monitoring species abundance is a critical tool for identifying trends in wildlife populations. Using data collected in the San Francisco Bay Area between 1995 and 2019, we evaluated trends in nesting abundance of four Ardeid species across the entire study area and in 10 sub-regions, while accounting for the effect of rainfall. Overall, Great Egret (*Ardea alba*) nest abundance increased by 27% (95% confidence interval -1%, 54%) from 783 to 993 nests. Great Blue Heron (*Ardea herodias*) and Snowy Egret (*Egretta thula*) nesting abundance was similar across the study period, averaging approximately 503 and 509 nests, respectively, but Snowy Egret abundance was highly variable between years. Finally, Black-crowned Night-Heron (*Nycticorax nycticorax*) abundance declined -22% (95% confidence interval -59%, 15%) from 682 to 535 nests. At the sub-regional scale, trends were variable within species, and no species had consistent positive or negative trends

across all 10 sub-regions, although it appears the distribution of all species except Great Blue Heron shifted among sub-regions. Our results suggest conservation action may be warranted to recover the Black-crowned Night Heron population in our study area, but there is uncertainty on the magnitude of their decline and the reasons for it. Further investigation of the mechanisms for demographic change is needed to guide effective actions. In the absence of that information, protection of the few colony sites occupied by Black-crowned Night Herons and Snowy Egrets—especially islands in San Francisco Bay and two large urban colonies in Santa Rosa and Fairfield—is a prudent immediate action.

KEY WORDS

Abundance trend, *Ardea alba*, *Ardea herodias*, Black-crowned Night-Heron, *Egretta thula*, Great Blue Heron, Great Egret, *Nycticorax nycticorax*, Snowy Egret

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INTRODUCTION

The Ardeidae (herons and egrets) are a highly visible and recognizable feature of the North American breeding bird landscape because of their large size, mobility, propensity to breed colonially, and their cosmopolitan distribution, ranging from wilderness areas to densely

populated urban centers (Kushlan and Hafner 2000; Kushlan 2018). This is also a family of birds that has faced significant conservation challenges. In the United States, in the late 1800s, fashion trends drove the excessive killing of herons and egrets and led to some of the country's strongest laws protecting wild birds, resulting in the recovery of many Ardeidae populations (Merchant 2010; Kushlan 2018). However, despite strong legislative protection, in the past 5 decades (1970–2017) 58% of the 12 Ardeidae species that breed in North America have declined, and the total population size of breeding Ardeidae has decreased by 28% (Rosenberg et al. 2019).

To determine heron and egret populations of conservation interest requires monitoring programs done at various spatial scales (Kushlan 2000). Currently, there is no North America-wide monitoring effort dedicated to the Ardeidae; trend estimates for ardeids come mainly from several continent-wide monitoring programs aimed at all bird taxa, including Breeding Bird Surveys (BBSs) and Christmas Bird Counts (CBCs; Kushlan 2012). In California, the California Department of Fish and Game (now called Department of Fish and Wildlife) intermittently surveyed heron and egret rookeries throughout the state from 1969 to 1982 (Schlorff 1982). In general, long-term monitoring of Ardeidae populations to determine trends remains rare, particularly in the West (Shuford et al. 2020).

A West Coast exception began in 1967, with Helen Pratt's pioneering monitoring work on breeding Ardeidae at Bolinas Lagoon in Marin County, California (Pratt 1970, 1983; Pratt and Winkler 1985). This effort was later expanded to include monitoring breeding colonies of Great Egret (*Ardea alba*), Great Blue Heron (*A. herodias*), Snowy Egret (*Egretta thula*), and Black-crowned Night Heron (*Nycticorax nycticorax*) across the San Francisco Bay Area (Kelly et al. 1993, 2007). The most recent summarized trend results from this work, from 1991 to 2005, found the regional nest abundances of all four species to be stable or increasing (Kelly et al. 2007). In contrast, ardeid population trends measured during winter from 1972 to 2015 at Bolinas Lagoon—a key waterbird

site in the San Francisco Bay Area—were more varied (Stenzel and Page 2018). Black-crowned Night Herons significantly decreased during this period, while Great Egret increased. However, for Snowy Egrets, overall positive trends during the first part of that study reversed around 1997, while negative trends for Great Blue Herons also switched direction around 1997, so that for both species there were about the same number of birds in 2015 as in 1972.

In the San Francisco Bay Area, nesting abundance of herons and egrets is related to rainfall in the current year and up to 2 years prior (Kelly and Condeso 2014). Depending on the lag considered, species generally show either a quadratic response to rainfall, with highest abundance in years of intermediate total rain or rainfall volatility, or a negative relationship, with highest abundance in years of lower rain or rainfall volatility (Kelly and Condeso 2014). Elsewhere in the world, some studies have shown wading bird nesting abundance and productivity to be positively related to rainfall (Bildstein et al. 1990; Maddock and Baxter 1991), while others have shown little relationship between rainfall and nesting abundance, particularly where birds have access to human-managed and estuarine foraging areas (e.g., Tourenq et al. 2000). Previous analysis of part of the dataset considered here has shown that ardeid population trends in the San Francisco Bay region vary by watershed or sub-region (Kelly et al. 2007), and that declines of ardeid nest abundances on a sub-regional level can result from the loss of a single large colony site (Kelly et al. 2018).

Here, we expand on the temporal results of monitoring heron and egret breeding colonies in the San Francisco Bay area, providing an updated synthesis of monitoring data from 1995 to 2019 for this region. Our goals were to (1) estimate annual abundance over this time for Great Egret, Great Blue Heron, Snowy Egret, and Black-crowned Night-Heron, while accounting for the effect of rainfall on annual abundance; (2) describe trends in abundance across the entire study area and in ten distinct sub-regions; and (3) identify any

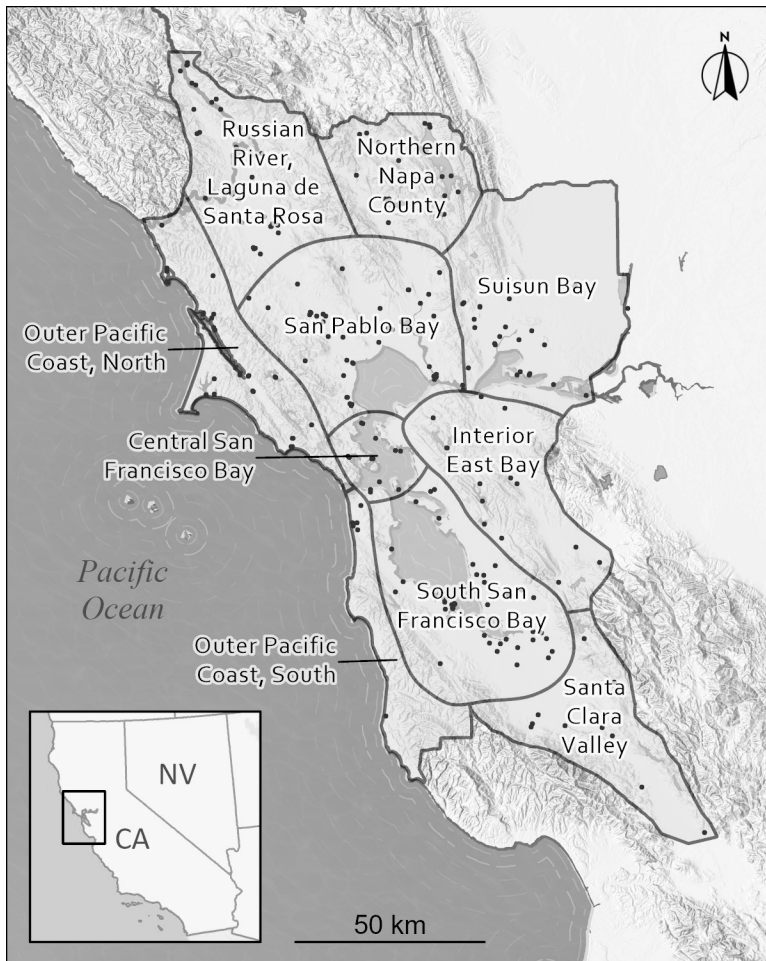


Figure 1 Study area where heron and egret colonies were monitored 1995–2019. Shown are sub-region names and boundaries, and colony locations are indicated by dots (not all locations were occupied every year).

strong negative trends in nesting abundance that may warrant conservation effort.

METHODS

Study Area

Known ardeid nesting colonies were monitored in the central coastal region of California around the San Francisco Bay Estuary (Figure 1), covering an area of approximately 13,705 km². The study area was divided into ten sub-regions based on major wetland areas (Kelly et al. 1993, 2007; Figure 1). Although Cattle Egret (*Bubulcus ibis*) and Little Blue Heron (*Egretta caerulea*) are monitored by our study, these species only nest occasionally, in small numbers, or in few colonies, and were thus excluded from this analysis. Green Heron (*Butorides virescens*), American Bittern (*Botaurus lentiginosus*), and Least Bittern (*Ixobrychus*

exilis), are generally solitary nesters that are not monitored by our program.

Surveys

From 1995 to 2019, between March and June, staff and trained volunteers of Audubon Canyon Ranch and the San Francisco Bay Bird Observatory monitored colonies. Although monitoring throughout the study area began in 1989 and data for 1991–1994 were included in the last trend analysis (Kelly et al. 2007), we excluded these first 4 years of data because several new colonies were discovered as a result of increasing surveillance and search effort during those years, and inclusion of those data added a positive bias to our trend estimates. Each year, most colonies were visited every 2 to 4 weeks from the first weekend in March through June, or until chicks were old enough to estimate pre-fledging brood size.

Some nesting sites, particularly those with Black-crowned Night-Herons or Snowy Egrets, were visited weekly. Sites that were only accessible by boat or where other logistical constraints permitted one visit per year were visited in May, which generally corresponds to peak colony attendance (Kelly et al. 2007). Colonies were monitored with binoculars and scopes from the ground or by boat from 50 to 200 m. To reduce human disturbance, colonies were rarely entered, but occasionally entrance was required to obtain accurate counts. On each visit, the number of active nests in each colony was counted [see Kelly et al. (2007) for a full description of our study area and field methods].

