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Status, Trends, and Implications for the Conservation of Heron and Egret Nesting Colonies in the San Francisco Bay Area

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Abstract.—Nesting distribution, abundance, and reproductive success of colonially nesting herons and egrets in the central coastal region of California surrounding the San Francisco Estuary were analyzed from 1991 to 2005. Nesting activity among nine major wetland subregions was compared with regard to nesting distribution, nest survivorship, productivity of successful nests, habitat characteristics, and intraseasonal timing. An average of 73 active colony sites ^y¹ supported approximately 62 Great Blue Heron (*Ardea herodias*) colonies, 25 Great Egret (*Ardea alba*) colonies, 13 Black-crowned Night-Heron (*Nycticorax nycticorax*) colonies and twelve Snowy Egret (*Egretta thula*) colonies each year. Regional nest abundances were stable or increasing in all species. Annual changes in nest abundance were consistent with shifts in colony site preference as wetland suitability and disturbance patterns fluctuate across years and over space. Decreases in colony size were significantly related to higher rates of nest mortality, suggesting that conspecific nest failure may stimulate shifts in breeding distribution. A sharp decline in regional nest abundances suggested the effects of reduced recruitment associated with increased juvenile mortality in winter, rather than a decline in productivity. Persistence of colony site use increased substantially at sites that reached at least 20 active nests. Subregional increases in nesting abundance coincided with the restoration of tidal marshes. Significant declines in regional reproductive success of Great Blue Herons, Black-crowned Night-Herons, and Snowy Egrets resulted primarily from declining nest survivorship, which coincided with regional increases in abundances of Common Ravens (*Corvus corax*). We found small but significant subregional differences in nest survivorship, productivity, and overall reproductive success. Local and subregional productivity of successful Great Blue Heron and Great Egret nests fluctuated within larger-scale variation across the region, whereas nest survivorship was associated with processes at local or subregional scales. Received 26 October 2006, accepted 20 May 2007.

Key words.—Ardeidae, distribution, monitoring, habitat, disturbance, reproductive success.

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Nest abundance and reproductive performance at heron and egret colony sites are likely to depend on small-scale processes that influence local conditions for feeding and nesting, as well as larger-scale processes that affect regional populations within which colonies exchange birds (Parnell *et al.* 1988). Such processes may involve nest predation, colony disturbance, weather, hydrology, quality or availability of feeding or nesting habitat, availability or intraseasonal timing of food, environmental contaminants, or shifts in nesting distribution (Frederick and Spalding 1994; Gibbs and Kinkel 1997; Custer 2000; Kushlan 2000a; Kushlan and Hancock

2005). Because these processes operate at different spatial scales, local or subregional changes in nest abundance or reproductive success may not reflect regional rates. Therefore, the appropriate unit for monitoring and management is often a regional "population," even though the geographic extent of the interbreeding group is usually unknown (Parnell *et al.* 1988; Kushlan 1992). Because regional rates buffer the dynamics of individual heronries and subregions, a thorough assessment of regional status includes underlying subregional patterns and trends.

Several authors have described the challenges of effective monitoring of colonial

waterbird abundance (Dodd and Murphy 1995; Frederick *et al.* 2006; Kushlan 2000b) and reproductive success (Erwin and Custer 1982; Parnell *et al.* 1988). In most cases, basic demographic parameters are poorly known (Kushlan 2000b), and regional monitoring is often limited to aerial surveys that do not provide intensive information on colonies (Parnell *et al.* 1988; Rodgers *et al.* 2005).

The extensive tidal wetlands of the San Francisco Bay region are an important habitat area for herons and egrets in North America (Butler *et al.* 2000). The work presented here summarizes continuing efforts to monitor colonially nesting herons and egrets throughout the central coastal region of California surrounding the San Francisco Estuary (Kelly *et al.* 1993). Prior to this work, information on colonially nesting herons and egrets in the San Francisco Bay area was limited to isolated monitoring of individual colony sites and less extensive surveys of colony size within subregional areas (Pratt 1983; Pratt and Winkler 1985; Harvey *et al.* 1992; Kelly *et al.* 1993; Ryan and Parkin 1998).

The goals of this report are to (1) present a method for intensive monitoring of regional abundance and reproductive success of herons and egrets, (2) evaluate the regional and subregional status of herons and egrets in the San Francisco Bay area with regard to patterns and trends in nesting abundance and reproductive performance, and (3) consider regional, subregional, and local implications for conservation. Specifically, we present information based on field observations from 1991 to 2005 on regional distributions, nest survivorship, productivity, nesting habitat, intraseasonal timing, human disturbance, nest predation, and management concerns at all known heronries in the San Francisco Bay area. The primary study species are Great Blue Heron (*Ardea herodias*), Great Egret (*Ardea alba*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Snowy Egret (*Egretta thula*), and Cattle Egret (*Bubulcus ibis*).

STUDY AREA

The study area extends from the outer Pacific Coast eastward to the confluence of the Sacramento and San Joaquin rivers, and from the Russian River and north-

ern Napa County southward through the Santa Clara Valley (Fig. 1). The study area covers approximately 13,705 km² and includes most of the area in nine shoreline counties of the San Francisco Estuary: Marin, Sonoma, Napa, Solano, Contra Costa, Alameda, San Francisco, San Mateo, and Santa Clara.

