



# Effects of rainfall during winter and nesting seasons on the rate of change in heron and egret nest abundance and implications of climate change

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## INTRODUCTION

Changes in the structure and composition of wetland systems as a consequence of rising global temperatures have been hypothesized, yet little is known about how the resulting climate change might impact top wetland predators. Rainfall is one aspect of climate with the potential to affect wintering and breeding populations of herons and egrets—important predators in wetland systems. Rainfall can enhance the availability of seasonal wetland feeding areas, however heavy winter rain may reduce heron and egret foraging efficiency. Therefore, climate variation may enhance or reduce the availability of food during the nesting season and in winter. We investigated annual changes in heron and egret nesting abundance (Figure 1) in relation to rainfall variation, over 18 years at all known nesting colonies in the northern San Francisco Bay area. We also investigated rainfall effects on nest survivorship and the productivity of successful nests. We used monthly rainfall estimated for each colony site to account for local and subregional variation, using data generated by the PRISM Climate Group, Oregon State University. Analyses were conducted at regional and subregional scales (Figure 2).

## METHODS

We visited most heronries at least four times each nesting season, 1991-2008. We estimated regional and subregional nest abundance each year as the sum across heronries of seasonal peak counts of active nests. Field observations were made from the ground or from boats, often by trained volunteers.

We estimated annual production as peak annual nest abundance  $\times$  mean survivorship of focal nests  $\times$  mean productivity of successful nests. We estimated nest survivorship based on annual samples of focal nests ( $n = 53 \pm 5\%$  of regional nest abundance for Great Blue Heron,  $39 \pm 3\%$  for Great Egret,  $14 \pm 4\%$  for Snowy Egret, and  $22 \pm 2\%$  for Black-crowned Night-Heron). Nests were considered successful if at least one chick survived to minimum fledging age. Because Snowy Egret and Black-crowned Night-Heron nestlings begin to wander away from the nest when relatively young, we considered their nests to be successful at 14 or 15 days after first hatch, respectively. We estimated the productivity in successful nests as pre fledging brood size when nestlings were  $>5$  weeks old, for Great Blue Herons and Great Egrets ( $n = 49 \pm 1\%$  and  $31 \pm 2\%$  of regional nest abundance, respectively), 7-14 days old for Snowy Egrets ( $n = 13 \pm 4\%$ ) and 7-15 days old Black-crowned Night-Herons ( $n = 13 \pm 4\%$ ).

## STATISTICAL ANALYSIS

We used a first order autoregressive (AR[1]) model to account for density-dependent population growth in relation to rainfall variation, with the realized annual rate of change in nest abundance as the dependent variable:

$$X_t - X_{t-1} = r = \alpha_0 + \alpha_1 X_{t-1} + \sum \omega_{i,t-d} C_{i,t-d} + \epsilon_t$$

where  $X_t$  is  $\log_e$ -transformed nest abundance ( $\ln N$ ) in the current ( $t$ ) or previous ( $t-1$ ) year,  $r$  is the realized annual  $\log_e$  rate of change in nest abundance ( $\ln(N_t/N_{t-1})$ ),  $\alpha_0$  is the intrinsic rate of increase in nest abundance without density dependence or climatic influences,  $\alpha_1$  is the strength of direct (first-order) density dependence,  $C_{i,t-d}$  is the value of climate (seasonal rainfall) term  $i$  at lags of up to  $d$  years, and  $\omega_{i,t-d}$  is the associated strength of the climate effect. To focus the analysis on the interannual effects and to avoid spurious results related to nonstationary time series, we de-trended all variables prior to analysis. We used the residuals from best-fit linear or polynomial regressions against year as the de-trended values. To account for potential influences on recruitment associated with climate-related variation in hatching-year production and first-winter juvenile survival, we considered climate effects at lags of up to two years.

We developed a set of eight *a priori* candidate models with particular combinations of rainfall terms (Table 1). Each *a priori* combination was considered to have reasonable potential to account for variation in reproductive performance or overwinter survival, based on published accounts of rainfall effects on herons or egrets and on our experience with these species and associated wetland systems (Kelly et al. 2007, 2008).

