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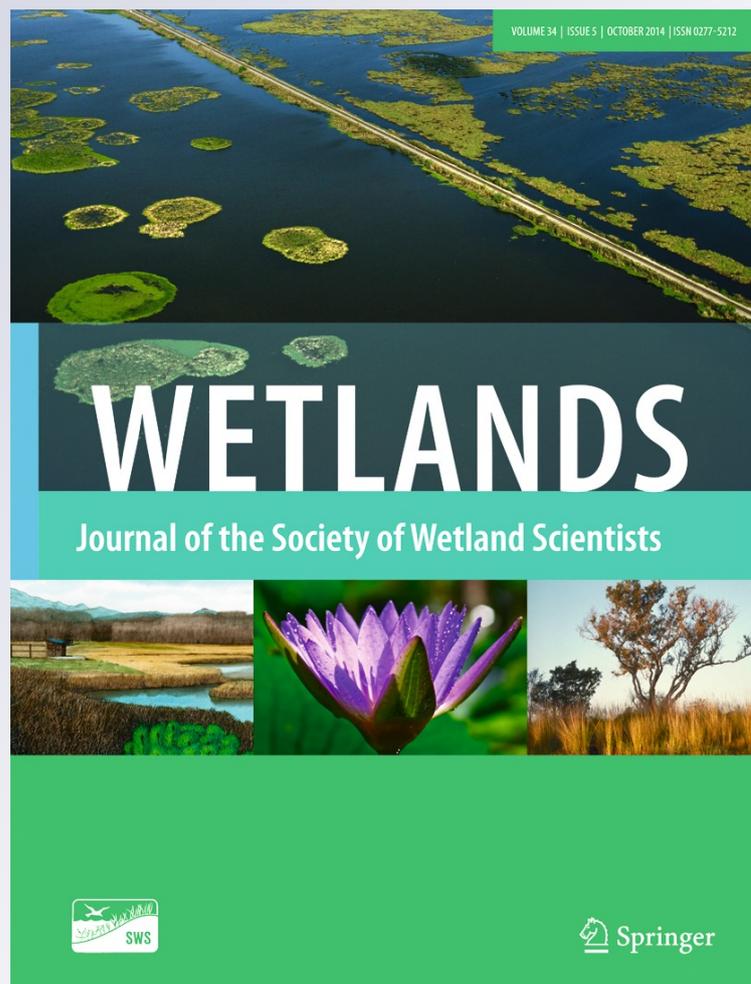
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Rainfall Effects on Heron and Egret Nest Abundance in the San Francisco Bay Area

John P. Kelly · T. Emiko Condeso

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Abstract Twelve models addressing the current and delayed effects of seasonal rainfall and rainfall volatility (a measure of storm intensity) were used to evaluate changes in nest abundances of herons and egrets in the San Francisco Bay area, from 1991 to 2010. Wetter- or drier-than-average conditions, two winters before nesting, were associated with reduced growth rates of Great Egret (*Ardea alba*) nest abundance. Similarly, growth rates of Great Blue Heron (*Ardea herodias*) nest abundance were maximized near average levels of rainfall volatility two winters prior nesting. Annual growth rates of Snowy Egret (*Egretta thula*) and Black-crowned Night-Heron (*Nycticorax nycticorax*) abundances declined with heavier-than-usual winter rainfall volatility immediately prior to nesting and with increases in spring rainfall volatility 2 years prior to nesting. The dynamics of heron and egret nest abundances were not associated with annual production of fledglings within the region. The results suggest the possibility of regional declines in the growth or resilience of heron and egret abundances with increasingly rainy or stormy seasonal conditions in northwestern California.

Keywords Ardeidae · Climate · Nesting · Population · San Francisco Bay · Wetlands

Introduction

General assessments of avian susceptibilities to climate change impacts have suggested that the sensitivities of herons and egrets may be relatively “low” (Foden et al. 2008), or below the upper 35th percentile of bird species ranked

according to climate change sensitivity and exposure (Gardali et al. 2012). However, changes in the extent or intensity of seasonal rainfall and associated changes in surface-water dynamics are known to have strong effects on heron and egret foraging rates and reproductive success (Frederick and Collopy 1989; Maddock and Baxter 1991; Bennetts et al. 2000; but see Herring et al. 2010) and may lead to significant changes in regional distributions and abundances (Hafner et al. 2001; Russell et al. 2002; Fasola et al. 2010). Such rainfall sensitivity is reflected in storm-related wind and thermal effects on the survival of nests and nestlings (personal observations) and in the responses of nesting and foraging herons and egrets to rainfall-related changes in water depth (Frederick and Collopy 1989; Gawlik 2002), vegetation structure (Bancroft et al. 2002; Pierce and Gawlik 2010), hydrologic processes that influence circulation, drainage, and extent of wetland feeding areas (Kushlan 2000; Combes 2003; Maccarone and Brzorad 2005), and the availability of prey (Bancroft et al. 1988; Maddock and Baxter 1991). Important concerns include the modification and loss of tidal marsh feeding areas as a consequence of sea level rise, including interactions with runoff that result in episodic coastal flooding, especially in human-altered landscapes (Scavia et al. 2002; Hughes 2004; Calloway et al. 2007). In addition, because herons and egrets are top predators in wetland systems, climate-induced changes in regional abundance might enhance or depress top-down influences on prey populations and the structure of wetland communities (Kushlan 1976; Master 1992; Frederick 2002).

Feeding conditions for herons and egrets may be enhanced if reduced seasonal rainfall confines potential prey to receding ponds or if increased rainfall alters runoff patterns to create confluences, eddies, flooded fields, or isolated ponds that enhance foraging rates, or extends hydroperiods needed for the production or survival of prey (Bancroft et al. 2002; Master et al. 2005; Beerens et al. 2011). Interactions between

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these processes and rainfall volatility, a measure of storm intensity, may enhance or reduce the availability of prey or opportunities for foraging in ephemeral wetland feeding areas (Scavia et al. 2002; Bromirski et al. 2003). Alternatively, foraging efficiency may decline if flooding or turbidity related to extreme rainfall events reduces the supply or availability of prey (Thompson 1978; Cezilly 1992). In Florida, Great Egrets (*Ardea alba*) shift their nesting distribution from areas undergoing drought conditions immediately prior to nesting to areas where surface water is sufficient to sustain wetland feeding areas (Bancroft et al. 1994). In California, winter rainfall is needed to sustain seasonal wetlands, and substantial amounts of winter rainfall enhance the extent of wetland feeding areas through both non-breeding and breeding periods (Heitmeyer et al. 1989). Therefore, changes in the amount or pattern of winter or spring rainfall may lead to regional changes in nesting abundance (Maddock and Baxter 1991; Bancroft et al. 1994).