We did not conduct a systematic search of the study area each year to discover unknown colonies, and our data may not represent the true total number of nesting herons and egrets. However, because of the long duration of our study, our wide network of volunteers, and the relatively high density of bird watchers in our study area, we believe most new or unknown colonies were generally identified within a few years of becoming established (Kelly et al. 2007). Colonies missed for a few years may still depress our estimates, but because data were aggregated up to the sub-region scale, missed colonies were unlikely to substantially affect the overall shape of our long-term trend estimates.

Data Preparation and Analyses

For each colony, we took the highest number of active nests observed across all visits each year as the nesting abundance for that species in that year. We then summed these colony abundances for all colonies in each sub-region to calculate a total number of observed nests in each sub-region each year. We used the same sub-region boundaries as prior analyses of these data (Kelly et al. 1993, 2007, 2018) so that our results could be compared to prior studies. We also summed all nests for the entire study area to evaluate trends at that spatial scale.

Annual rainfall has gradually declined across most of the study area since 1995, although annual rainfall is highly variable, and the study

area experienced prolonged droughts (Figure 2). The relationships between rainfall and nesting abundance were previously investigated using part of this dataset (Kelly and Condeso 2014). Thus, our objectives here were to account for any potential effect of rainfall while estimating annual nesting abundance for each species. We extracted the monthly total rainfall for the 4-km PRISM (PRISM Climate Group) cells where each colony was located. Because nesting in our study area has generally concluded by July, we assumed that rainfall from July the prior year through June in the current year would best represent the effect of annual rainfall on current year nesting abundance. We then calculated annual rainfall for each sub-region as the average of July-June rain for all colonies in that sub-region. Informed by prior analysis of part of this dataset (Kelly and Condeso 2014) and other studies (Bildstein et al. 1990; Stenzel and Page 2018), we wanted to include rainfall in the current year and up to 2 years prior to account for possible effects of multi-year drought. Stenzel and Page (2018) found support for a diminishing effect of prior years' rainfall on heron and egret abundance, but Kelly and Condeso (2014) did not consider a diminishing effect of prior years' rain. Although the analysis of Kelly and Condeso (2014) is more similar to ours because they also investigated nesting abundance (rather than winter abundance), we nevertheless agree with the reasoning of Stenzel and Page (2018) that the effects of prior years' rainfall are likely less strong than the effects of current year rainfall. Thus, we calculated a cumulative, weighted rainfall index comprising the current and 2 prior years as:

$$R_s = r_{s,t} + (r_{s,t-1}/2) + (r_{s,t-2}/3) \quad \text{Eq 1}$$

where R_s is the rainfall index for sub-region s , $r_{s,t}$ is the rainfall in sub-region s in the current year, $r_{s,t-1}$ is rainfall the prior year, and $r_{s,t-2}$ is rainfall 2 years prior.

We only estimated abundance trends where a species was observed nesting in a sub-region for > 5 years, although all observed nests were included in the estimate of abundance for the entire study area. We used generalized

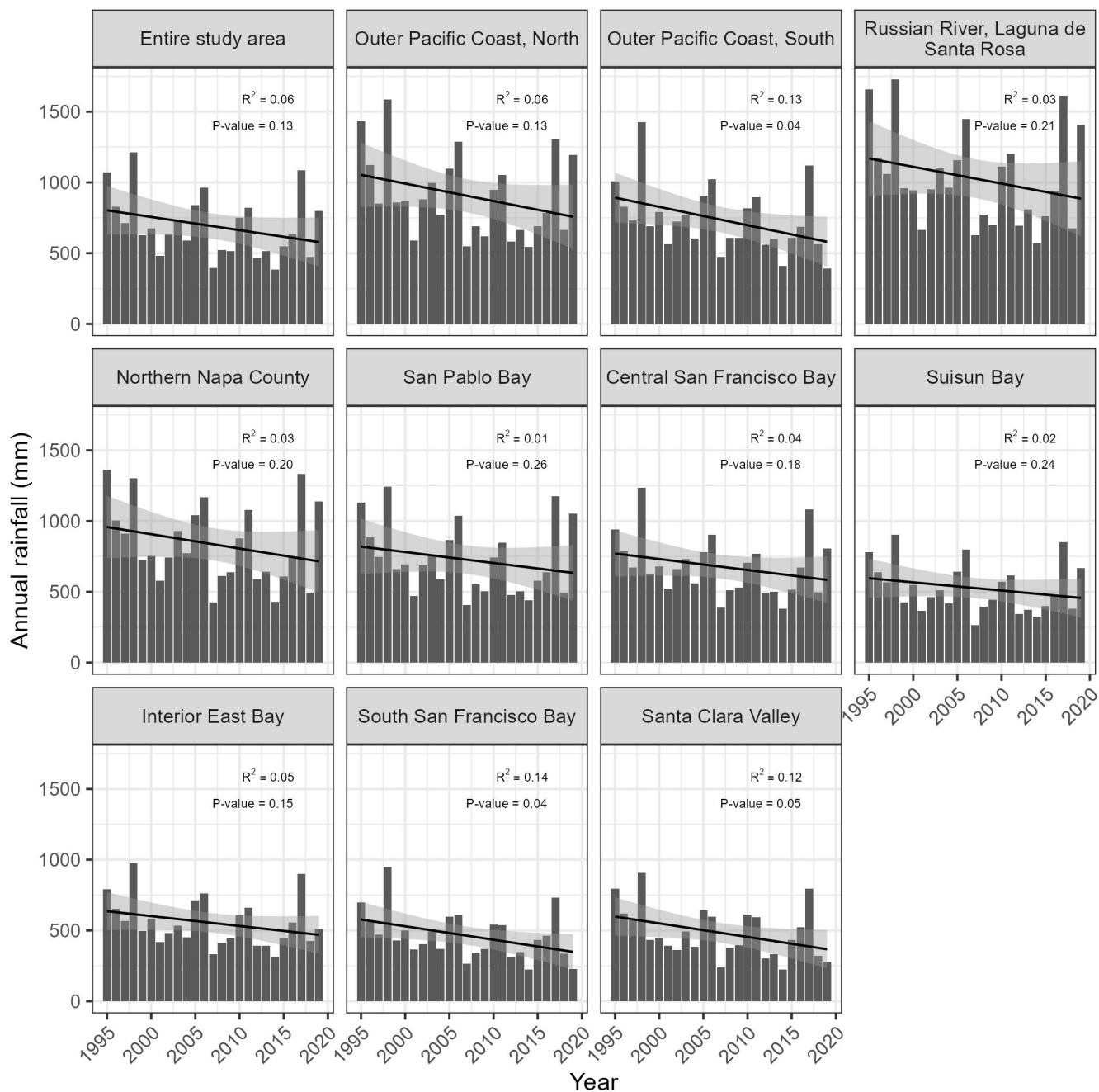


Figure 2 Cumulative rainfall from July of the previous year to June of the current year by sub-region in the San Francisco Bay Area, 1995–2019. The *black line* represents the fit of a linear model to the data, and the *gray ribbon* is the 95% confidence interval for that fitted line. Also shown are the adjusted R^2 and P-value for that linear model.

linear models with a negative binomial error distribution (Zuur et al. 2009) to estimate changes in the average number of observed nests in each sub-region and the entire study area across the study period. Data visualization suggested a quadratic year effect would adequately capture changes in nest abundance while not overfitting the data. As described above, nesting abundance was previously found to be related to both the linear and quadratic effect of rainfall (Kelly and Condeso 2014). Thus, we created a set of candidate models with all the additive combinations of linear and quadratic year and linear and quadratic rain effects, those four predictors individually, plus the intercept-only model. We fit this candidate set of eight models to the data for each of the four species and each of the 10 sub-regions where the species was observed nesting for >5 years plus the entire study area, for a total of 36 parallel model sets. The only exception was for Snowy Egrets in the Suisun Bay sub-region, where the maximum likelihood routine for the $\text{Year}^2 + \text{Rain}^2$ model would not converge, and that model was removed from the candidate set.

For each species and sub-region, we evaluated the relative support for each model by comparing Akaike information criterion (AIC) values corrected for small sample size (AICc; Burnham and Anderson 2002). We then used AICc model weights to calculate model-averaged estimates of annual nesting abundance from the full candidate model set for each species and sub-region, holding the weighted rainfall index at its average for each sub-region. We calculated the absolute and percent change in observed nest abundance from the first year a species was observed nesting in a sub-region to the last year that species was observed nesting in that sub-region. If year effects were among competitive models ($\Delta\text{AICc} \leq 2$), we concluded there was good evidence for a change in abundance. If year effects were not competitive, or if the intercept-only model had $\Delta\text{AICc} \leq 2$, we concluded there was not good evidence for abundance change. We used R (R Core Team 2020) for all data management and analysis, and specifically used the MASS package (Venables and Ripley 2002) to fit the GLM models. Unless otherwise specified we report model-

averaged estimates of nesting abundance and absolute and percent change, and their 95% confidence intervals.

RESULTS

Data Summary

Rainfall during our study period was variable—generally higher along the coast and in the northern part of the study area—and was characterized by multiple drought periods with consecutive years of below-average rainfall (Figure 2). There was also a gradual negative trend in annual rainfall in all sub-regions during our study period, and this trend was generally stronger in the southern part of our study area. We monitored between 50 and 74 total nesting sites per year across the entire study area, with the largest number of colonies during the middle of our study period (Figures 3 through 6). Several colonies contained nests of multiple species (mean 1.5 species per colony, range 1-4), and generally only Great Blue Heron formed single-species colonies. The average number of colonies per sub-region across years was 3.9 (SD=2.2, range 1-10) for Great Egret, 6.8 (SD=3.4, range 1-19) for Great Blue Heron, 2.4 (SD=1.8, range 1-10) for Snowy Egret, and 2.5 (SD=1.4, range 1-8) for Black-crowned Night Herons. The average colony size (across the entire study area) was 31.0 nests (SD=40.9, range 1-261) for Great Egret, 7.4 nests (SD=6.3, range 1-49) for Great Blue Heron, 35.8 nests (SD=45.0, range=1-278) for Snowy Egret, and 38.3 nests (SD=50.6, range=1-341) for Black-Crowned Night Heron (Figures 3 through 6).