We determined the most likely model for rainfall effects on nest abundance on the basis of the lowest Akaike information criterion score corrected for small sample sizes ( $AIC_c$ ; Table 2). Because of non-independence among predictor variables, we used bootstrap standard errors of predictor coefficients ( $n = 10,000$ ) and calculated unconditional confidence intervals that incorporated model uncertainty.

To investigate the extent to which rainfall might directly affect reproductive output, we performed three additional sets of regression analyses, with annual mean reproductive success, focal nest survivorship, and productivity of successful nests as response variables, and  $X_{t-1}$  and seasonal rainfall variables as predictors. To directly consider the effects of production on changes in nest abundance, we ran multiple regressions with  $r_t$  as the response variable and  $X_{t-1}$  and reproductive success variables as predictors.

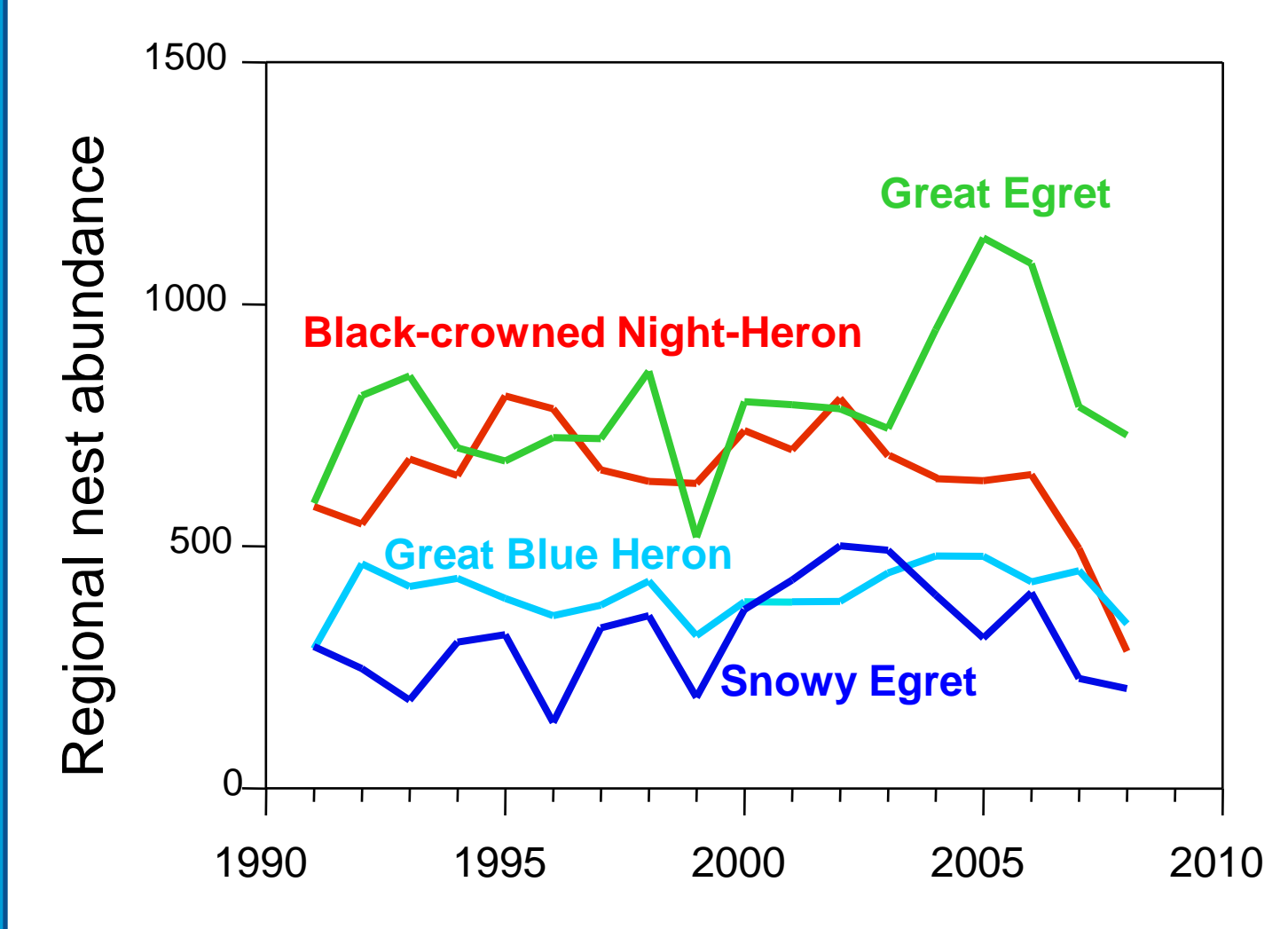


Figure 1. Annual variation in nest abundance of (A) Great Blue Herons (B) Great Egrets, (C) Snowy Egrets, and (D) Black-crowned Night-Herons in the northern San Francisco Bay area, 1991-2008.

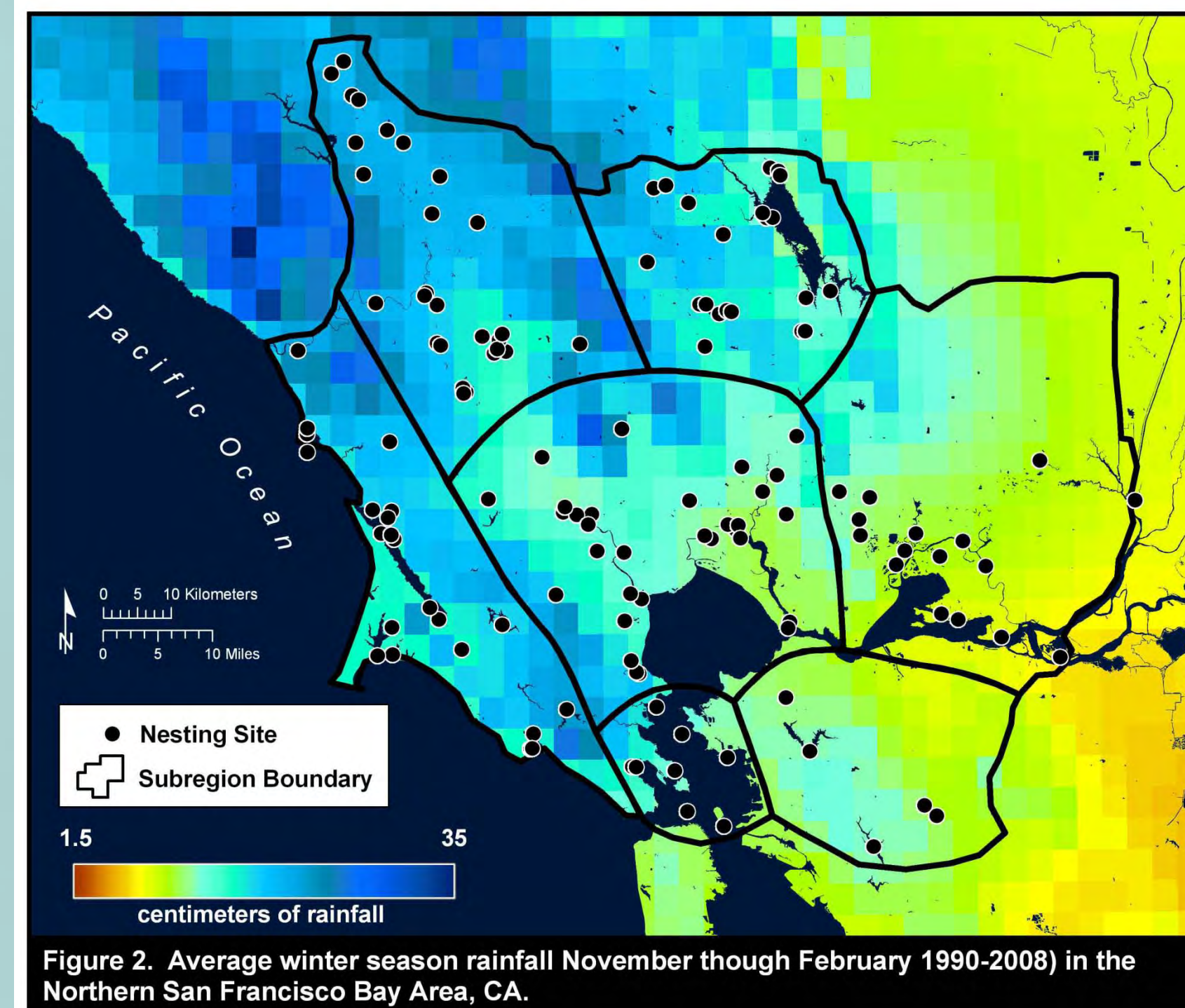


Figure 2. Average winter season rainfall November through February 1990-2008) in the Northern San Francisco Bay Area, CA.