In this study, we used first-order autoregressive population models to analyze the effects of total winter and spring rainfall, and rainfall volatility, at various time lags, on changes in heron and egret nesting abundances. We further examined whether the effects of rainfall on reproductive success might influence regional changes in nest abundance. The analysis was based on 20 years of nesting data from all known colony sites in the northern San Francisco Bay area (Kelly et al. 2007). To consider the long-term effects of climate change on nesting abundances in California, the results were compared with changes in seasonal rainfall predicted by regional climate models (Kueppers et al. 2005; Cayan et al. 2008; Pan et al. 2010).

Methods

Study Area

The study area covers the northern portion (approximately 9,950 km²) of the San Francisco Bay area, from the outer Pacific Coast eastward to the confluence of the Sacramento and San Joaquin rivers, and from the Russian River and northern Napa County southward through the interior East Bay hills and Central San Francisco Bay (Fig. 1; Kelly et al. 2007). The area includes extensive tidal marsh systems as well as historic wetlands that have been diked and drained, managed as marshes or ponds for flood control or duck hunting, or restored to tidal action (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). Broad alluvial terraces that surround tidal and non-tidal marshes function as seasonal wetlands, many of which are grazed or cultivated. The northern portion of the study area extends across the hillsides and lower slopes of the Coast Range, with

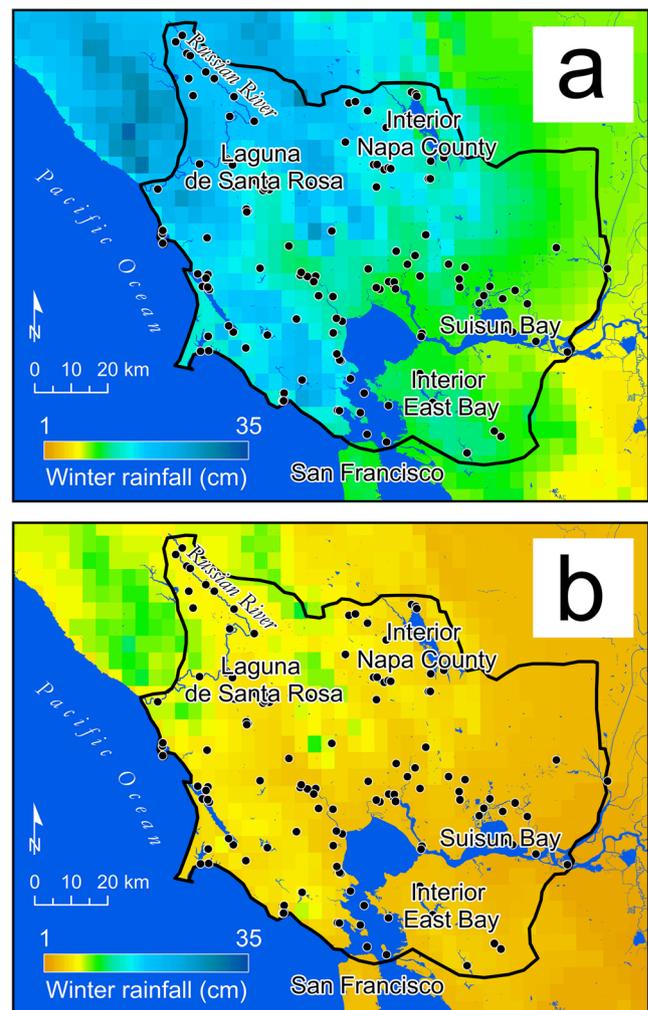


Fig. 1 Mean monthly rainfall in the northern San Francisco Bay area, in **a** winter (November–February) and **b** spring (March–June), 1989–2010, based on high-resolution estimates developed by the PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>). Filled circles indicate the locations of heron and egret nesting colonies; bold line indicates the study area boundary

freshwater marshes, rivers and streams, vernal wetlands, farm ponds and reservoirs.

Nest Abundance

The locations of all known colony sites (heronries) in the study region (1991–2010; 57±1.1 active sites year⁻¹, SE) were determined using aerial searches, supplemented by systematic annual, ground-based searches. Newly established sites were rarely revealed by these searches because they were usually detected first through regular communications with state, regional, and local natural resource managers, county breeding bird atlas project coordinators, and local bird watching networks (Kelly et al. 2007). Most sites were visited at least four times each breeding season, generally at monthly or more frequent intervals. Sites that could be visited only

once in a given year ($13 \pm 0.7\% \text{ year}^{-1}$) were observed in May or early June when nests and broods were conspicuous and likely to provide a close estimate of peak nest abundance (Kelly et al. 2007). The peak number of active nests observed at each colony site, summed annually across sites, was used to estimate annual nest abundances from 1991 to 2010 (Table 1).

Reproductive Success

Overall reproductive success was calculated as the product of focal nest survivorship (proportion fledging at least one young) and the mean number of young fledged in successful nests (Kelly et al. 2007). Focal nests were observed from initiation or early in the incubation period ($n=58 \pm 1.9\%$ of regional nest abundance for Great Blue Heron, $41 \pm 1.9\%$ for Great Egret, $16 \pm 4.0\%$ for Snowy Egret, and $23 \pm 2.1\%$ for Black-crowned Night-Heron [1993–2010]). Because Snowy Egret and Black-crowned Night-Heron nestlings wander away from the nest when relatively young, their nests were considered successful if at least one nestling survived to 14 d or 15 d, respectively (Custer et al. 1983; Frederick and Collopy 1989). The productivity in successful nests was estimated based on prefledging brood size, when nestlings were old enough to have survived the period when most brood reduction occurs (5–8 weeks for Great Blue Herons and 5–7 weeks for Great Egrets; Pratt 1970; Pratt and Winkler 1985) or to the age when they begin to wander away from nest sites (7–14 days old in Snowy Egrets and 7–15 days old for Black-crowned Night-Herons; Custer et al. 1983, Frederick and Collopy 1989).