Colonies were grouped into nine major wetland subregions: (1) Outer Pacific Coast, (2) Russian River and Laguna de Santa Rosa, (3) Northern Napa County, (4) Suisun Bay, (5) San Pablo Bay, (6) Central San Francisco Bay, and (7) South San Francisco Bay; (8) Interior East Bay, and (9) Santa Clara Valley (Fig. 1). The Laguna de Santa Rosa is the southern-most tributary of the Russian River, with an 8,100-ha freshwater wetland system composed of seasonal and perennial marshes, open water, vernal pools, riparian forest, willow groves, grasslands, and oak woodlands. Central San Francisco Bay includes several rocky islands used by nesting herons and egrets. Large tidal marshes occur in Suisun, San Pablo, and South San Francisco Bays; much of the historic marshland in these areas has been diked and drained, or converted to salt evaporation ponds, although some has been restored to tidal action. Habitats and topography are further described in Kelly *et al.* (1993) and in the San Francisco Bay Area Wetlands Ecosystem Goals Project (1999).

METHODS

All known colony sites in the region from 1991 to 2005 were included in the study. The locations of colony sites were determined through ongoing communications with state, regional, and local natural resource managers, county breeding bird atlas project coordinators, and local bird watching networks. In addition, region-wide aerial and ground-based searches were conducted for new breeding sites in 1991 and ground-based searches in remote areas of the region in most other years. Searches for new heronries were concentrated in May and June, when colony sites are relatively conspicuous because of adults actively feeding nestlings, nestlings large enough to be easily seen or heard, and guano accumulations beneath nests. Because systematic annual surveys for undiscovered colony sites were not conducted, the results reflect patterns among all known heronries in the region but may be biased toward conspicuous heronries and therefore may not accurately represent overall populations.

A colony site or heronry was defined as a group of active heron or egret nests within 500 m of each other. GPS or USGS 7.5-min topographic quads were used to record the geographic position of each heronry (NAD83). With the assistance of trained volunteer field observers, attempts were made to visit all colony sites during each of five, three-d observation periods each year, scheduled as closely as possible to 10-12 March, 10-12 April, 10-12 May, 3-5 June, and 20-22 June. All colonies were observed from the ground or from boats using binoculars and telescopes. Observers visited most colony sites at least four times each breeding season, with an average of 6.0 ± 0.3 (SE) visits per site annually ($N = 1,361$). Sites visited only once in a given year ($19 \pm 1.4\% \text{ y}^{-1}$) were usually observed in May or early June when nests and broods were the most conspicuous. The annual percent of colony sites that were visited at least ten times was $15 \pm 0.6\% \text{ y}^{-1}$. The duration of colony site visits averaged 1.4 ± 0.04 h ($N = 1,070$), with longer periods of observation