Model Selection

Year or Year^2 effects were in the best supported and/or competitive models for 33 species/sub-region combinations, but for eight of these the intercept-only model was also best supported or competitive (Table 1; Table A1). A further three species/sub-regions had the intercept-only model best supported, and no year effects among any competitive models (Table 1; Table A1). Thus, we found good evidence for change in abundance for 25 species/sub-region combinations, including Great Egret and Black-crowned Night Heron across the entire study area, and weak

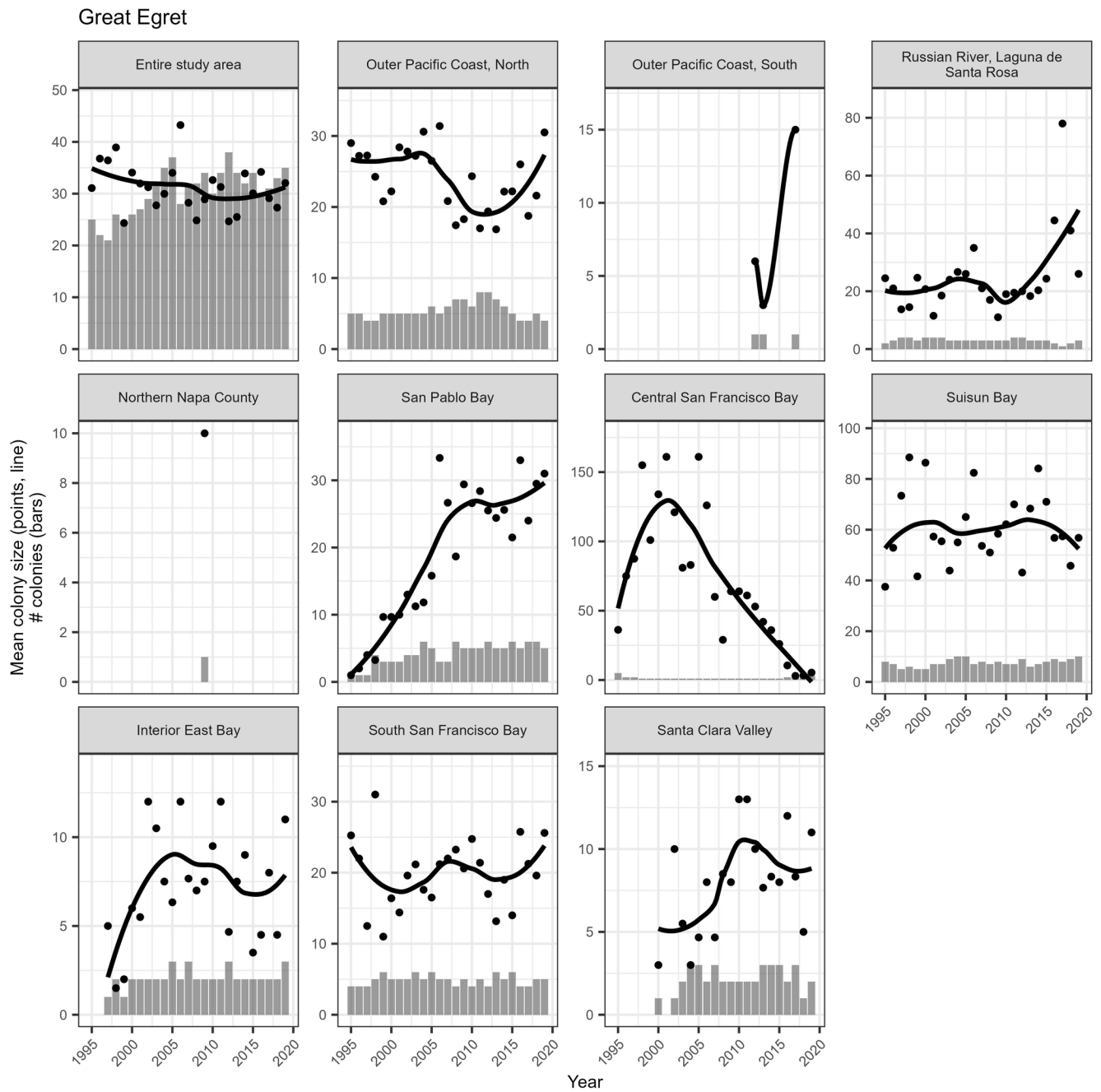


Figure 3 Number of Great Egret colonies (*bars*) and average number of nests per colony (*points, line*) in the San Francisco Bay Area and in 10 sub-regions, 1995–2019. The *line* is a loess smoother to aid visualization of patterns. Note different y-axis scales.

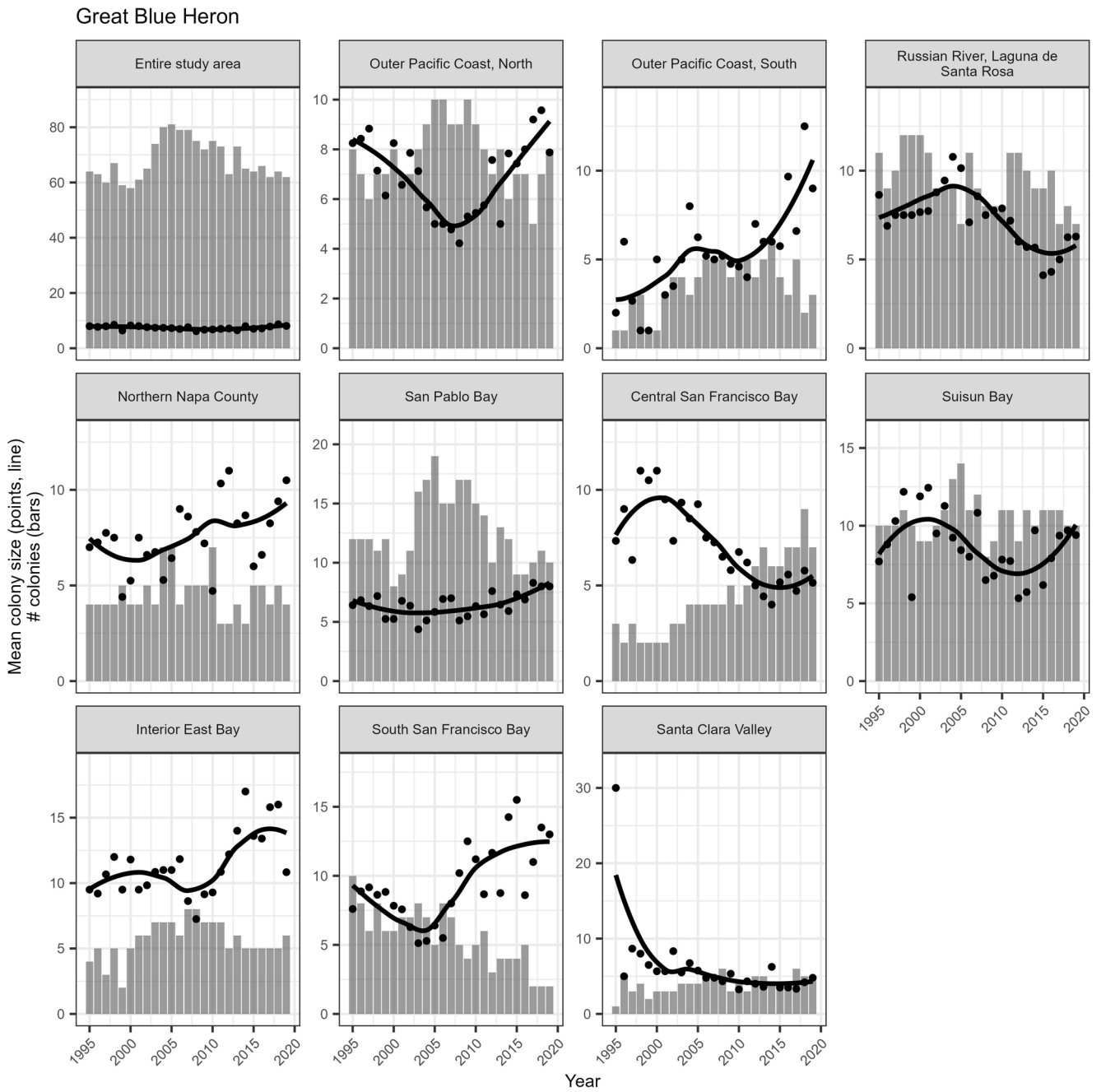


Figure 4 Number of Great Blue Heron colonies (*bars*) and average number of nests per colony (*points, line*) in the San Francisco Bay Area and in 10 sub-regions, 1995–2019. The *line* is a loess smoother to aid visualization of patterns. Note different y-axis scales.