Rainfall

Seasonal rainfall totals for winter (November through February) and spring (March through June) were estimated at each colony location using the high-resolution precipitation climate data sets developed by the PRISM Climate Group (C. Daly, Spatial Climate Analysis Service, Oregon State University;

<http://prism.oregonstate.edu>). The spatial resolution of the data is 2.4 arc minutes (approximately 4 km), which captured the local rainfall conditions experienced by the foraging herons and egrets associated with individual colony sites (Fig. 1; Kelly et al. 2008). To estimate the seasonal rainfall conditions experienced by each species, regional means of colony-site rainfall estimates were weighted by colony-site nest abundances (Table 1). These estimates assume that relative distributions across San Francisco Bay area landscapes were similar in winter and spring (Gill and Mewaldt 1979, Hom 1983), although unknown differences may occur.

Winter rainfall volatility was estimated as the standard deviation of residuals from linear trends in cumulative daily rainfall. These estimates were calculated by multiplying the coefficient of variation of residuals of daily cumulative rainfall trends in San Francisco, as an index of regional rainfall variation (CV, estimated as the standard deviation of residuals/mean cumulative rainfall; Golden Gate Weather Services, P. O. Box 3,071, Saratoga, CA 95,070; www.ggweather.com), by the estimated linear mean of cumulative regional rainfall, based on seasonal totals at each colony site as described above.

Statistical Analysis

A first order autoregressive (AR[1]) model was used to account for density-dependent population growth in relation to climate variation (Post et al. 2009):

$$X_t = \alpha_0 + (1 + \alpha_1)X_{t-1} + \sum \omega_{i,t-d} C_{i,t-d} + \varepsilon_t, \quad (1)$$

where X is the \log_e -transformed nest abundance in the current (t) or previous ($t-1$) year, α_0 is the intrinsic rate of increase in nest abundance without density dependence or climatic influences, α_1 is the strength of direct (first-order) density

Table 1 Regional means and standard errors (SE) of variables used in regression models of rainfall effects, 1989–2010, on annual changes in heron and egret nest abundance, 1991–2010, in the northern San Francisco Bay area. Differences in rainfall values among species reflect

differences in annual distribution of nesting abundance (see text). Rainfall volatility is estimated as the standard deviation of the residuals of linear trends in cumulative daily rainfall

Variable	Great Blue Heron		Great Egret		Snowy Egret		Black-crowned Night-Heron	
	Mean	(SE)	Mean	(SE)	Mean	SE	Mean	SE
Nest abundance (\log_e) ^a	5.99	(0.030)	6.67	(0.401)	5.72	(0.079)	6.43	(0.051)
Winter rainfall total (cm)	54.02	(4.336)	46.31	(3.575)	49.53	(3.895)	49.01	(3.818)
Spring rainfall total (cm)	18.31	(2.382)	15.35	(1.98)	16.59	(2.209)	16.21	(2.159)
Winter rainfall volatility (cm)	5.34	(0.430)	4.57	(0.351)	4.87	(0.361)	4.84	(0.373)
Spring rainfall volatility (cm)	1.73	(0.266)	1.46	(0.227)	1.58	(0.258)	1.55	(0.261)

^a Back-transformed 1991–2010 means, 95 % confidence intervals: 401, 375.9–426.7 (Great Blue Heron); 785, 724.4–854.6 (Great Egret); 304, 258.2–358.8 (Snowy Egret); 623, 559.6–693.4 (Black-crowned Night-Heron)

dependence, $C_{i,t-d}$ is the value of climate term i (rainfall amount or rainfall volatility) at lags of up to d years, $\omega_{i,t-d}$ is the associated strength of the climate effect, and ε_t is the error variation in nest abundance. This model assumes a linear relationship between the realized annual “per capita” (per nest) growth in nest abundance and the natural log of nest abundance in the prior year. It includes current and delayed effects of climate as external drivers. To model rainfall effects specifically on interannual rates of change in nest abundance, the model was re-expressed in this form:

$$r = \alpha_0 + \alpha_1 X_{t-1} + \sum \omega_{i,t-d} C_{i,t-d} + \varepsilon_t, \quad (2)$$

where $r = X_t - X_{t-1}$, the realized annual rate of change in nest abundance [$\ln(N_t/N_{t-1})$]. All variables were detrended prior to analysis, using the residuals from best-fit linear or polynomial regressions against year as the detrended values. After detrending, annual changes in nest abundance were not significantly autocorrelated ($P > 0.05$) and were determined to be stationary.

The heron and egret study species normally do not breed until the second spring after their hatching year (Parsons and Master 2000; Hothem et al. 2010; McCrimmon Jr et al. 2011; Vennesland and Butler 2011). Therefore, to account for potential, climate-related influences on the production, survival, and recruitment of juveniles, and for possible lags in the development of wetland food supplies relative to changes in seasonal rainfall, rainfall effects were considered at lags of up to 2 years.

A set of 12 *a priori* models was used to evaluate rainfall effects and applied identically to each of the study species (Table 2). To avoid over-fitting models to a relatively limited data series (Burnham and Anderson 2002), the candidate models were structured as simple combinations of two predictor variables. Each *a priori* combination was considered to have a reasonable potential to account for variation in nest abundance, based on published accounts of rainfall effects on heron or egret reproductive performance, overwinter survival, or immigration/emigration (e.g., Frederick and Collopy 1989; Maddock and Baxter 1991; Fasola et al. 2010), and on our experience with these species and associated wetland systems (Kelly et al. 2007, 2008). Scatter plots, residual plots, and partial regression plots were visually inspected, using LOWESS smoothers (Cleveland 1979). The relationships between response variables and predictor variables were determined to be approximately linear and to satisfy the assumptions of normality and equal variance.