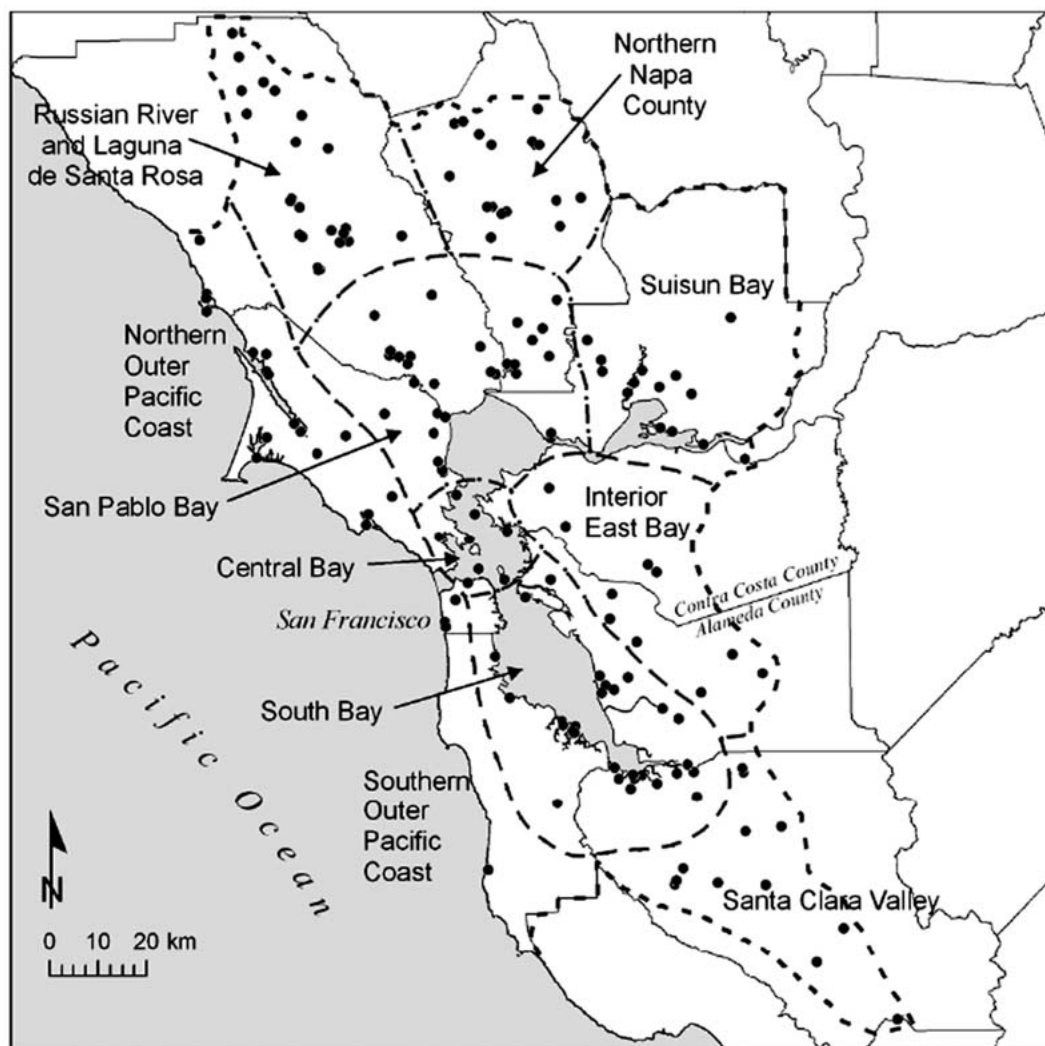


Figure 1. Distribution of heron and egret nesting colony sites in the San Francisco Bay area, 1991-2005. Bold, dashed line indicates the study area boundary; thin, dashed lines within the study area separate heronries associated with the labeled wetland subregions.

required at larger colonies, especially in May and June when brood sizes were recorded ($h = 1.25 + 0.004 \times \text{peak annual nest abundance}$; $F_{1,801} = 54.9$, $P < 0.001$).

The peak number of active nests were used as an estimate of annual colony size. Before 1 April, nests were assumed to be active if two adults were present, an adult carrying nest material was present, an adult was incubating or caring for eggs, or chicks were present. After 1 April, all occupied nests were assumed to be active. Observations at colonies visited weekly indicated that monthly visits normally detected peak colony size accurately and that even a single visit during the peak of the nesting season were likely to provide a close estimate of peak nest abundance. In addition, consistent counts of Great Blue Heron and Great Egret nests at sites visited by different observers suggested that nests were generally detectable enough to accurately estimate colony size, although a slight bias toward conspicuous nests could have

occurred. Counts of Snowy Egret and Black-crowned Night-Heron nests included an unmeasured bias associated with the difficulty of counting nests concealed in dense vegetation and, therefore, they may have been lower than the actual number of nests. At the Marin Islands in Central San Francisco Bay, where nest abundance was estimated from approximately 100 m away by boat, nest counts were multiplied by a factor of 5.4, derived from differences between counts conducted by boat and counts obtained by intensive nest searches within the colony in 1990 and 1991 (R. Hothem, pers. comm.).

Habitat characteristics were analyzed at active heronries in 2003 (Tables 1 and 2). Colony site boundaries were determined by the minimum convex polygon indicated by nest locations. Trees within the colony site boundaries were allocated into dbh classes (diameter at breast height, 1.3 m above ground) using a reach stick (James and Shugart 1970): (1) 3-10 cm, (2) 11-50 cm,

Table 1. Percent of Great Blue Heron, Great Egret, Snowy Egret and Black-crowned Night-Heron colony sites associated with nesting substrates and land forms (and the regional percent of nests that occurred in those sites) in the San Francisco Bay area in 2003. Values <0.5% are indicated by “+”.

Characteristic	Great Blue Heron N = 58 (504)	Great Egret N = 27 (856)	Snowy Egret N = 17 (846)	Black-crowned Night-Heron N = 15 (1,113)	All species N = 73 (3,332)
Nesting substrate					
Tree	95 (96)	90 (97)	82 (85)	67 (90)	90 (91)
<i>Eucalyptus</i> spp.	57 (69)	72 (76)	53 (64)	27 (47)	53 (62)
<i>Quercus agrifolia</i>	2 (2)	7 (12)	18 (46)	20 (38)	4 (28)
<i>Aesculus californica</i>	2 (2)	3 (9)	6 (12)	7 (25)	1 (14)
<i>Pinus radiata</i>	3 (9)	10 (4)	6 (4)	7 (10)	4 (7)
<i>Sequoia sempervirens</i>	14 (11)	7 (9)	6 (1)	0 (0)	11 (4)
<i>Cupressus macrocarpa</i>	7 (5)	7 (5)	6 (+)	0 (0)	5 (2)
<i>Quercus lobata</i>	5 (7)	3 (4)	0 (0)	0 (0)	4 (2)
<i>Pseudotsuga menziesii</i>	10 (6)	0 (0)	0 (0)	0 (0)	8 (1)
<i>Pinus sabiniana</i>	5 (4)	0 (0)	0 (0)	0 (0)	4 (1)
<i>Pinus muricata</i>	2 (2)	3 (2)	0 (0)	0 (0)	1 (1)
<i>Lithocarpus densiflorus</i>	0 (0)	0 (0)	0 (0)	7 (+)	1 (1)
Shrub (0.5-5 m in height)	3 (2)	10 (13)	24 (23)	40 (42)	8 (24)
Snag	9 (8)	3 (9)	6 (12)	7 (25)	7 (15)
Artificial structures	3 (3)	3 (5)	6 (22)	7 (21)	4 (14)
<i>Schoenoplectus</i> or <i>Typha</i> spp.	0 (0)	3 (+)	12 (6)	20 (3)	4 (2)
Land form					
Island	7 (6)	17 (14)	35 (30)	53 (53)	14 (30)
with bridge	2 (3)	3 (2)	0 (0)	7 (1)	3 (1)
without bridge	5 (3)	14 (13)	35 (30)	47 (53)	11 (29)
Flood plain	29 (27)	28 (29)	35 (38)	7 (9)	27 (24)
Wetland	10 (15)	17 (12)	12 (26)	20 (24)	12 (20)
Levee	16 (15)	21 (37)	0 (0)	0 (0)	12 (12)
Hillside	28 (34)	14 (5)	0 (0)	7 (+)	23 (7)