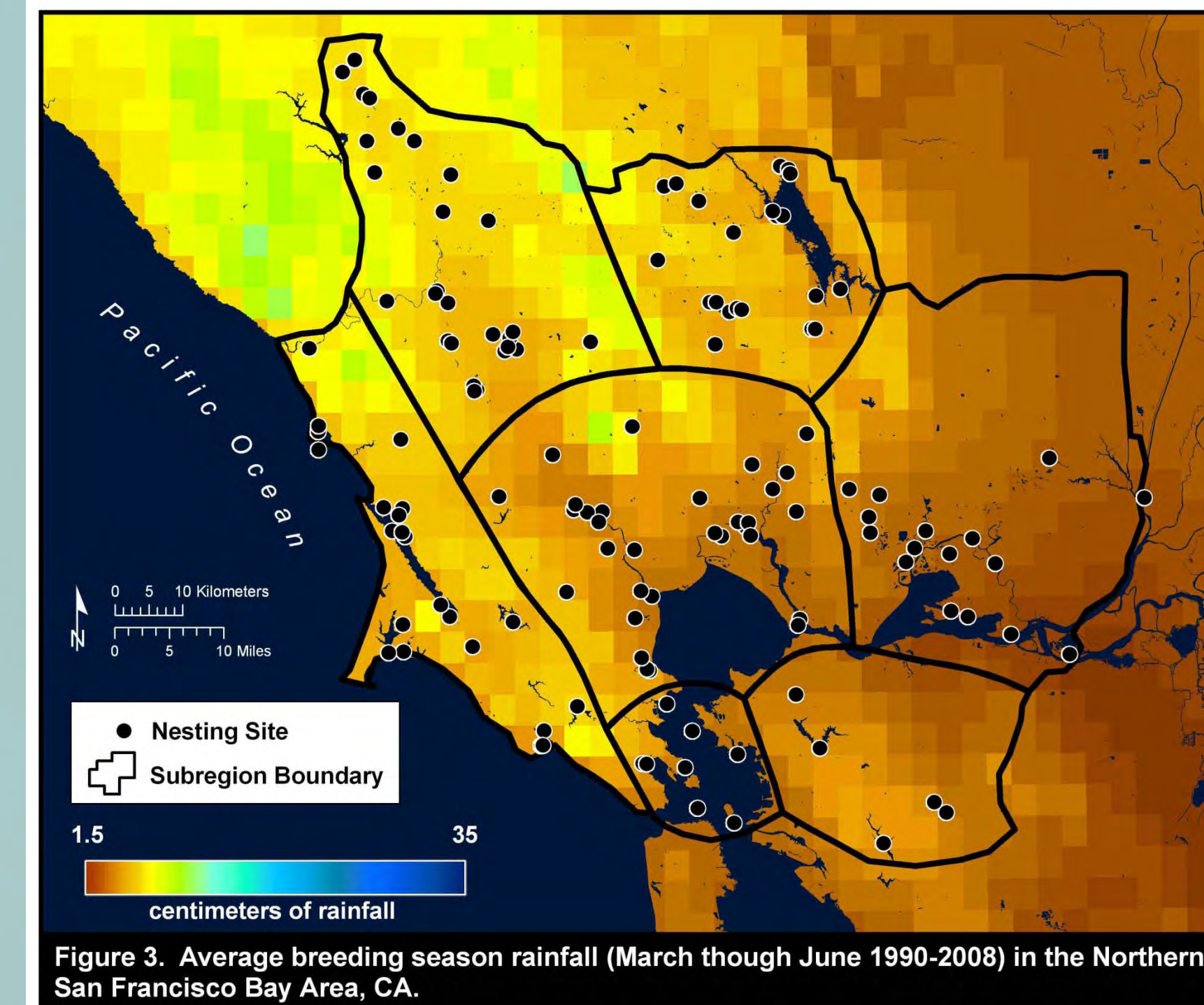


Figure 3. Average breeding season rainfall (March through June 1990-2008) in the Northern San Francisco Bay Area, CA.