To linearize the effects of seasonal rainfall on annual nest abundance, the effects of total rainfall were modeled as rainfall suitability, with a quadratic decline during increasingly wet or dry years, relative to long-term average rainfall: $x' = -(x - \bar{x})^2$. This approach was based on observations of regional nesting

activity and habitat selection patterns suggesting that the availability of ephemeral feeding areas and suitable water depths for foraging increase to, or decrease from, an optimum level with the extent of rainfall and associated runoff (Bancroft et al. 2002; Russell et al. 2002; Beerens et al. 2011). Predictors for rainfall volatility were squared to model increased response rates with greater volatility. To ensure that modeled rainfall effects were linear, residual plots were inspected and associated improvements in predictive strength were confirmed.

The most parsimonious model for rainfall effects on nest abundance was determined based on the lowest Akaike Information Criterion score corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). The predictive information in each variable in each set of (species specific) models was evaluated by calculating its model-averaged coefficient as the sum across all models in which it occurred, multiplied by Akaike weights (w_i ; relative measures of model support that sum to 1 across models), and confidence intervals that incorporated model uncertainty (Burnham and Anderson 2002).

After running the set of candidate models, exploratory quadratic analyses (Burnham and Anderson 2002) were used to verify the extent to which hypothesized optimum (average) rainfall totals were consistent with maximum rates of growth in nest abundance. Because comparisons among candidate models must be based on fixed data (Burnham and Anderson 2002), we examined the stability of the models by comparing the results with those from median and robust regressions, which are less sensitive to outliers, and by fitting the best models ($\Delta AIC_c < 2$) to the data separately, to consider the potential effects of influential cases with high leverage or large residuals. We used partial regressions on each of the strongest predictors (controlling for the model-averaged effects of other predictors) to verify the extent to which rainfall variables independently predicted linear or quadratic trends in annual nest abundance.

To investigate whether density-dependent variation in nest abundance, which may involve spatial and temporal changes in abundance, could have included additional responses to rainfall conditions, we examined interactions between nest abundance in the previous year and each rainfall variable, using general linear models. To consider the extent to which changes in nest abundance may be related to rainfall effects on reproductive output within the region, two additional sets of analyses were run: (1) linear and quadratic regressions of overall reproductive rates against winter or spring rainfall variables, with \log_e nest abundance in the current year (X_t) as a covariate, and (2) AR (1) models relating changes in X_t to lagged effects of regional production (product of overall reproductive success and nest abundance) during the hatching year ($t-2$) of first-time breeders.

Table 2 *A priori* combinations of predictors used to model rainfall effects on annual change in heron and egret nest abundance. Variable names reflect winter (W; November-February) and spring (S; March-

June) rainfall total (TOT) or volatility (VOL; see text); *t* refers to the current breeding season (spring) or the winter *immediately prior* to the current breeding season

Model	Independent variables	Description
1	W-TOT (<i>t</i>), W-VOL (<i>t</i>)	Winter rainfall conditions immediately prior to nesting
2	W-TOT (<i>t</i> -1), W-VOL (<i>t</i> -1)	Rainfall conditions two winters before nesting, potentially associated with the development of prey or with first-winter juvenile survival or emigration/immigration
3	W-TOT (<i>t</i> -2), W-VOL (<i>t</i> -2)	Rainfall conditions three winters before nesting, potentially associated with the development of prey or with foraging conditions prior to the production of first-time breeders
4	S-TOT (<i>t</i> -2), S-VOL (<i>t</i> -2)	Rainfall conditions during the natal spring of first-time breeders
5	S-TOT (<i>t</i> -2), W-TOT (<i>t</i> -1)	} Rainfall conditions associated with nesting or foraging during the natal spring and first winter of first-time breeders
6	S-VOL (<i>t</i> -2), W-VOL (<i>t</i> -1)	
7	W-TOT (<i>t</i>), W-TOT (<i>t</i> -1)	} Rainfall totals or volatility during the previous two winters, potentially affecting the development or availability of prey
8	W-VOL (<i>t</i>), W-VOL (<i>t</i> -1)	
9	W-TOT (<i>t</i> -2), S-TOT (<i>t</i> -2)	} Winter and spring rainfall two years before nesting, potentially affecting development of prey or production of first-time breeders
10	W-VOL (<i>t</i> -2), S-VOL(<i>t</i> -2)	
11	W-TOT (<i>t</i>), W-TOT (<i>t</i> -2)	} Winter rainfall immediately prior to the current nesting season and the natal spring of first-time breeders
12	W-VOL (<i>t</i>), W-VOL (<i>t</i> -2)	

Most of the nests in the region were within a 10-km foraging range of tidal feeding areas (63±0.6 %, 92±0.7 %, 89±1.6 %, 85±2.2 % of nests y^{-1} for Great Blue Heron, Great Egret, Snowy Egret, and Black-crowned Night-Heron, respectively). To investigate the extent to which responses to seasonal rainfall may have differed in locations associated primarily with freshwater feeding areas (within 10 km), we used general linear models to measure potential interactions between tidal vs. nontidal conditions and each of the best-performing rainfall variables.

Results

Initial comparisons of the most likely models, given the data ($\Delta AIC_c < 2$), and the best-performing predictors suggested that regional growth of nest abundance declined with increasing winter rainfall volatility, for Great Blue Herons, and with wetter- or drier-than-average winters for Great Egrets (Tables 3 and 4, Fig. 2). These effects were strongest two winters (*t*-1) before nesting. The best-performing models and predictors suggested that growth rates of regional Snowy Egret and

Table 3 *A priori* multiple regression models predicting the annual rate of change in heron and egret nest abundances in the northern San Francisco Bay region. The number of parameters (K), difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), relative Akaike weight (w_i ; $\sum w_i = 1$), and measure of model fit (R^2) are provided. The most likely models, given the data, are in bold type ($\Delta AIC_c < 2$). See Table 2 for model descriptions