(3) 51-100 cm, (4) 101-150 cm, (5) ≥ 150 cm. Vegetation cover was estimated at ground (<0.5 m), shrub (0.5-5 m), and tree canopy (>5 m) levels as the percent of vegetation “hits” viewed vertically through an ocular tube (James and Shugart 1970) at one-m transect intervals along the maximum diameter of the colony site and its longest perpendicular diameter. Human land uses (Table 1) were recorded within 200 m, a distance within which human activity might disturb nesting birds (Vos *et al.* 1985; Erwin 1989; Rodgers and Smith 1995) and 500 m, a distance within which human-altered landscape conditions might affect the locations of colony sites (Watts and Bradshaw 1994).

Reproductive success, intraseasonal timing, and rates of nest predation were measured at colonies in the northern portion of the study area (all subregions north of San Francisco, including Central San Francisco Bay, Contra Costa County in the Interior East Bay, and the Outer Coast north of San Francisco; Fig. 1). To compare intraseasonal timing among subregions, differences in the average proportion of nests observed in the egg-laying and incubation period, the parental guardian period (nestlings with adults continually present), and the post-guardian period (adults not continuously present) were estimated, weighted equally across years with adequate data, 1992-2005. Subregional comparisons of intraseasonal timing for each species were based on samples with at least ten nests per year or half of the active nests in each subregion.

Occurrences of predation or disturbance were classified by source (human, observer, avian, mammal, other predator, weather, or unknown) and level of response (colony abandonment, nest loss or nestling mortality, or behavioral response) and summarized as the mean proportion of occurrences among sites or site visits per year. However, observers rarely entered colony sites to search for evidence of nest predation or disturbance.

Reproductive Success

Estimates of nest survivorship were based on the apparent survivorship of focal nests observed from initiation or early in the incubation period. Panoramic photographs and sketches were used to identify and number individual nest locations and to track focal nests across repeated site visits. High daily survivorship of Great Egret and Great Blue Heron nests during the incubation period, from 2003 to 2005 at Audubon Canyon Ranch on the Outer Coast north of San Francisco, indicated that the potential (positive) bias resulting from occasional selection of focal nests one to two weeks into the 28-d incubation period was minor (daily nest survivorship for Great Egret: $99.8 \pm 0.1\%$ over 224 exposure d in the first seven d, $99.7 \pm 0.1\%$ over 2,617 exposure d in the first 14 d; Great Blue Heron: $99.8 \pm 0.1\%$ over 189 exposure d in the first seven d, $99.7 \pm 0.1\%$ over 371 exposure d in the first 14 d). In colonies with fewer than 15 active nests, all nests were treated as focal nests.

Table 2. Percent of Great Blue Heron, Great Egret, Snowy Egret and Black-crowned Night-Heron colony sites associated with human land uses (and the regional percent of nests that occurred in those sites) in the San Francisco Bay area in 2003. Values <0.5% are indicated by “+”.

Characteristic	Great Blue Heron N = 58 (504)	Great Egret N = 27 (856)	Snowy Egret N = 17 (846)	Black-crowned Night-Heron N = 15 (1,113)	All species N = 73 (3,332)
Land use within 200 m					
Grazing	22 (29)	21 (8)	12 (7)	7 (11)	19 (12)
Industrial	0 (0)	7 (5)	12 (27)	13 (32)	3 (19)
Orchard	2 (1)	0 (0)	0 (0)	0 (0)	1 (+)
Park or natural area	28 (24)	38 (30)	47 (46)	40 (40)	30 (36)
Residential, <3 houses ha ⁻¹	40 (41)	28 (19)	29 (5)	13 (1)	34 (13)
Residential, 3-10 houses ha ⁻¹	10 (6)	10 (4)	18 (39)	27 (23)	14 (20)
Residential, >10 houses ha ⁻¹	5 (6)	10 (7)	6 (4)	7 (10)	7 (8)
Sport or recreational field	0 (0)	7 (8)	6 (33)	7 (9)	3 (13)
Vineyard	7 (8)	3 (1)	6 (+)	0 (0)	5 (1)
Land use within 500 m					
Farm	2 (1)	3 (+)	0 (0)	7 (2)	3 (1)
Grazing	21 (33)	21 (12)	6 (1)	0 (0)	16 (8)
Industrial	2 (1)	10 (6)	18 (32)	20 (32)	5 (21)
Orchard	7 (7)	3 (+)	0 (0)	0 (0)	5 (1)
Park or natural area	29 (26)	38 (39)	47 (46)	40 (40)	30 (39)
Residential, <3 houses ha ⁻¹	43 (32)	28 (23)	29 (4)	7 (+)	37 (12)
Residential, 3 to 10 houses ha ⁻¹	17 (13)	21 (12)	29 (62)	40 (45)	22 (36)
Residential, >10 houses ha ⁻¹	10 (8)	14 (10)	18 (14)	20 (16)	12 (13)
Sport or recreational field	2 (1)	7 (4)	12 (37)	13 (18)	4 (17)
Vineyard	16 (17)	7 (5)	6 (+)	0 (0)	12 (4)