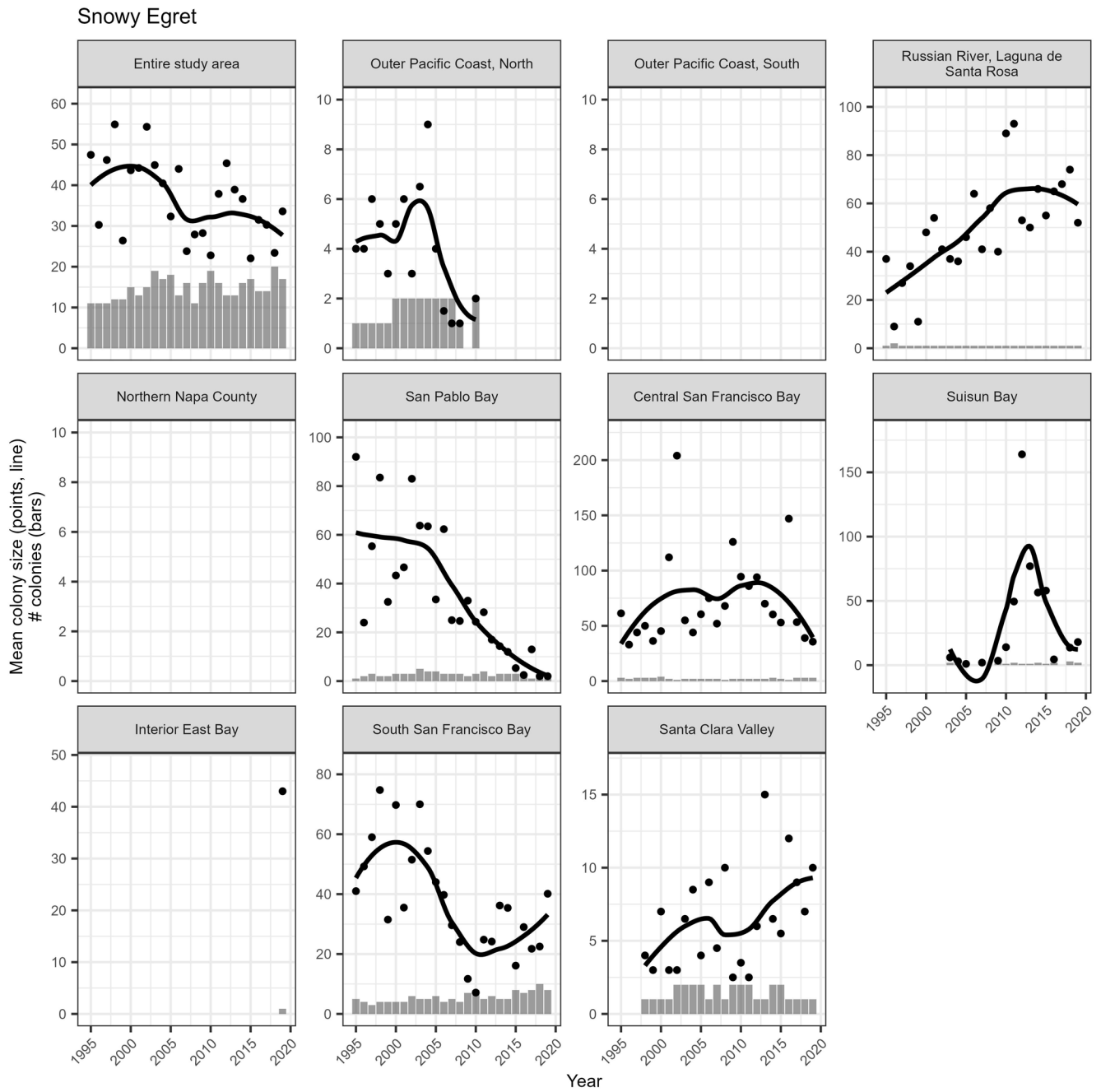


Figure 5 Number of Snowy Egret colonies (*bars*) and average number of nests per colony (*points, line*) in the San Francisco Bay Area and in 10 sub-regions, 1995–2019. The *line* is a loess smoother to aid visualization of patterns. Note different y-axis scales.

Black-crowned Night-Heron

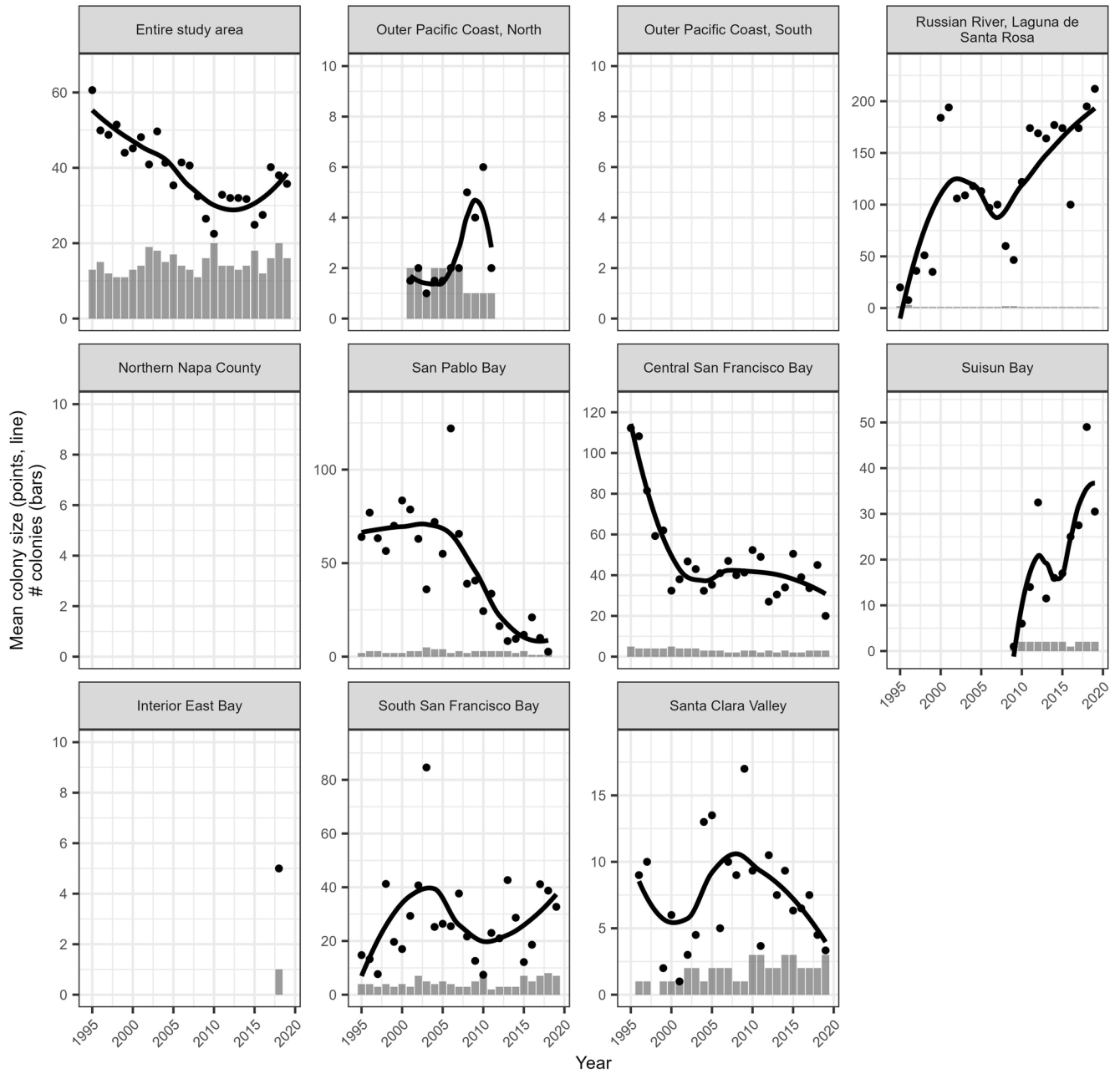


Figure 6 Number of Black-crowned Night Heron colonies (*bars*) and average number of nests per colony (*points, line*) in the San Francisco Bay Area and in 10 sub-regions, 1995–2019. The *line* is a loess smoother to aid visualization of patterns. Note different y-axis scales.

Table 1 Coefficient values for the best supported models (lowest AICc values) for estimating heron and egret abundance in the San Francisco Bay area (“Entire study area”), California, and 10 sub-regions, 1995-2019. Shown also for each model is the percent deviance explained (“% Dev. explained”). No coefficient values and “% Dev. explained = 0.00” indicates the intercept only model was best supported. Sub-regions with insufficient data for modelling are not shown.

Species	Sub-region	Year	Year ²	Rain	Rain ²	% Dev. explained
Great Egret	Entire study area	0.010 (0.002, 0.017)				18.60
	Outer Pacific Coast, North	-0.201 (-0.485, 0.083)	-0.386 (-0.663, -0.108)			26.22
	Russian River, Laguna de Santa Rosa	0.015 (0.004, 0.026)		0.525 (0.123, 0.929)	-0.441 (-0.811, -0.071)	36.61
	San Pablo Bay	4.941 (4.451, 5.446)	-2.200 (-2.641, -1.767)			93.54
	Central San Francisco Bay	-3.964 (-4.595, -3.337)	-1.085 (-1.695, -0.473)			84.86
	Suisun Bay	0.014 (0.003, 0.026)				18.51
	Interior East Bay	1.852 (0.778, 2.940)	-1.682 (-2.703, -0.670)			37.61
	South San Francisco Bay					0.00
	Santa Clara Valley	2.714 (1.975, 3.502)	-1.955 (-2.661, -1.282)			69.97
Great Blue Heron	Entire study area					0.00
	Outer Pacific Coast, North	-0.063 (-0.325, 0.199)	0.422 (0.155, 0.686)			34.34
	Outer Pacific Coast, South	3.096 (2.473, 3.757)	-1.554 (-2.125, -1.003)			79.23
	Russian River and Laguna de Santa Rosa	-1.183 (-1.462, -0.907)	-0.479 (-0.750, -0.210)			75.38
	Northern Napa County	0.012 (0.003, 0.022)				20.51
	San Pablo Bay					0.00
	Central San Francisco Bay	0.028 (0.017, 0.038)				59.15
	Suisun Bay					0.00
	Interior East Bay	0.921 (0.548, 1.295)	-0.517 (-0.887, -0.148)			50.08
	South San Francisco Bay	-0.024 (-0.037, -0.012)				35.18
	Santa Clara Valley	-0.013 (-0.027, 0.001)		0.021 (-0.460, 0.498)	0.513 (0.119, 0.888)	33.76
Snowy Egret	Entire study area					0.00
	Outer Pacific Coast, North	-1.911 (-3.476, -0.485)	-2.841 (-4.276, -1.542)			54.36
	Russian River, Laguna de Santa Rosa	1.444 (0.883, 2.007)	-0.516 (-1.067, 0.040)			50.34
	San Pablo Bay	-4.873 (-5.786, -3.971)	-3.627 (-4.527, -2.727)			84.16
	Central San Francisco Bay					0.00
	Suisun Bay	0.236 (0.039, 0.407)				20.33
	South San Francisco Bay					0.00
	Santa Clara Valley			-0.001 (-0.002, 0.000)		24.61
Black-crowned Night Heron	Entire study area	-0.552 (-0.971, -0.135)	0.395 (-0.010, 0.808)			28.51
	Outer Pacific Coast, North					0.00
	Russian River, Laguna de Santa Rosa	1.978 (1.218, 2.730)	-0.805 (-1.570, -0.017)			49.54
	San Pablo Bay	-5.111 (-5.835, -4.396)	-3.089 (-3.768, -2.412)			87.43
	Central San Francisco Bay	-2.226 (-2.671, -1.779)	1.163 (0.723, 1.610)			85.71
	Suisun Bay	3.667 (2.141, 5.228)	-2.025 (-3.618, -0.477)			60.07
	South San Francisco Bay					0.00
	Santa Clara Valley	2.346 (1.208, 3.513)	-1.736 (-2.854, -0.626)			40.60

or no evidence for change for the remaining 11, including Great Blue Heron and Snowy Egret across the entire study area (Table 2; Table A1). Across species/sub-regions where the intercept-only model was not best supported, the best-supported models explained 18.5% to 93.5% of the variation in our data (Table 1).