Model	Independent variables	K	ΔAIC_c^a	w_i	R^2
Great Blue Heron					
2	W-TOT (<i>t</i>-1), W-VOL (<i>t</i>-1)	4	0.00	0.520	0.73
7	S-VOL (<i>t</i> -2), W-VOL (<i>t</i> -1)	4	2.57	0.144	0.69
5	S-TOT (<i>t</i> -2), W-TOT (<i>t</i> -1)	4	2.80	0.128	0.69
4	S-TOT (<i>t</i> -2), S-VOL (<i>t</i> -2)	4	4.55	0.053	0.66
12	W-VOL (<i>t</i> -2), S-VOL (<i>t</i> -2)	4	4.96	0.044	0.65
8	W-VOL (<i>t</i>), W-VOL (<i>t</i> -1)	4	5.25	0.038	0.64
6	W-TOT (<i>t</i>), W-TOT (<i>t</i> -1)	4	5.99	0.026	0.63
10	W-TOT (<i>t</i> -2), S-TOT (<i>t</i> -2)	4	6.66	0.019	0.62
3	W-TOT (<i>t</i> -2), W-VOL (<i>t</i> -2)	4	8.21	0.009	0.58
9	W-TOT (<i>t</i>), W-TOT (<i>t</i> -2)	4	8.29	0.008	0.58
1	W-TOT (<i>t</i>), W-VOL (<i>t</i>)	4	8.90	0.006	0.57
11	W-VOL (<i>t</i>), W-VOL (<i>t</i> -2)	4	8.99	0.006	0.57
	Null - density dependence	2	5.23	0.037	0.56
Great Egret					
5	S-TOT (<i>t</i>-2), W-TOT (<i>t</i>-1)	4	0.00	0.498	0.67
2	W-TOT (<i>t</i>-1), W-VOL (<i>t</i>-1)	4	1.86	0.197	0.64
6	W-TOT (<i>t</i>), W-TOT (<i>t</i> -1)	4	2.40	0.150	0.63
4	S-TOT (<i>t</i> -2), S-VOL (<i>t</i> -2)	4	5.23	0.036	0.57
10	W-TOT (<i>t</i> -2), S-TOT (<i>t</i> -2)	4	5.66	0.029	0.56
7	S-VOL (<i>t</i> -2), W-VOL (<i>t</i> -1)	4	6.58	0.019	0.53
12	W-VOL (<i>t</i> -2), S-VOL (<i>t</i> -2)	4	6.61	0.018	0.53
1	W-TOT (<i>t</i>), W-VOL (<i>t</i>)	4	7.35	0.013	0.52
8	W-VOL (<i>t</i>), W-VOL (<i>t</i> -1)	4	7.49	0.012	0.51
9	W-TOT (<i>t</i>), W-TOT (<i>t</i> -2)	4	7.73	0.010	0.50
11	W-VOL (<i>t</i>), W-VOL (<i>t</i> -2)	4	7.80	0.010	0.50
3	W-TOT (<i>t</i> -2), W-VOL (<i>t</i> -2)	4	8.46	0.007	0.49
	Null - density dependence	2	5.32	0.034	0.46
Snowy Egret					
12	W-VOL (<i>t</i>-2), S-VOL (<i>t</i>-2)	4	0.00	0.211	0.63
11	W-VOL (<i>t</i>), W-VOL (<i>t</i>-2)	4	0.96	0.131	0.62
8	W-VOL (<i>t</i>), W-VOL (<i>t</i>-1)	4	1.49	0.100	0.60
4	S-TOT (<i>t</i>-2), S-VOL (<i>t</i>-2)	4	1.62	0.094	0.60
1	W-TOT (<i>t</i>), W-VOL (<i>t</i>)	4	1.70	0.090	0.60
10	W-TOT (<i>t</i> -2), S-TOT (<i>t</i> -2)	4	2.13	0.073	0.59
5	S-TOT (<i>t</i> -2), W-TOT (<i>t</i> -1)	4	2.16	0.072	0.63
2	W-TOT (<i>t</i> -1), W-VOL (<i>t</i> -1)	4	2.34	0.065	0.59
6	W-TOT (<i>t</i>), W-TOT (<i>t</i> -1)	4	2.47	0.062	0.58
7	S-VOL (<i>t</i> -2), W-VOL (<i>t</i> -1)	4	2.47	0.061	0.58
3	W-TOT (<i>t</i> -2), W-VOL (<i>t</i> -2)	4	3.96	0.029	0.55
9	W-TOT (<i>t</i>), W-TOT (<i>t</i> -2)	4	5.82	0.011	0.50
	Null - density dependence	2	1.87	0.083	0.50
Black-crowned Night-Heron					
12	W-VOL (<i>t</i>-2), S-VOL (<i>t</i>-2)	4	0.00	0.9979	0.90

Table 3 (continued)

Model	Independent variables	K	ΔAIC_c^a	w_i	R^2
11	W-VOL (<i>t</i>), W-VOL (<i>t</i> -2)	4	13.75	0.0010	0.80
7	S-VOL (<i>t</i> -2), W-VOL (<i>t</i> -1)	4	14.80	0.0006	0.79
4	S-TOT (<i>t</i> -2), S-VOL (<i>t</i> -2)	4	16.56	0.0003	0.77
1	W-TOT (<i>t</i>), W-VOL (<i>t</i>)	4	19.09	0.0001	0.73
8	W-VOL (<i>t</i>), W-VOL (<i>t</i> -1)	4	19.30	0.0001	0.73
5	S-TOT (<i>t</i> -2), W-TOT (<i>t</i> -1)	4	21.87	0.0000	0.69
10	W-TOT (<i>t</i> -2), S-TOT (<i>t</i> -2)	4	22.35	0.0000	0.68
3	W-TOT (<i>t</i> -2), W-VOL (<i>t</i> -2)	4	23.27	0.0000	0.67
6	W-TOT (<i>t</i>), W-TOT (<i>t</i> -1)	4	26.99	0.0000	0.60
2	W-TOT (<i>t</i> -1), W-VOL (<i>t</i> -1)	4	28.39	0.0000	0.57
9	W-TOT (<i>t</i>), W-TOT (<i>t</i> -2)	4	29.29	0.0000	0.54
	Null - density dependence	2	33.67	0.0021	0.52

^a AIC_c of best model: -29.33 (Great Blue Heron); -15.08 (Great Egret); 13.70 (Snowy Egret); -11.96 (Black-crowned Night-Heron)

Black-crowned Night-Heron nest abundances may decline with increasing rainfall volatility immediately before nesting and with increasing spring rainfall volatility 2 years (*t*-2) before nesting (Tables 3 and 4, Fig. 2). In addition, Snowy Egret nest abundance declined with greater spring rainfall 2 years before nesting (*t*-2). Direct, first-order density dependence was suggested by strongly negative, model-averaged coefficients for all species (Table 4).