In colonies with more than 15 active nests, a random subset of ten to 15 focal nests was selected. In some larger colonies most or all observable nests were selected as focal nests. A slight bias toward conspicuous nest sites could have influenced the monitoring of focal nests, but this was unlikely to be of concern because (1) almost all nests active early in the season were detected, based on observations later in the nesting cycle when nests and nestlings were more conspicuous, and (2) the survival of partially hidden nests could be successfully tracked by the presence or movements of adults or nestlings. Annual samples of focal nests represented $72 \pm 1.8\%$ of the active Great Blue Heron colonies, $63 \pm 3.0\%$ of Great Egret colonies, $39 \pm 4.6\%$ of Black-crowned Night-Heron colonies, and $47 \pm 4.9\%$ of Snowy Egret colonies in the northern portion of the study area (see above) each year (1993-2005).

Great Egret and Great Blue Heron nests were considered successful if at least one chick survived to seven weeks or eight weeks post-hatch, respectively (Pratt 1970; Pratt and Winkler 1985). Nests were considered to be successful at 14 d after first hatch for Snowy Egret (Frederick and Collopy 1989) and 15 d after first hatch for Black-crowned Night-Heron (Custer *et al.* 1983).

The productivity of successful nests was based on the size of completely visible broods when Great Blue Heron nestlings were five to eight weeks old and Great Egrets were five to seven weeks old. During these periods, nestlings were too young to hop away from their nests and old enough to have survived the period when most brood reduction occurs (Pratt 1970; Pratt and Winkler 1985). Samples of completely visible broods may have included a slight bias toward nest sites that were more visible, but nestlings at the appropriate age

were generally near adult size with tall profiles that allowed observers to determine pre fledging brood size at most nests. Brood size in successful Snowy Egret and Black-crowned Night-Heron nests was measured when the young were seven to 14 d old (Frederick and Collopy 1989; Parsons and Master 2000) and seven to 15 d old (Custer *et al.* 1983; Davis 1993), respectively. Estimates of the number of young in successful nests included (focal) nests followed through the nesting cycle as well as nests that were not followed but contained young known to have reached the appropriate age prior to fledging.

Statistical Analyses

Estimates of annual nest survivorship and productivity of successful nests were based on the fates of individual nests from a sampling universe equal to the number of nests (N) in a colony or group of colonies, with the sample size (n) often accounting for a relatively large proportion of the total number of nests. Because of the conspicuousness of colonially nesting herons and egrets, the sampling population of nests could be confidently estimated by counting the peak number of active nests (see above). Under these conditions, variance models based on sampling without replacement are more accurate than commonly used models that assume replacement, and benefit from standard errors that are substantially and appropriately reduced (Thompson 1992). Therefore, standard errors of pre fledging brood size and nest survivorship are based on sampling without replacement.

Comparisons of nest survivorship and number of young in successful nests between subregions, colony

sites, or species were based on the means and standard errors of individually monitored nests within groups, weighted equally across years. To evaluate the significance of multiple pairwise comparisons among groups, *t*-tests with Bonferroni adjustments for an experiment-wise error of $P < 0.05$ were used. Subregional comparisons of nest survivorship were based on annual samples of at least ten nests or half of the active nests in each subregion. Similarly, comparisons of the number of young in successful nests were based on annual samples of at least ten nests or half of the successful nests (number of active nests \times nest survivorship).

The proportions of focal nests or brood sizes sampled did not vary significantly with colony size ($|r| < 0.1$, $P > 0.05$). However, because the proportions were not constant, possible biases related to variation in sampling intensity among sites were examined by repeating the analyses using representative colony means of at least ten nests or half of the nests in each colony, weighted by colony size. Because the regional and subregional differences based on weighted colony means did not differ from those based on pooled samples of nests, the potential biases were considered to be minor.

Overall reproductive success (r_s) was estimated as the number of young produced per nest attempt, calculated as the product of estimates of focal nest survivorship (\hat{p}) and pre fledging brood size in successful nests (\hat{b}): $r_s = \hat{p} \cdot \hat{b}$ with a variance (Goodman 1960) of $\text{var}(r_s) = [(\hat{p})^2 \cdot \text{var}(\hat{b})] + [(\hat{b})^2 \cdot \text{var}(\hat{p})] - [\text{var}(\hat{b}) \cdot \text{var}(\hat{p})]$.

The approximate significance of subregional differences in overall reproductive success was determined by assuming a standard normal probability range (critical $t_{.05} = 1.96$) with Bonferroni adjustments for an experiment-wise error of $P < 0.05$.

Simple linear regression was used to measure trends in annual nest abundance and reproductive performance and to visually inspect scatter plots to check for evidence of nonlinear trends. Cleveland's robust locally weighted regression algorithm was used to examine relationships between colony size and persistence (LOWESS; Cleveland 1979; Chambers *et al.* 1983). The precision of results is presented as \pm SE unless indicated otherwise.

RESULTS

Nest Abundance and Distribution

From 1991 to 2005 ($N = 15$), an average of 73 ± 2.1 active colony sites y^{-1} ($N = 15$ y; Fig. 1) were recorded. These sites supported 62 ± 1.7 Great Blue Heron colonies, 25 ± 1.5 Great Egret colonies, 13 ± 0.7 Black-crowned Night-Heron colonies and 12 ± 1.0 Snowy Egret colonies. The average annual number of nests in the region from 1994 to 2005 ($N = 12$) was 516 ± 14.9 for Great Blue Heron, 878 ± 49.6 for Great Egret, 834 ± 39.3 for Black-crowned Night-Heron, and 587 ± 48.1 for Snowy Egret.