## RESULTS AND DISCUSSION

**Regional patterns.** Changes in Great Blue Heron and Great Egret nest abundance were influenced more strongly by rainfall during winter than during the nesting season. The strongest effects of winter rainfall were lagged one year and appeared in each of the top three models for these two species (Tables 2 and 3), suggesting rainfall-induced declines in survival (or increased emigration) of juveniles during their first winter. Results for Snowy Egret and Black-crowned Night-Heron were more complex and lacked strong predictors, but the best models consistently reflected lagged rainfall effects on hatch-year or first-winter conditions (Table 2).

Direct, first-order density dependence was suggested by negative, approximately linear ( $\log_e$ ) trends and negative coefficients for nest abundance in the previous year, in all models for all species, although 95% confidence intervals excluded zero only for Great Egret and Black-crowned Night-Heron (Figure 4). Because data were limited to only 18 years, confidence intervals tended to be wide, and annual variation in nest abundance may not reflect long-term patterns.

**Reproduction.** We found no distinguishable effects of regional winter or spring rainfall on annual nest survival, brood size in successful nests, or overall reproductive output. Therefore, rainfall effects on nest abundance may be more closely related to juvenile or adult survivorship, or inter- or intraregional movement between nesting years, possibly through effects on wetland foraging conditions, than to variation in reproductive rate.

**Subregional patterns.** The most likely models at subregional scales were generally consistent with regional patterns, with reduced growth in nest abundance related to lagged effects of increased winter rainfall during the first winter of first-time breeders. Subregional variation was complex and requires more intensive investigation. For example, growth in Great Blue Heron nest abundance declined with two-year lags in nesting season rainfall in the Russian River and Laguna de Santa Rosa, but increased with two-year lags in nesting season rainfall along the Outer Pacific Coast. In contrast with the regional pattern, increased winter rainfall may lead to increases in nest abundance in seasonally dynamic, non-tidal landscapes, possibly through enhanced juvenile survival or immigration. Such areas include the diked marshes of Suisun Bay and the drier wetland landscape of northern Napa County. Differential rainfall effects among subregions may contribute to dynamic shifts in nesting distribution among San Francisco Bay area heronries (Kelly et al. 2007).

**Implications of climate change.** Regional climate models predict future increases in precipitation in northwest California, but decreases in spring (April-August) rainfall (Kueppers et al 2005), implying increased precipitation during the winter months. Our results suggest that long-term increases in the extent of winter rainfall may depress regional rates of population growth in herons and egrets. In addition, predicted increases in flood frequency, storminess, and loss of tidal marsh feeding areas associated with sea level rise, highlight the sensitivity of herons and egrets to rainfall patterns during their first winter.