Exploratory investigation after the *a priori* analyses verified the relative strengths of seven of the eight best performing predictors (the suggested effects of rainfall volatility three winters before nesting on Black-crowned Night-Herons were eliminated by analysis of partial residuals and outliers; Fig. 2). For Great Blue Herons and Great Egrets, annual growth in nest abundance declined with greater-than-average winter rainfall volatility (Tables 1 and 5, Fig. 3). The growth of Great Egret nest abundance was maximized at 45.0 cm of winter rainfall, two winters before nesting, which was near the regional average of 46.3 cm (1989–2010; Table 1, Fig. 3). Total winter rainfall was not among the strongest model-averaged predictors for other species (Fig. 2), but positive correlations with winter rainfall volatility ($r=0.43$ – 0.54 for all species, 1989–2010) suggests that heavy winter rainfall may also lead to lagged declines in heron and egret nest abundance. The growth rate of Snowy Egret nest abundance exhibited a linear decline with increasing spring rainfall and a linear or quadratic decline with increasing winter rainfall volatility, especially when volatility exceeded the regional average (Fig. 3, Tables 1 and 5). The annual growth of Black-crowned Night-Heron nest abundance was maximized when total spring rainfall reached 4.6 cm, which was near the regional average of 4.8 cm. (Table 1, Fig. 3). The results for night-herons also suggested a linear decline with increasing spring rainfall 2 years before the current nesting season (Fig. 3, Table 5).

Table 4 Model-averaged multiple regression coefficients predicting the effects of seasonal rainfall on the annual rate change in heron and egret (\log_e) nest abundance. Unconditional standard error (SE), standardized (beta) coefficient, and relative importance based (sum of Akaike weights [Σw_i] across all models that include variable) are provided. Coefficients for first-order density dependence (X_{t-1}) are included in all models. Variables in bold have coefficients with 95 % confidence intervals^a that exclude zero. See Table 2 for variable descriptions

Independent variable	Coefficient	SE	Beta coefficient	Σw_i
Great Blue Heron				
W-VOL (<i>t</i>-1)	-0.011961	0.005768	-0.30	0.70
S-TOT (<i>t</i> -2)	0.000160	0.000125	0.21	0.20
W-TOT (<i>t</i> -1)	-0.000038	0.000057	-0.17	0.67
W-VOL (<i>t</i> -2)	-0.002921	0.004104	-0.07	0.06
W-TOT (<i>t</i>)	-0.000013	0.000037	-0.06	0.04
W-TOT (<i>t</i> -2)	0.000007	0.000046	0.03	0.04
W-VOL (<i>t</i>)	-0.000500	0.006866	-0.01	0.05
S-VOL (<i>t</i> -2)	-0.008425	0.013684	0.00	0.24
X_{t-1}	-0.939666	0.450320	-0.75	1.00
Great Egret				
W-TOT (<i>t</i>-1)	0.0002318	0.0000937	0.38	0.85
S-VOL (<i>t</i> -2)	-0.0252921	0.0212351	-0.23	0.07
S-TOT (<i>t</i> -2)	0.0004691	0.0003342	0.22	0.56
W-VOL (<i>t</i>)	-0.0133711	0.0142500	-0.17	0.04
W-TOT (<i>t</i> -2)	-0.0001038	0.0001261	-0.17	0.05
W-VOL (<i>t</i> -1)	-0.0077190	0.0125577	-0.10	0.23
W-TOT (<i>t</i>)	-0.0000238	0.0001085	-0.04	0.17
W-VOL (<i>t</i> -2)	-0.0003706	0.0140508	-0.02	0.04
X_{t-1}	-0.8844094	0.2128345	-0.67	1.00
Snowy Egret				
S-VOL (<i>t</i>-2)^a	-0.0424918	0.0245305	-0.40	0.37
S-TOT (<i>t</i>-2)^a	0.0008966	0.0005411	0.40	0.24
W-VOL (<i>t</i>)^a	-0.0507281	0.0285922	-0.30	0.32
W-TOT (<i>t</i> -1)	0.0002585	0.0001642	0.27	0.20
W-VOL (<i>t</i> -2)	0.0306632	0.0304279	0.20	0.37
W-TOT (<i>t</i> -2)	0.0000644	0.0001702	0.10	0.11
W-VOL (<i>t</i> -1)	-0.0077029	0.0288972	-0.04	0.23
W-TOT (<i>t</i>)	-0.0000220	0.0001696	-0.02	0.16
X_{t-1}	-1.0817424	0.2627280	-0.78	1.00
Black-crowned Night-Heron				
S-VOL (<i>t</i>-2)	-0.0424820	0.0071398	-0.48	1.00
W-VOL (<i>t</i>-2)	0.0308965	0.0063435	0.40	1.00
W-VOL (<i>t</i>)	-0.0314221	0.0102743	-0.38	0.00
W-VOL (<i>t</i> -1)	0.0217606	0.0160036	0.28	0.00
S-TOT (<i>t</i> -2)	0.0004891	0.0004152	0.20	0.00
W-TOT (<i>t</i> -1)	0.0000603	0.0000865	0.11	0.00
W-TOT (<i>t</i>)	0.0000361	0.0000797	0.06	0.00
W-TOT (<i>t</i> -2)	-0.0000069	0.0000862	0.02	0.00
X_{t-1}	-1.1736285	0.1223116	-0.78	1.00

^a The strongest model-averaged predictors for Snowy Egrets excluded zero from 90 % confidence intervals