Active colony sites were separated by about six km (mean nearest-neighbor dis-

tance = 6.0 ± 4.8 km SD; $N = 1,116$, sites weighted equally among years; species pooled). Great Blue Heron colonies tended to be small and widely distributed in the region ($44 \pm 1.9\%$ with < 6 nests y^{-1} ; $35 \pm 1.4\%$ of those occurred at sites with colonies of other species). Great Egret nesting abundance was concentrated at several colony sites in the Suisun Bay subregion, with other important colony sites in Central and South San Francisco Bay and along the Outer Pacific Coast (Fig. 2). Cattle Egrets nested in low numbers of one to 23 nests at one or two sites each year, from 1994 to 2005 (Laguna de Santa Rosa and South San Francisco Bay). Single pairs of Little Blue Herons nested in South San Francisco Bay in 1990, 1993, and 1996. Detailed accounts of colony sites are reported in Kelly *et al.* (2006).

The number of years heron or egret colonies were active was related to colony size and nesting species. Great Blue Heron colonies that remained smaller than six nests generally became inactive within five years, but colonies persisted, on average, for twelve years or more if maximum abundance was greater than 20 nests (Fig. 3). The persistence of Great Egret, Black-crowned Night-Heron, and Snowy Egret colonies increased substantially only after reaching an abundance of 20-30 nests per species. Colony sites with less than ten nests of all species combined tended to become inactive within approximately eight years (Fig. 4). These general patterns underestimate average persistence because some colonies were active prior to discovery or were likely to remain active beyond the 15-y monitoring period.

The nest abundances of all species were stable or increasing in the region from 1994 to 2005 (Fig. 2). Great Blue Heron nest numbers showed no significant linear trend from 1994 to 2005 ($F_{1,10} = 1.1$, n.s.), but increased significantly by an average of 25 ± 2.8 nests y^{-1} from 1999 to 2005 ($F_{1,4} = 82.4$, $P < 0.001$; Fig. 2). The number of Great Egret nests in the region increased significantly from 1994 to 2005 ($b = 32 \pm 11.2$ nests y^{-1} , $F_{1,10} = 8.2$, $P = 0.02$), reflecting primarily a sharp increase in 2004 and 2005 (Fig. 2). Black-crowned Night-Heron nest numbers did not increase