Rain effects were in the best model for only two species/sub-regions (Table 1) but were among competitive models for 18 of 36 species/sub-regions (Table A1). Rain effects were included in competitive models at about the same frequency as for sub-regions with only freshwater wetlands (the Russian River and Laguna de Santa Rosa, Northern Napa County, the Interior East Bay, and the Santa Clara Valley) as those that also had tidal wetlands (Table A1).

Status

Holding our rainfall index at its average, and using model-averaged coefficient values, we estimate that there were 2,540 heron and egret nests within our study area in 2019 compared to 2,506 in 1995. Our 2019 estimate includes 993 (845, 1163) Great Egret nests (Table 2), 503 (471-537) Great Blue Heron nests (Table 3), 509 (416-619) Snowy Egret nests (Table 4), and 535 (422, 674) Black-crowned Night Heron nests (Table 5). In 2019, Great Egrets nested in eight of 10 sub-

regions, and were most abundant in the Northern Outer Pacific Coast and in the Suisun, San Pablo, and South San Francisco bays (Table 2; Figure 7), whereas Great Blue Herons were present and distributed relatively evenly across all sub-regions (Table 3; Figure 8). Snowy Egret and Black-crowned Night Heron were nesting in the same six sub-regions at the end of our study period, and both species were most abundant in the Russian River and Laguna de Santa Rosa and in the South and Central San Francisco bays (Tables 4 and 5; Figures 9 and 10).

Trends

Across the entire study area, Great Egret nest abundance increased by an estimated 27% (-1%, 54%), although this increase mostly occurred between 1995 and 2010 (Table 2; Figure 7). The 95% confidence interval on this estimated change overlaps 0 slightly, so although this percent change is somewhat large there is uncertainty in its magnitude. Among sub-regions, the largest percent increase was observed in San Pablo Bay where abundance increased 2671% (2144%, 3197%) from 5 nests in 1995 to 131 nests in 2019. The largest absolute increase was observed in Suisun Bay where abundance went from 355 (253, 487) to 487 (381, 619) nests. The largest absolute and percent decrease in Great Egret nest abundance was in Central San Francisco Bay where

Table 2 Changes in estimated number of Great Egret nests by sub-region in the San Francisco Bay area, 1995–2019. Shown for each sub-region are the years Great Egrets were observed nesting, the absolute and percent change across those years, and the estimated abundance in the final observed year. Estimates are shown with their 95% confidence Intervals. Sub-regions marked with * and with no values had insufficient data for modeling.

Sub-region	Years observed nesting	Absolute change	% change	Final year estimated abundance
Entire study area	1995-2019	210 (-5, 425)	27% (-1%, 54%)	993 (845, 1163)
Outer Pacific Coast, North	1995-2019	-13 (-40, 15)	-10% (-33%, 12%)	110 (86, 138)
Outer Pacific Coast, South*	—	—	—	—
Russian River, Laguna de Santa Rosa	1995-2019	19 (-7, 46)	32% (-12%, 76%)	81 (63, 102)
Northern Napa County*	—	—	—	—
San Pablo Bay	1995-2019	126 (101, 151)	2671% (2144%, 3197%)	131 (108, 158)
Central San Francisco Bay	1995-2019	-149 (-207, -90)	-93% (-129%, -56%)	12 (8, 17)
Suisun Bay	1995-2019	133 (-15, 280)	37% (-4%, 79%)	487 (381, 619)
Interior East Bay	1996-2019	9 (1, 18)	224% (21%, 426%)	13 (7, 24)
South San Francisco Bay	1995-2019	4 (-18, 26)	5% (-19%, 29%)	95 (81, 111)
Santa Clara Valley	1999-2019	13 (8, 18)	607% (368%, 846%)	15 (11, 21)

Table 3 Changes in estimated number of Great Blue Heron nests by sub-region in the San Francisco Bay area, 1995–2019. Shown for each sub-region are the years Great Blue Herons were observed nesting, the absolute and percent change across those years, and the estimated abundance in the final observed year. Estimates are shown with their 95% confidence Intervals. Sub-regions marked with * and with no values had insufficient data for modeling.

Sub-region	Years observed nesting	Absolute change	% change	Final year estimated abundance
Entire study area	1995-2019	1 (- 43, 44)	0% (- 8%, 9%)	503 (471, 537)
Outer Pacific Coast, North	1995-2019	- 2 (- 14, 10)	- 4% (- 24%, 16%)	58 (49, 70)
Outer Pacific Coast, South	1995-2019	21 (15, 27)	676% (484%, 867%)	24 (19, 31)
Russian River, Laguna de Santa Rosa	1995-2019	- 42 (- 57, - 27)	-53% (- 72%, - 34%)	38 (31, 45)
Northern Napa County	1995-2019	9 (- 1, 18)	31% (- 3%, 64%)	37 (31, 44)
San Pablo Bay	1995-2019	6 (- 13, 24)	8% (- 18%, 34%)	78 (66, 93)
Central San Francisco Bay	1995-2019	20 (12, 27)	99% (63%, 135%)	40 (34, 47)
Suisun Bay	1995-2019	- 6 (- 31, 20)	-6% (- 33%, 21%)	89 (74, 106)
Interior East Bay	1995-2019	32 (16, 49)	85% (41%, 128%)	71 (56, 90)
South San Francisco Bay	1995-2019	- 31 (- 48, - 14)	- 48% (- 75%, - 21%)	33 (26, 43)
Santa Clara Valley	1995-2019	- 5 (- 13, 4)	- 20% (-57%, 17%)	19 (14, 24)

Table 4 Changes in estimated number of Snowy Egret nests by sub-region in the San Francisco Bay area, 1995–2019. Shown for each sub-region are the years Snowy Egrets were observed nesting, the absolute and percent change across those years, and the estimated abundance in the final observed year. Estimates are shown with their 95% confidence Intervals. Sub-regions marked with * and with no values had insufficient data for modeling.

Sub-region	Years observed nesting	Absolute change	% change	Final year estimated abundance
Entire study area	1995-2019	- 30 (- 172, 111)	-6% (- 32%, 21%)	509 (416, 619)
Outer Pacific Coast, North	1995-2011	- 2 (- 5, 1)	- 76% (-185%, 34%)	1 (0, 2)
Outer Pacific Coast, South*	—	—	—	—
Russian River, Laguna de Santa Rosa	1995-2019	43 (22, 65)	161% (80%, 241%)	70 (50, 98)
Northern Napa County*	—	—	—	—
San Pablo Bay	1995-2019	- 70 (- 105, - 34)	- 96% (- 145%, - 47%)	3 (2, 5)
Central San Francisco Bay	1995-2019	- 1 (- 38, 36)	- 1% (- 26%, 25%)	144 (119, 175)
Suisun Bay	2002-2019	106 (- 187, 398)	1168% (- 2061%, 4398%)	115 (8, 749)
Interior East Bay*	—	—	—	—
South San Francisco Bay	1995-2019	- 18 (- 114, 77)	- 9% (- 54%, 37%)	192 (145, 254)
Santa Clara Valley	1997-2019	3 (- 2, 9)	61% (- 45%, 168%)	9 (5, 14)

abundance dropped from 160 (112-227) to 12 (8-17) nests, representing a - 93% (- 129%, - 56%) decrease.

For Great Blue Heron across the entire study area, the intercept-only model was the best supported, indicating no evidence for change in nesting abundance during our monitoring period (Tables 1 and 3; Figure 8). By sub-region, the largest Great Blue Heron percent increase was in the outer Pacific Coast, South, where abundance

increased 676% (484%, 867%) from 3 (2 to 5) nests in 1995 to 24 (19 to 31) nests in 2019. The largest absolute increase was observed in Interior East Bay where abundance went up by 32 (16, 49) nests to 71 (56 to 90) nests. The largest percent decreases in Great Blue Heron nest abundance were in the Russian River and Laguna de Santa Rosa, and South San Francisco Bay, where nesting abundance decreased by - 53% (- 72%, - 34%) and - 48% (- 75%, - 21%), respectively. The decrease in the Russian River and Laguna de Santa Rosa

Table 5 Changes in estimated number of Black-crowned Night Heron nests by sub-region in the San Francisco Bay area, 1995–2019. Shown for each sub-region are the years Black-crowned Night Heron were observed nesting, the absolute and percent change across those years, and the estimated abundance in the final observed year. Estimates are shown with their 95% confidence intervals. Sub-regions marked with * and with no values had insufficient data for modeling.

Sub-region	Years observed nesting	Absolute change	% Change	Final year estimated abundance
Entire study area	1995-2019	-147 (-400, 106)	-22% (-59%, 15%)	535 (422, 674)
Outer Pacific Coast, North	2000-2012	0 (-2, 2)	14% (-68%, 95%)	3 (1, 6)
Outer Pacific Coast, South*	—	—	—	—
Russian River, Laguna de Santa Rosa	1995-2019	131 (56, 207)	234% (100%, 369%)	188 (120, 289)
Northern Napa County*	—	—	—	—
San Pablo Bay	1995-2019	-124 (-171, -76)	-97% (-134%, -60%)	4 (3, 7)
Central San Francisco Bay	1995-2019	-365 (-488, -242)	-78% (-104%, -51%)	106 (82, 136)
Suisun Bay	2008-2019	55 (-25, 134)	933% (-417%, 2283%)	61 (17, 183)
Interior East Bay*	—	—	—	—
South San Francisco Bay	1995-2019	41 (-77, 158)	37% (-71%, 145%)	150 (87, 252)
Santa Clara Valley	1995-2019	10 (0, 20)	324% (-1%, 649%)	13 (6, 26)

appears to have been mostly in the last 15 years of the study. The largest absolute decrease was observed in the Russian River and Laguna de Santa Rosa where abundance dropped by -42 (-57, -27) nests, from 80 (67 to 96) to 38 (31 to 45).

As with Great Blue Heron, our data suggested no overall change in Snowy Egret nesting abundance across the entire study area, with the intercept-only model being the best supported (Tables 1 and 4; Figure 9). By sub-region, the largest absolute and percent increase in modeled nest abundance was in Suisun Bay. However, data for this sub-region were highly variable, leading to large confidence intervals on estimates, and the intercept-only model was also competitive, so caution should be exercised when interpreting these trend estimates (Table 4). Otherwise, the largest percent and absolute increase in Snowy Egret nesting abundance was in the Russian River and Laguna de Santa Rosa, where abundance increased by 43 (22, 65) nests to 70 (50 to 98) in 2019, a 161% (80%, 241%) increase. The largest absolute and percent decrease in Snowy Egret nest abundance was in San Pablo Bay where abundance dropped by -70 (-105, -34) nests to only 3 (2 to 5) in 2019, a -96% (-145%, -47%) decrease.