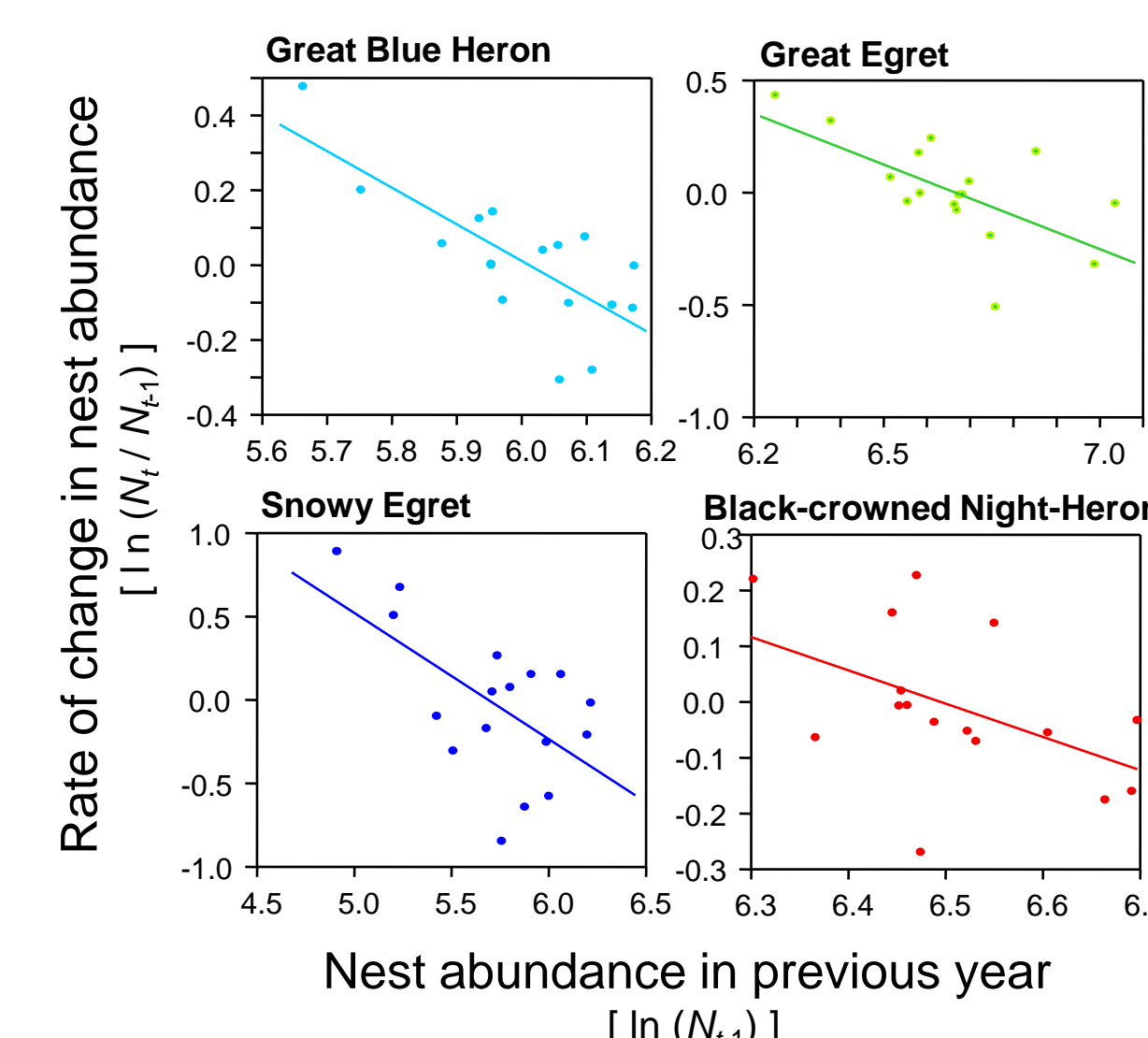


Figure 4. Dependence of realized rate of change in heron and egret nest abundance on the number of nests in the previous year.