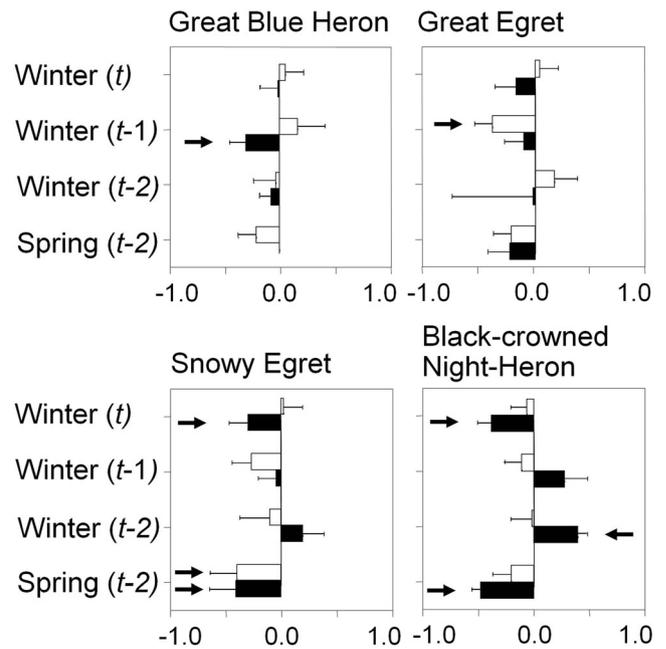


Fig. 2 *A priori* comparison of annual differences in regional heron and egret nest abundance with increasing winter rainfall volatility (solid bars) and increasing deviation of total seasonal rainfall from the 1989–x average (open bars; opposite of modeled suitability). Bars represent model-averaged multiple regression (standardize beta) coefficients (\pm SE); *t* refers to the current breeding season (spring) or the winter immediately prior to the current breeding season. Arrows indicate potentially important predictors selected for exploratory analysis after the *a priori* analyses

Regional production (2 years prior to nesting) had no substantial effect on changes in nest abundance in any of the study species (partial eta-square [η^2] values < 0.01; 95 % confidence intervals included zero).

The effects of rainfall on changes in nest abundance were not detectable unless the models accounted for density dependence. Density-dependent interactions with rainfall conditions were evident only in Great Blue Herons, suggesting increasing (negative) density dependence with greater winter rainfall volatility during the current year ($b = -3.0 \pm 0.91$) and 2 years prior to nesting ($b = -1.1 \pm 0.02$); however, these predictors were relatively unimportant in the overall analysis. No other substantial interactions between rainfall conditions and density dependence were found (95 % confidence intervals included zero). Responses to the best performing rainfall predictors were consistent across tidal and freshwater foraging areas (95 % confidence intervals of interactions included zero).

Discussion

The annual growth or resilience of heron and egret nest abundances in the northern San Francisco Bay area declined with heavier-than-usual winter or spring rainfall or rainfall

Table 5 Partial regressions of the (\log_e) rate of change in heron and egret nest abundance on key rainfall predictors (controlling for the model-averaged effects of other predictors). See Table 2 for variable descriptions and Fig. 3 for regression plots

Independent variable	Model	n	R^2	Beta	Coefficient	SE	95 % Confidence interval		ΔAIC_c
Great Blue Heron									
W-VOL ($t-1$)	quadratic response ^a	19	0.29	0.54	3.404	1.280	0.703	6.105	
	quadratic effect (a)			-2.93	-0.013	0.005	-0.024	-0.002	
	linear effect (b)			2.77	0.143	0.060	0.016	0.269	
Great Egret									
W-TOT ($t-1$)	quadratic response ^a	19	0.46	0.68	2.189	0.579	0.967	3.412	
	quadratic effect (a)			-3.40	-0.0004	0.0001	-0.001	-0.0001	
	linear effect (b)			3.02	0.034	0.012	0.009	0.059	
Snowy Egret									
W-VOL (t)	linear response	18	0.23	-0.48	-0.094	0.042	-0.184	-0.004	0.00
	quadratic response ^a	18	0.28	0.53	3.619	1.464	0.505	6.723	1.91
	quadratic effect (a)			-1.55	-0.029	0.031	-0.096	0.038	
	linear effect (b)			1.04	0.203	0.324	-0.487	0.894	
S-TOT ($t-2$)	linear response	17	0.49	-0.70	-0.017	0.004	-0.026	-0.007	0.00
	quadratic response ^a	17	0.49	0.59	2.900	1.030	0.702	5.094	2.77
	quadratic effect (a)			-0.32	-0.0002	0.0004	-0.001	0.0007	
	linear effect (b)			-0.39	-0.009	0.018	-0.047	0.029	
S-VOL ($t-2$)	linear response	18	0.23	-0.48	-0.073	0.033	-0.143	-0.003	
Black-crowned Night-Heron									
S-VOL ($t-2$)	linear response	19	0.50	-0.71	-0.089	0.022	-0.135	-0.044	0.00
	quadratic response ^a	19	0.52	0.71	2.059	0.484	1.039	3.080	2.08
	quadratic effect (a)			-0.40	-0.010	0.012	-0.035	0.015	
	linear effect (b)			-0.34	-0.043	0.059	-0.168	0.082	
W-VOL (t)	quadratic response ^a	19	0.43	0.66	2.330	0.650	0.955	3.697	
	quadratic effect (a)			-3.30	-0.023	0.007	-0.038	-0.007	
	linear effect (b)			2.97	0.214	0.076	-0.053	0.325	

^a Overall quadratic ($ax^2 + bx$) response reflects independent linear and quadratic effects

volatility. Winter storms in central coastal California often impose harsh conditions that may degrade foraging habitat quality, reduce food availability, or increase thermal stress. The lagged, negative effects of heavy rainfall conditions two winters before nesting in Great Blue Herons and Great egrets suggest the possibility of negative effects on foraging conditions encountered by juveniles during their first winter, although such conditions might also affect adults. Similar responses immediately before nesting by Snowy Egrets and Black-crowned Night-Herons suggest the possibility of reduced food availability affecting nesting efforts by adults. However, we did not investigate the movements or survival rates of juveniles or adults. Others have suggested that thermal stress during winter may reduce the survival of juveniles and the growth of heron and egret nesting populations (North 1979; Butler 1994; Cezilly 1997). This possibility is supported by relatively low foraging proficiencies in juvenile herons (Butler 1995). North and Morgan (1979) found that reduced numbers of resident heron and egret species in Britain were associated with reduced overwinter survival of first-year birds.

Lagged responses to rainfall may reflect the timing of wetland processes that enhance populations of fishes or other wetland prey targeted by foraging herons and egrets. Great Egret nest abundances, which are concentrated in the Suisun Bay subregion (Fig. 1; Kelly et al. 2007), declined with unusually low rainfall two winters before nesting, which is consistent with the relative unavailability of crayfish (*Procambarus clarkii*) during dry periods (Penn 1943, Bildstein et al. 1990) and first-winter foraging stress in juveniles that potentially nest after their second winter; crayfish are normally abundant in that area with widespread evidence of crayfish prey remains in heronries (personal observations). Such effects may be complicated by other processes beyond the scope of this study that affect food supply or availability at larger spatial scales or in other regions, such as California's Central Valley.