Across the entire study area, Black-crowned Night Heron nesting abundance declined by -22% (-59%, 15%), a loss of approximately -147 (-400, 106) nests (Table 5; Figure 10). However, these estimates have 95% CI broadly overlapping 0, so there was substantial uncertainty in the statistical significance and magnitude of these changes. Like Snowy Egrets, Black-crowned Night Heron abundance in Suisun Bay was quite variable, and our estimates of abundance and change had 95% CI broadly overlapping 0. Otherwise, the largest absolute and percent increase in Black-crowned Night Herons was observed in the Russian River and Laguna de Santa Rosa where abundance increased by 131 (56, 207) nests to 188 (120 to 289) in 2019, a change of 234% (100%, 369%). The largest declines in Black-crowned Night Heron nest abundance were in San Pablo Bay, where abundance declined by -124 (-171, -76) nests or -97% (-134%, -60%), to only 4 (3 to 7) nests in 2019, and Central San Francisco Bay where abundance declined by -365 (-488, -242) nests or -78% (-104%, -51%), to 106 (82 to 136) nests in 2019. The steepest decline in Central San Francisco Bay occurred at the same time as an increase in San Pablo Bay, and then the decrease in both of those sub-regions through the second half of our study coincided with the increase in the Russian River and Laguna de Santa Rosa.

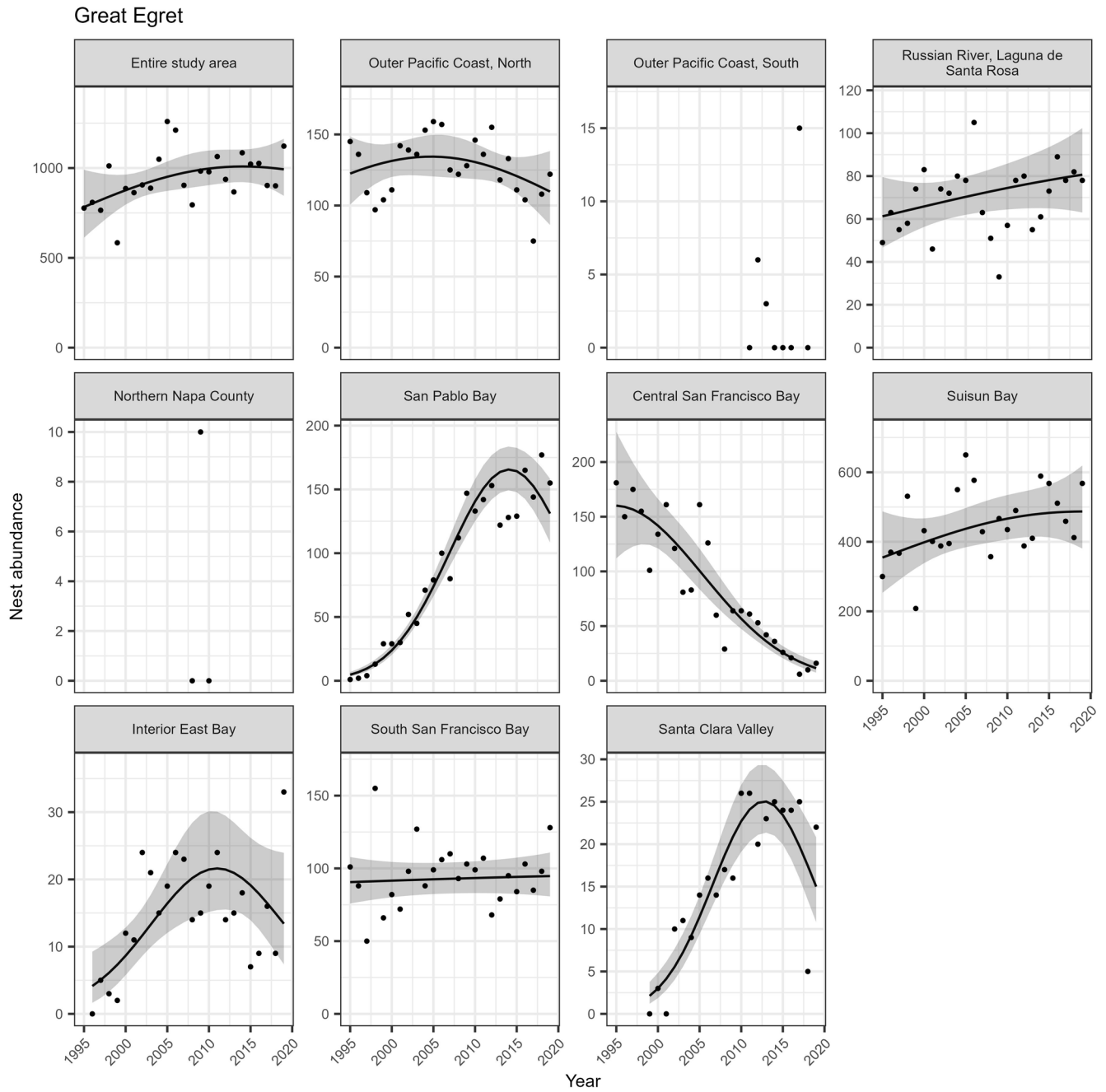


Figure 7 Changes in nest abundance of Great Egret by sub-region in the San Francisco Bay Area, 1995-2019. Shown are the estimated mean abundance (*line*) and 95% confidence interval (*gray ribbon*) calculated by averaging across a candidate set of generalized linear models while holding the sub-region-specific rainfall index at its mean value. *Black dots* show the raw data to which the models were fitted. Note different y-axis scales.

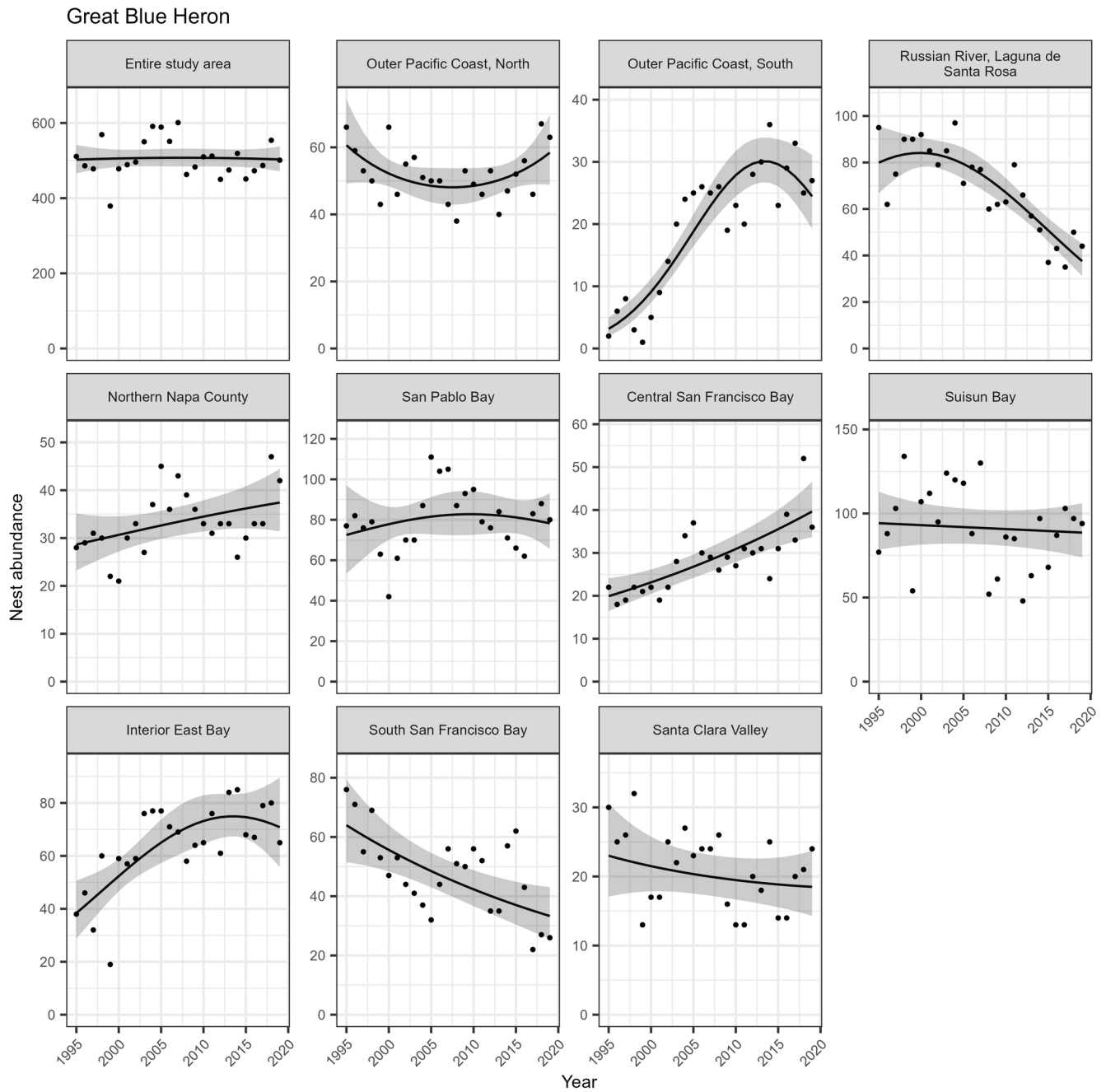


Figure 8 Changes in nest abundance of Great Blue Heron by sub-region in the San Francisco Bay Area, 1995–2019. Shown are the estimated mean abundance (*line*) and 95% confidence interval (*gray ribbon*) calculated by averaging across a candidate set of generalized linear models while holding the sub-region-specific rainfall index at its mean value. *Black dots* show the raw data to which the models were fitted. Note different y-axis scales.