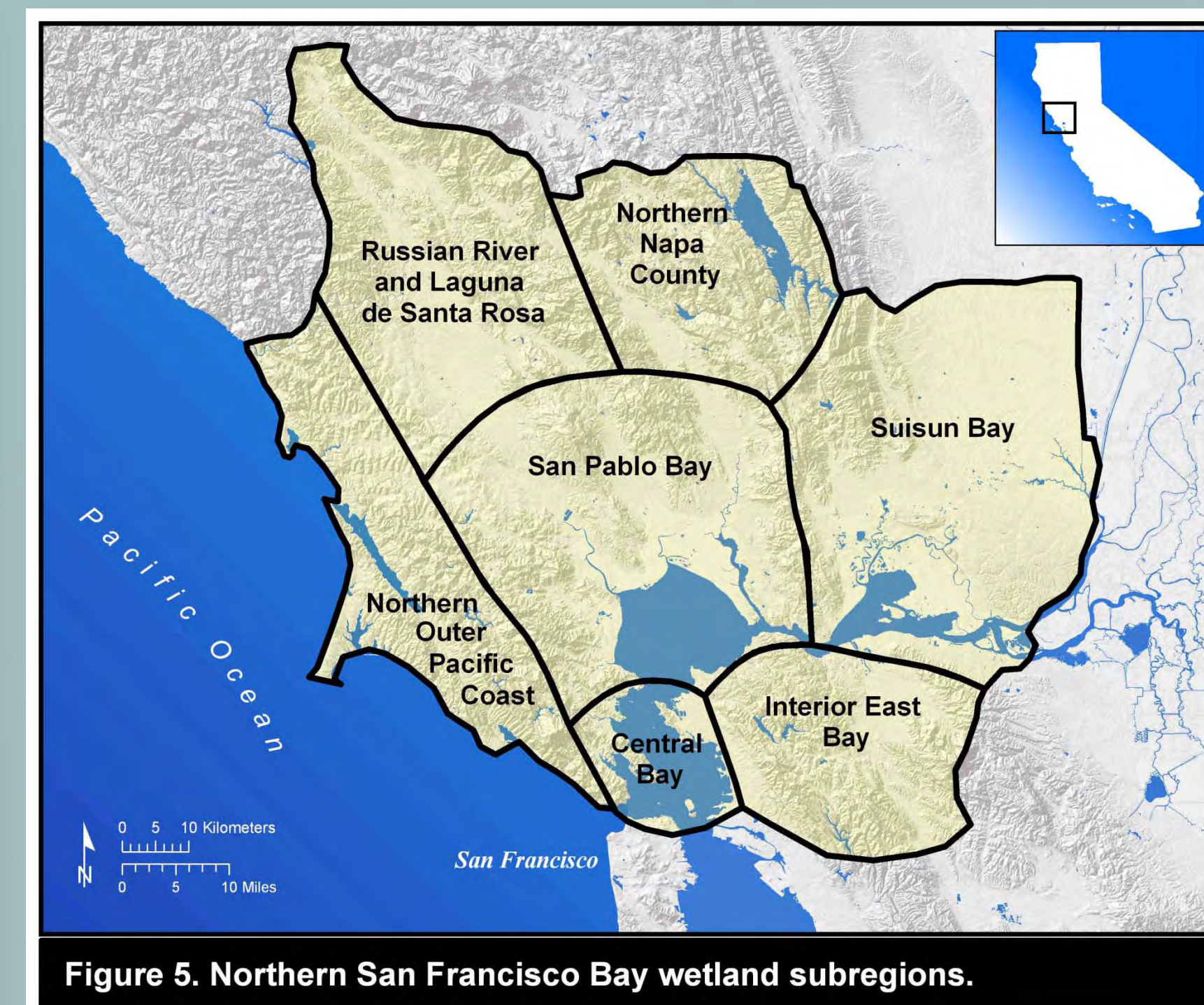


Figure 5. Northern San Francisco Bay wetland subregions.

**Table 2.** Multiple regression models predicting annual rate of change in nest abundance. The number of model parameters (K, including first order density dependence and constant), difference in Akaike's Information Criterion adjusted for small sample size ( $\Delta AIC_c$ ), relative Akaike weight ( $w_i$ , sums to 1), and measure of model fit ( $R^2$ ) are provided. Most likely models, given the data, are indicated in red ( $\Delta AIC_c < 2$ ).