Fasola et al. (2010) found that the migratory populations of Black-crowned Night-Heron and Squacco Heron (*Ardeola ralloides*) nesting in southern Europe increased with increasing rainfall in their African wintering range, and they

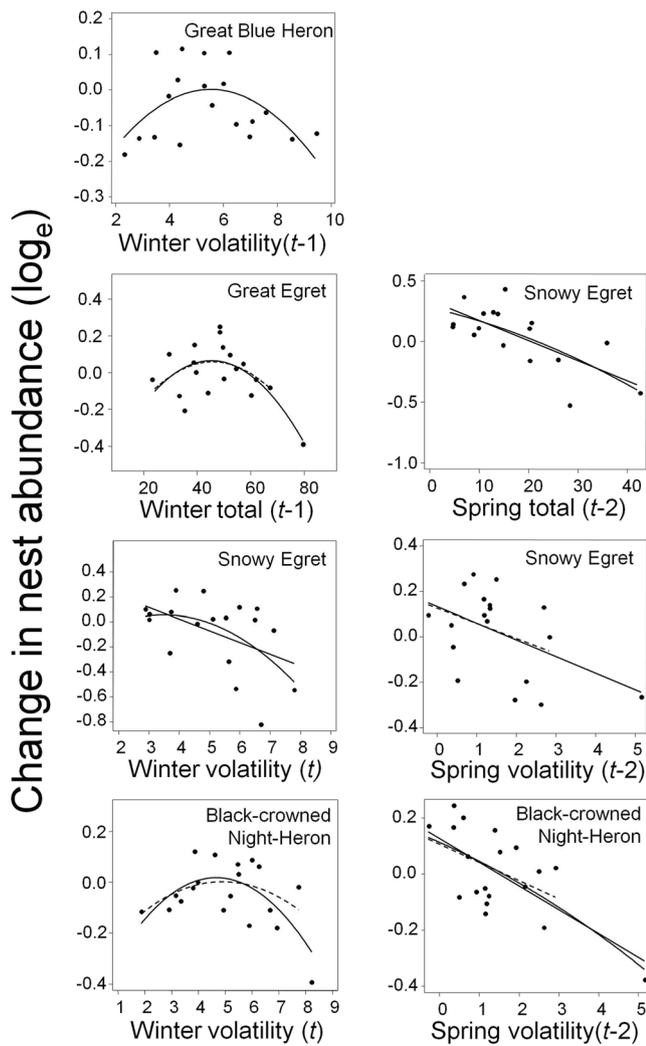


Fig. 3 Partial linear and quadratic regression plots (solid lines) of the log_e rate of change in heron and egret nest abundance on key model-averaged predictors for total winter (November–February) or spring (March–June) rainfall and winter rainfall volatility (see text). Dashed lines illustrate the consistency of the trends if relatively extreme values with acceptable influence are omitted; *t* refers to the current breeding season (spring) or the winter immediately prior to the current breeding season. See Table 5 for the regression results

attributed the changes to the enhancement of wetlands and improved food supplies in winter. In the Florida Everglades, Great Egret foraging distributions vary with dynamic hydrological conditions, and nesting abundances are associated with local foraging distributions prior to nesting (Bancroft et al. 1994). In the San Francisco Bay area, relatively stable tidal foraging conditions suggest that nesting birds may be less likely to move to more hydrologically pulsed freshwater areas, where conditions can fluctuate greatly between years (Frederick 2002, Kelly et al. 2007). We found no differences in responses to rainfall between tidal and non-tidal areas, but nesting declines associated with periods of relatively low rainfall suggest that herons and egrets nesting in seasonally dynamic, non-tidal systems in drier parts of California, such as

the San Joaquin Valley, may exhibit more severe, drought-induced nesting declines.

The dynamics of heron and egret populations operate over large spatial scales involving complex, interregional patterns of reproduction, survival, seasonal dispersal, and emigration/immigration. The seasonal movements of herons and egrets nesting in the San Francisco Bay area are poorly known, but they likely involve dispersal within the region during winter with some movement into the Central Valley or other regions of California (Gill and Mewaldt 1979). Because such processes are likely to be open or partially open at regional scales, their effects may not substantially influence changes in regional nest abundance. More information is needed to understand the extent to which the regional responses reflect influxes or losses of nesting birds to or from other areas and whether responses to rainfall variation by herons and egrets in the San Francisco Bay area are similar to those in the Central Valley or other regions.

Implications of Climate Change

Based on our results, increases in the volatility or amount of seasonal rainfall may reduce the annual growth or resilience of heron and egret nest abundances. Consecutive years with higher-than-usual winter or spring rainfall may exponentially degrade annual growth rates. Such effects may further depend on changes in the seasonal timing of rainfall within breeding and non-breeding periods.

Regional climate models for northwestern California predict increases in precipitation during winter, especially north of San Francisco, and decreases during spring (April–August; Kueppers et al. 2005; Pan et al. 2010). Extreme rainfall events are expected to increase in frequency and intensity (Cayan et al. 2008; Moser et al. 2009; Pan et al. 2010), suggesting declines in the growth or resilience of heron and egret nest abundance. The results presented here suggest that negative effects of increased winter rainfall on Snowy Egrets and Black-crowned Night-Herons, may be partially offset by benefits related to decreasing spring rainfall. However, predicted changes in precipitation within regions of California remain an area of considerable uncertainty (Knowles and Cayan 2002; Scavia et al. 2002).

Predictions of climate-related increases in flood frequency, storminess, and loss of tidal marsh feeding areas associated with sea level rise (Scavia et al. 2002; Frederick 2002; Stralberg et al. 2011) highlight the rainfall sensitivity of juvenile and adult herons and egrets. The possible importance of first-winter juvenile survival or emigration is consistent with vital demographic rates predicted by other studies (Butler 1994; Cezilly 1997; Arthur 2011). Conservation efforts that improve the resilience of wetland landscapes to episodic flooding and enhance winter foraging conditions for juveniles and

adults during wetter-than-average winters may be important to ensure the growth or resilience of heron and egret populations.

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