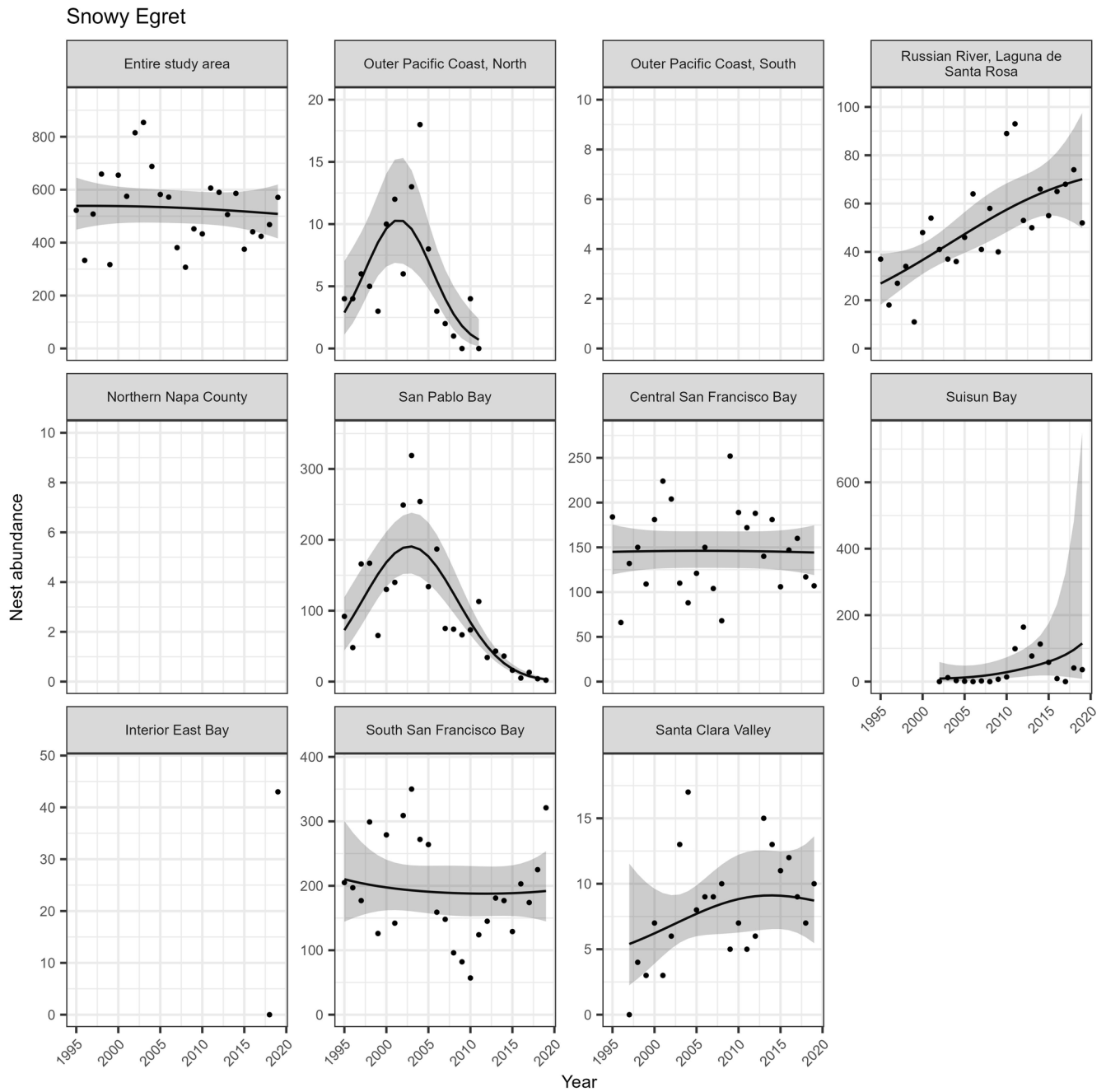


Figure 9 Changes in nest abundance of Snowy Egret by sub-region in the San Francisco Bay Area, 1995–2019. Shown are the estimated mean abundance (*line*) and 95% confidence interval (*gray ribbon*) calculated by averaging across a candidate set of generalized linear models while holding the sub-region-specific rainfall index at its mean value. *Black dots* show the raw data to which the models were fitted. Note different y-axis scales.

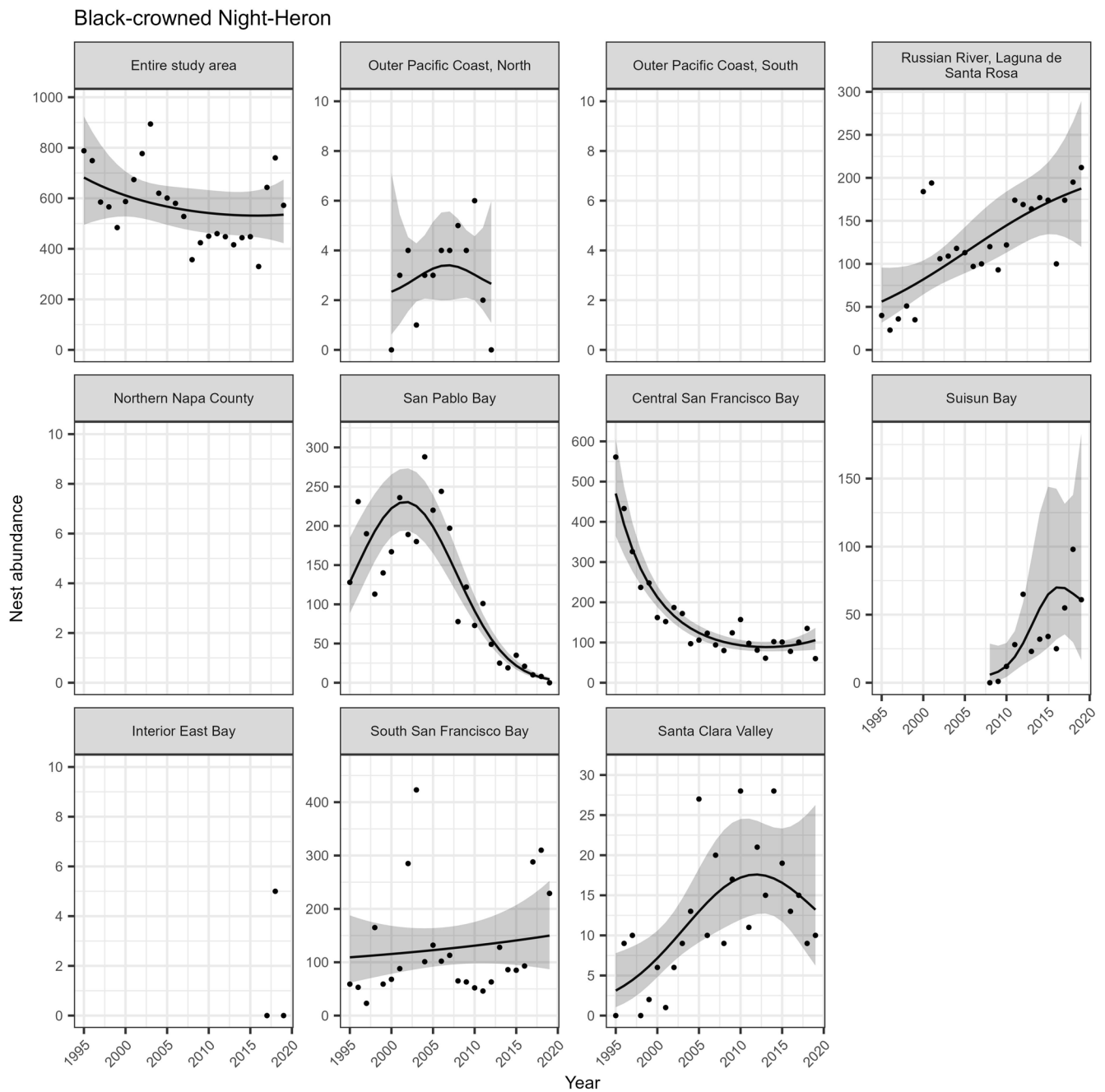


Figure 10 Changes in nest abundance of Black-crowned Night Heron by sub-region in the San Francisco Bay Area, 1995–2019. Shown are the estimated mean abundance (*line*) and 95% confidence interval (*gray ribbon*) calculated by averaging across a candidate set of generalized linear models while holding the sub-region-specific rainfall index at its mean value. *Black dots* show the raw data to which the models were fitted. Note different y-axis scales.

Changes in nesting abundance were most often associated with changes in average colony size, rather than changes in the number of colonies in each sub-region (e.g., Great Egret in San Pablo and Central San Francisco bays and the Santa Clara Valley, [Figure 3](#); Snowy Egret in the Russian River and Laguna de Santa Rosa and San Pablo Bay, [Figure 5](#)). The number of colonies per sub-region was generally stable across the study period for all four species, with the main exceptions being Great Blue Heron in Central and South San Francisco bays ([Figure 4](#)). Mean colony size was generally most stable for Great Blue Heron (but again, note Central and South San Francisco bays), whereas there were big shifts in multiple sub-regions for the other three species.

DISCUSSION

While total numbers of herons and egrets in North America have significantly decreased (Rosenberg et al. 2019), in the San Francisco Bay region, the abundance of ardeids has generally remained consistent between 1995 and 2019. This is encouraging, given that heron and egret breeding colonies are sensitive to human disturbance (Carney and Sydeman 1999) and the human population of the Bay Area increased by over 20%, from 6.02 to 7.75 million, during this monitoring period (Bay Area Census 2022). However, we nevertheless observed mixed trends for each species at the sub-regional scale within our study area, with abundance increasing in some sub-regions while decreasing in others.

On the positive side, Great Egret breeding populations in the San Francisco Bay region increased from 1995 until about 2005, after which abundance seemed to be stable. At Bolinas Lagoon, a site in the Outer Pacific Coast, North sub-region of our study area, winter trends of Great Egrets have also been positive (Stenzel and Page 2018). Nationally, Breeding Bird Survey (BBS) data from 1993 to 2019 show Great Egrets to be increasing (Ziolkowski et al. 2022), as is the case for wintering numbers of Great Egrets in California, Oregon, and Washington based on Christmas Bird Counts (CBCs; National Audubon Society 2020). However, eBird data collected from

2012 to 2022 show Great Egrets to be declining in California's Central Valley and in much of the lower Mississippi Basin and the Eastern Seaboard (Fink et al. 2022).