Model	K	$\Delta AIC_c$	$w_i$	$R^2$
<b>Great Blue Heron</b>				
NOVFEB <sub>t-1</sub>	3	0.00	0.599	0.60
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-1</sub>	4	2.73	0.153	0.61
NOVFEB <sub>t-1</sub> , MARJUN <sub>t-2</sub>	4	3.49	0.105	0.60
NOVFEB <sub>t-1</sub>	3	4.50	0.063	0.47
MARJUN <sub>t-2</sub>	3	5.55	0.037	0.44
NOVFEB <sub>t-2</sub>	3	6.17	0.027	0.43
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-2</sub>	4	7.95	0.011	0.49
NOVFEB <sub>t-2</sub> , MARJUN <sub>t-2</sub>	4	9.61	0.005	0.43
<b>Great Egret</b>				
NOVFEB <sub>t-1</sub>	3	0.00	0.485	0.63
NOVFEB <sub>t-1</sub> , MARJUN <sub>t-2</sub>	4	1.08	0.283	0.68
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-1</sub>	4	2.18	0.163	0.66
MARJUN <sub>t-2</sub>	3	6.14	0.023	0.47
NOVFEB <sub>t-1</sub>	3	6.16	0.022	0.47
NOVFEB <sub>t-2</sub>	3	6.78	0.016	0.46
NOVFEB <sub>t-2</sub> , MARJUN <sub>t-2</sub>	4	9.81	0.004	0.47
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-2</sub>	4	9.97	0.003	0.47
<b>Snowy Egret</b>				
MARJUN <sub>t-2</sub>	3	0.00	0.437	0.35
NOVFEB <sub>t-1</sub> , MARJUN <sub>t-2</sub>	4	0.80	0.293	0.45
NOVFEB <sub>t-2</sub> , MARJUN <sub>t-2</sub>	4	1.98	0.163	0.45
NOVFEB <sub>t-1</sub>	3	4.08	0.057	0.18
NOVFEB <sub>t-1</sub>	3	6.06	0.021	0.08
NOVFEB <sub>t-2</sub>	3	6.49	0.017	0.08
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-1</sub>	4	7.57	0.010	0.18
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-2</sub>	4	9.98	0.003	0.08
<b>Black-crowned Night-Heron</b>				
NOVFEB <sub>t-1</sub>	3	0.00	0.228	0.55
MARJUN <sub>t-2</sub>	3	0.20	0.206	0.54
NOVFEB <sub>t-2</sub>	3	0.31	0.195	0.42
NOVFEB <sub>t-1</sub>	3	0.34	0.192	0.54
NOVFEB <sub>t-1</sub> , MARJUN <sub>t-2</sub>	4	2.93	0.053	0.56
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-2</sub>	4	3.12	0.048	0.44
NOVFEB <sub>t-1</sub> , NOVFEb <sub>t-1</sub>	4	3.31	0.044	0.55
NOVFEB <sub>t-2</sub> , MARJUN <sub>t-2</sub>	4	3.76	0.035	0.42

**Table 3.** Model-averaged regression coefficients for winter and spring rainfall (cm) predictor variables in multiple regression models of annual rate change in heron and egret nest abundance. See Table 1 for variable descriptions. Unconditional bootstrap standard error (SE), 95% confidence interval (CI), and relative importance based on sum of Akaike weights across all models in which the variable was present ( $\sum w_i$ ) are provided.

Variable	Coefficient	Unconditional SE	95% CI	$\sum w_i$
<b>Great Blue Heron</b>				
NOVFEB <sub>t-1</sub>	-0.006	0.003	-0.012 - 0.0006 <sup>a</sup>	0.856
NOVFEB <sub>t-1</sub>	0.002	0.002	-0.003 - 0.007	0.227
MARJUN <sub>t-2</sub>	0.000	0.005	-0.011 - 0.010	0.147
NOVFEB <sub>t-2</sub>	-0.002	0.003	-0.007 - 0.003	0.044
<b>Great Egret</b>				
NOVFEB <sub>t-1</sub>	-0.013	0.006	-0.024 - -0.002	0.932
MARJUN <sub>t-2</sub>	-0.014	0.015	-0.044 - 0.015	0.310
NOVFEB <sub>t-1</sub>	-0.005	0.006	-0.017 - 0.006	0.189
NOVFEB <sub>t-2</sub>	-0.001	0.010	-0.020 - 0.018	0.023
<b>Snowy Egret</b>				
MARJUN <sub>t-2</sub>	-0.008	0.005	-0.019 - 0.002	0.892
NOVFEB <sub>t-1</sub>	-0.003	0.003	-0.008 - 0.002	0.359
NOVFEB <sub>t-2</sub>	0.002	0.003	-0.005 - 0.008	0.183
NOVFEB <sub>t-1</sub>	0.000	0.016	-0.032 - 0.032	0.034
<b>Black-crowned Night-Heron</b>				
NOVFEB <sub>t-1</sub>	-0.002	0.003	-0.007 - 0.004	0.324
MARJUN <sub>t-2</sub>	-0.002	0.004	-0.010 - 0.006	0.294
NOVFEB <sub>t-1</sub>	0.001	0.003	-0.004 - 0.006	0.283
NOVFEB <sub>t-2</sub>	-0.002	0.002	-0.006 - 0.003	0.278

<sup>a</sup>93% Confidence interval excludes zero: -0.0013 to -0.0004.

## LITERATURE CITED

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