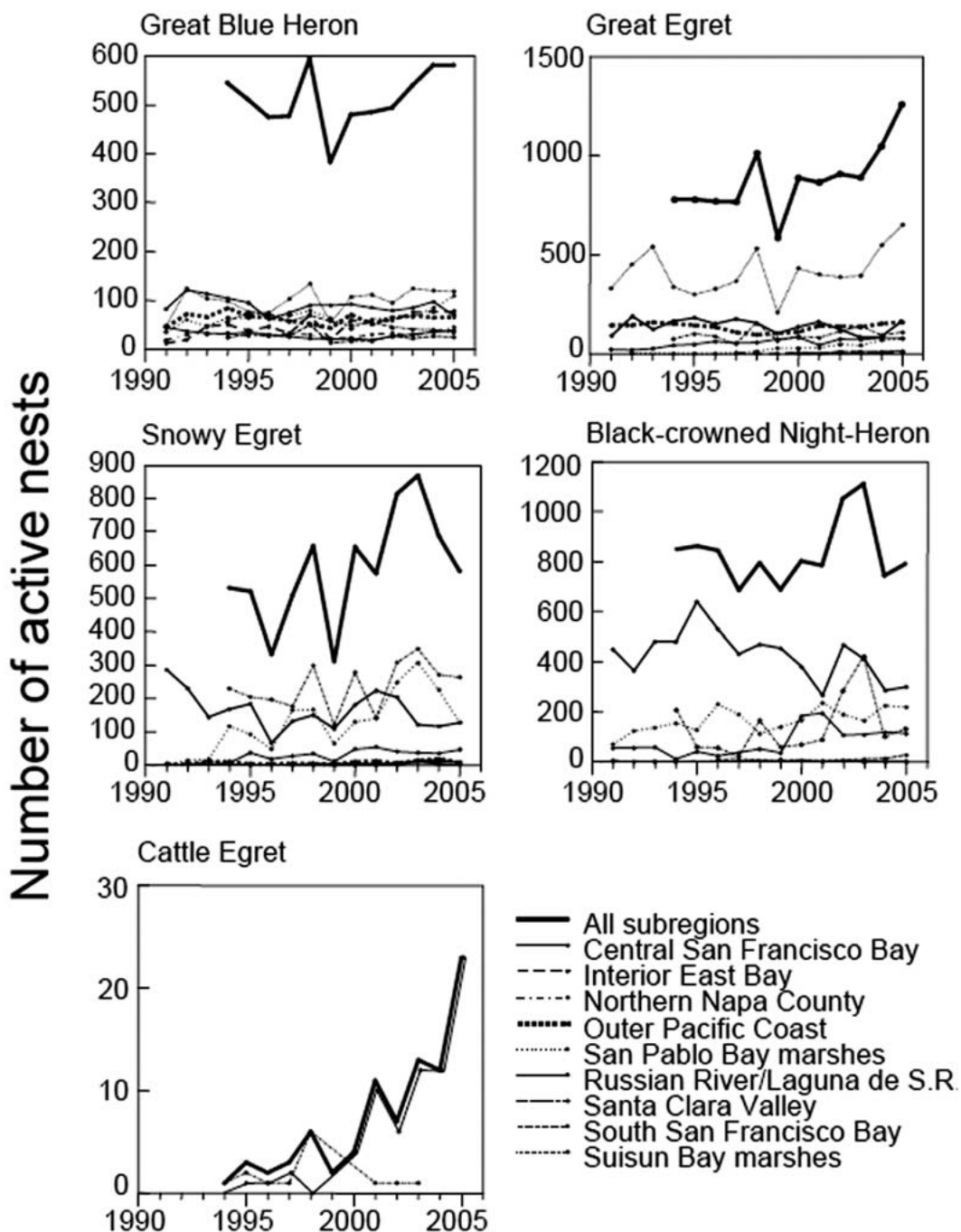


Figure 2. Peak number of active heron and egret nests observed annually within wetland subregions of the San Francisco Bay area. See Figure 1 for locations of subregions.

significantly ($F_{1,10} = 0.4$, n.s.), but a marginally significant linear increase was evident in the number of Snowy Egret nests from 1994 to 2005 ($F_{1,10} = 4.5$, $P = 0.057$; Fig. 2). Signifi-

cant increases in the small number of nesting Cattle Egrets resulted from an increase in the number of nests at a heronry in the Laguna de Santa Rosa ($F_{1,10} = 26.4$, $P < 0.001$).

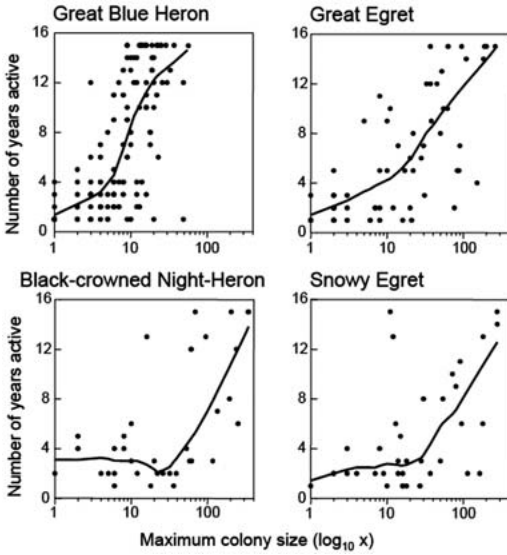


Figure 3. Relationships between persistence and maximum size of heron and egret nesting colonies (\log_{10} scale) in the San Francisco Bay area, 1991-2005. Lines represent LOWESS trends with smoothing parameter $f = 0.6$.

Regional declines in the peak number of active nests occurred in all species in 1999 (Fig. 2). These declines were associated with unusual conditions two years earlier, during the hatching year for individuals reaching reproductive age in 1999. These first-time breeders were produced during an unusual breeding-season drought in 1997 (Fig. 5) but the dry breeding conditions were not associated with regionwide declines in nest survivorship or the productivity of successful nests (Figs. 6 and 7). Those individuals also endured unusually heavy rainfall and extended rainstorms and during their first winter (Fig. 5) but juvenile survival or recruitment was not measured.

Nesting Habitat

Trees were used as nesting substrates in 90% of the active colony sites (Table 1). Non-native eucalyptus trees were used as nesting substrate at 53% of sites and were the predominant tree species near wetland habitats (JPK, pers. observation). In addition, Snowy Egrets and Black-crowned Night-Herons nested in substantial numbers in Coast Live Oaks (*Quercus agrifolia*), shrubs, and tule (*Schoenoplectus*

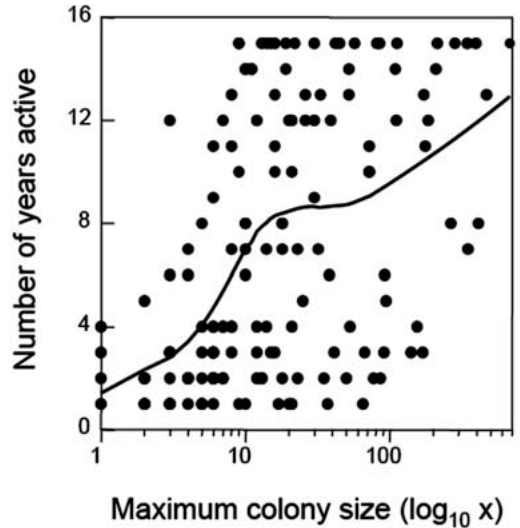


Figure 4. Relationship between persistence and maximum size of heronries (\log_{10} scale, all species combined) in the San Francisco Bay area, 1991-2005. Line represents LOWESS trend with smoothing parameter $f = 0.6$.

spp.) or cattail (*Typha* spp.) marshes (Table 1). Sites with trees as nest substrates averaged $47 \pm 2.6\%$ canopy cover, $14 \pm 2.8\%$ shrub cover, and $30 \pm 3.7\%$ ground cover ($N = 63$). Of 66 sites with trees as nest substrates, 32 (48%) included one or more trees that were one m dbh or larger and 13 (20%) included one or more trees larger than 1.5 m dbh.