We found region-wide Great Blue Heron abundance to be stable, and the Bolinas Lagoon data show increasing wintering trends as with Great Egret (Stenzel and Page 2018). Beyond our study area, BBS and CBC data for California (National Audubon Society 2020; Ziolkowski et al. 2022) and the Central Valley (Pandolfino and Handel 2018) show Great Blue Herons to be significantly declining, although the Central Valley decline is relatively small. As with Great Egret, eBird data show Great Blue Heron declines across much of the continent (Fink et al. 2022). For these two species, the San Francisco Bay Area appears to be one of the few regions in North America where populations are stable.

We found little evidence that Snowy Egret nesting abundance has changed across our study area, but our data for them are more variable, yielding a less precise trend estimate. Elsewhere, winter numbers of Snowy Egrets in the Central Valley have significantly increased (Pandolfino and Handel 2018), although California trends based on CBC and BBS data show non-significant negative trends (National Audubon Society 2020; Ziolkowski et al. 2022). More worrisome, it appears Black-crowned Night-Heron abundance has declined by over 21% over the last 30 years in the San Francisco Bay Area, although we also observed significant annual variation in abundance; and, consequently, there is some uncertainty in the statistical significance and magnitude of this decline. Nevertheless, the decline we observed mirrors significant local declines of wintering night herons on Bolinas Lagoon (Stenzel and Page 2018) and significant BBS declines for all of California (Ziolkowski et al. 2022). Since 2012, eBird data show both of these smaller ardeids have declined in most of the areas where they occur in North America (Fink et al. 2022).

Our data reveal that no single sub-region has experienced significant increases or declines for

all four species. All four species we considered have broad habitat requirements and use a range of wetland and upland habitats for foraging and to locate their colonies near (Hothem et al. 2020; McCrimmon et al. 2020; Parsons and Master 2020; Vennesland and Butler 2020). A lack of consistent trends for all species in any sub-region or across the entire study area suggests there were no large-scale losses of wetland extent or quality during our study. However, two sub-regions nevertheless had notable declines in multiple species. In Central San Francisco Bay, Great Egrets declined from approximately 150 to being largely absent, and Black-crowned Night Herons declined from > 500 to around 100. Similarly, in San Pablo Bay, Snowy Egrets and Black-crowned Night Herons both declined from > 100 nests to not nesting in the sub-region. This may be the result of a re-distribution of nesting birds from these sub-regions elsewhere in the study area (see below), but we are unsure of the mechanisms for these changes. The Outer Pacific Coast, South is somewhat unique in that it only has a single species (Great Blue Heron) consistently nesting. This area is generally more forested, with steeper topography and smaller wetlands than the other sub-regions in our study area, and these habitat factors likely explain the relative lack of nesting herons and egrets.

We found sub-regional changes in nesting abundance were more often associated with changes in average colony size than with the number of colonies in that sub-region. A prior analysis of this dataset found that acute disturbance events at individual colonies that caused a loss of nesters at that colony were also associated with sudden declines at the sub-regional scale (Kelly et al. 2018). Our results indicate that less-sudden changes in abundance at the colony scale (both up and down) are likely also driving longer-term patterns in sub-regional nesting abundance. Taken together, the results presented here and those of Kelly et al. (2018) indicate that maintaining sustainable heron and egret populations will likely require conservation actions that affect nesting abundance over short (e.g., acute disturbance) and long (i.e., overall wetland health) time-scales.

Some of the changes in nesting abundance we observed may be explained by birds moving among sub-regions. Although colonial nesting birds generally have high site fidelity (Cézilly et al. 2000), fidelity in herons and egrets is not well documented (McCrimmon et al. 2020; Parsons and Master 2020). The scant data available for Black-crowned Night Herons suggests these birds may move ≥ 60 km between breeding seasons (Hothem et al. 2020). The decline in Great Egret abundance in Central San Francisco Bay was mirrored by an increase of similar magnitude in San Pablo Bay, just to the north. This strongly suggests a shift in Great Egret distribution from the more urbanized portion of the Bay to less-developed areas, although the precise causes for this apparent shift are not known. Our data also appear to show a shift in Black-crowned Night Heron distribution, first from Central San Francisco Bay to San Pablo Bay from 1995 until the early 2000s, then from San Pablo Bay to the Russian River and Laguna de Santa Rosa over the final 10 to 15 years of our study. They may have shifted southward into the Santa Clara Valley during this time, as well. However, these apparent shifts in breeding distribution do not entirely make up for the large loss in nest numbers we observed in Central San Francisco Bay. Snowy Egret also appeared to shift distribution from San Pablo Bay to the Russian River and Laguna de Santa Rosa sub-region. This apparent shift of these smaller heron and egret species from colonies along the San Francisco Bay northward into the Russian River drainage represents a shift from tidal to freshwater wetlands, despite an overall decline in annual rainfall. All sub-regions in the study area were subject to both extensive land conversion for human purposes as well as many wetland restoration projects (San Francisco Estuary Partnership 2015, 2019). There is also some anecdotal evidence from our monitoring that predator disturbance was elevated above normal levels in Central San Francisco Bay from about 2000 to 2005, but these data may represent a biased sample of disturbance events and should be interpreted with caution. Evaluating the possible effects of these interacting factors on heron and egret nesting abundance dynamics would be particularly helpful in better

understanding these apparent distribution shifts between sub-regions.

Another possible explanation for the divergent sub-regional trends we observed is that they reflect different patterns of productivity and survival at the sub-regional level. Short-term changes in abundance in our study area appear driven more by variation in overwinter survival (inferred from relationships between recruitment and winter weather) than by prior year productivity (Kelly and Condeso 2014). Thus, we do not believe that sub-regional differences in nest success and subsequent recruitment (if they existed) were responsible for the patterns we observed. Additionally, because our entire study area experiences similar rainfall and other weather, and because rainfall was equally supported as a predictor of nesting abundance in sub-regions with and without tidal wetlands, we also do not believe that sub-regional differences in weather-related overwinter survival explain our results. There may be other sub-regional habitat differences that contribute to varying survival among sub-regions. However, herons and egrets are highly mobile species. In a separate study, we observed GPS-tagged Great Egrets regularly moving among Bay Area sub-regions (Lumpkin et al. 2022), and we feel that movement of breeding individuals or dispersal of juveniles between sub-regions is a likely explanation for the divergent trends we observed in neighboring sub-regions. However, we remain unsure what habitat or other factors may be driving these patterns. Kelly et al. (2018) found that all four ardeids monitored in this study increased locally on Tomales Bay, part of the Outer Pacific Coast, North sub-region, in years after winters with high numbers of Pacific Herring (*Clupea pallasii*) in Tomales Bay. Otherwise, we have little data linking prey dynamics with numbers of ardeids in the San Francisco Bay region.

Along with apparent distribution shifts within our study area, movements in and out of our study area may also explain some of our results, especially along the eastern edge of the study area. We observed abundance of Snowy Egret and Black-crowned Night Heron in the Suisun

Bay to be highly variable year to year. Snowy Egret abundance regularly varied by 1 to 2 orders of magnitude in consecutive years, and Black-crowned Night Heron abundance regularly varied by 20 to 40 nests in consecutive years (representing ~40% to 65% annual changes). It may be that our data represent the true nesting behavior of these two species in the Suisun Bay, with many individuals skipping breeding in certain years. Additionally, as a result of logistical constraints, most of the Suisun sub-region is surveyed by a single annual boat trip, and this area is less well visited by birdwatchers than other sub-regions, so it may be that we failed to detect or be made aware of additional colonies within this sub-region. These species also have less synchronous nesting phenology, so we may have missed the peak with only a single visit. Alternatively, it could be that individuals of both species have relatively low fidelity to nesting colonies, and regularly move eastward, outside our study area, to breed. The Suisun Bay is at the edge of our study area, and just to the east lies California's Central Valley where both species nest in multiple colonies (Shuford et al. 2020). Black-crowned Night Herons in the Bay Area are not thought to be migrants, but they do disperse into the Central Valley (Gill and Mewalt 1979). For both species, the size and density of colonies outside our study area to the north of Sacramento are among the largest in the state. Shorebirds move between the Central Valley and more coastal areas in response to annual rainfall patterns (Warnock et al. 1995; Takekawa et al. 2002), and herons and egrets may do the same. Unfortunately, detailed trend data for the Central Valley do not exist to address this question.

Weather and climate can also strongly affect ardeid numbers and breeding success (Frederick and Collopy 1989; Fasola et al. 2009; Kelly and Condeso 2014). Heron and egret nest abundance in the San Francisco Bay region was previously shown to be lowest during or just after unusually dry or wet years, and highest when rainfall was at intermediate levels, although rain effects were only supported when density-dependent effects of nesting abundance were also accounted for (Kelly and Condeso 2014). While we accounted

for rainfall in our analysis, we did not formally investigate whether long-term trends in annual rainfall might be driving changes in ardeid nesting abundance. At Bolinas Lagoon, winter numbers of Great Blue Herons, Great Egrets, and Snowy Egrets declined after years with higher-than-average rainfall, while numbers of Black-crowned Night Herons were positively related to the previous year's rainfall amount (Stenzel and Page 2018). Average annual rainfall in our study area declined during the study period, though this decline was only statistically significant for two sub-regions. If rainfall declines continue, it may cause a shift of ardeids from freshwater wetlands in our study area to the more hydrologically predictable tidal areas. However, our data do not seem to show such a response over the last 25 years. Indeed, as described above, Black-crowned Night Herons and Snowy Egrets appear to be making the opposite shift (tidal to fresh).

In our study area, Black-crowned Night-Herons and Snowy Egrets nest in a relatively small number of large, multi-species nesting sites (generally just one to two colonies per sub-region). Protecting the current and previously occupied nesting sites—and unoccupied sites with similar characteristics (see Kelly et al. 2007)—from acute disturbance (predation, human harassment) and habitat degradation (i.e., loss of trees) is likely important for sustaining these populations (Kelly et al. 2018), allowing them to shift nesting location in response to annual changes in food availability or other factors. Since these two species have either negative or uncertain trends, we suggest this is the most important conservation measure to take for ardeid species over the next 5 to 10 years. Great Egrets, and especially Great Blue Herons, tend to nest in more colonies across the study area, which makes their overall nesting abundance less sensitive to loss of a single colony. Although protecting Great Egret and Great Blue Heron colonies remains important, overall wetland health is likely a more important driver of their population dynamics.

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