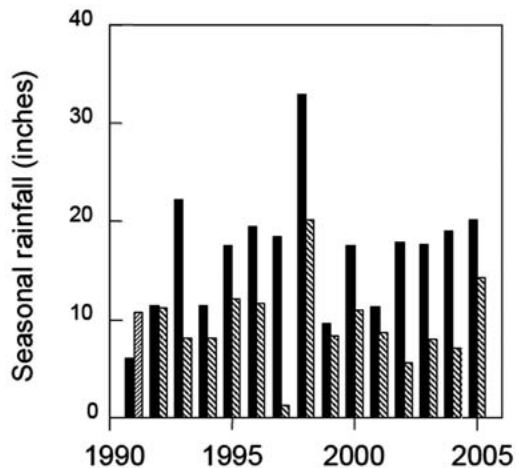


Figure 5. Cumulative rainfall in winter (November-February; solid bars) and in the nesting season (February-June; striped bars), 1991-2005, recorded in San Francisco (California Data Exchange Center, California Department of Water Resources).

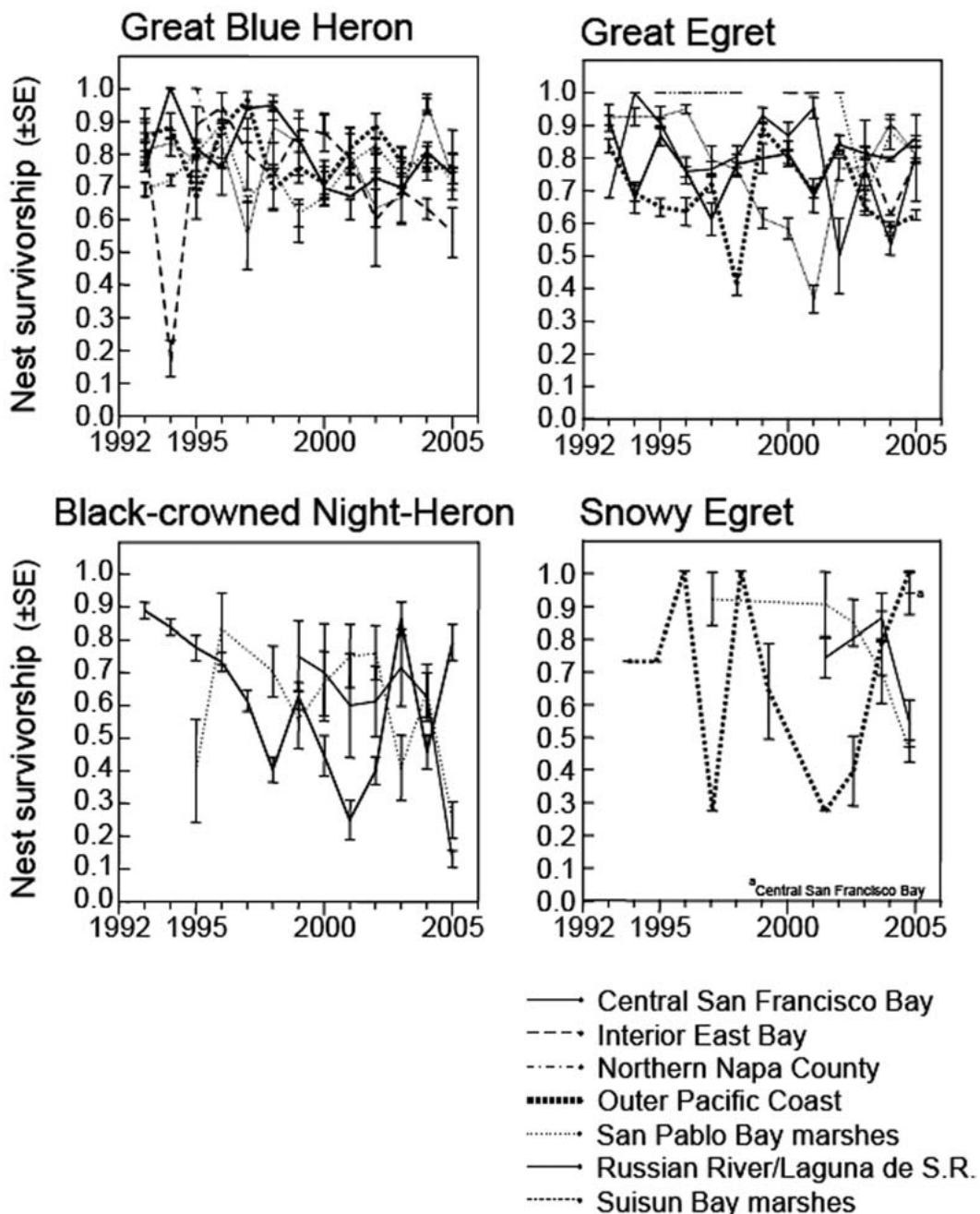


Figure 6. Annual mean survivorship (\pm SE) of Great Blue Heron, Great Egret, and Black-crowned Night-Heron nests, by subregion, in the San Francisco Bay area, 1993-2005.

Only twelve percent of colony sites were in wetland habitat (Table 1). Great Egrets and Great Blue Herons nested in heronries associated with a variety of landforms and were the most important species in heronries on levees and hillsides. Islands, primarily

without bridges, accounted for over half of the colony sites used by Black-crowned Night-Herons and a third of those used by Snowy Egrets. The predominant human land uses near colony sites were cattle grazing, parks or natural areas, and low-to-medi-

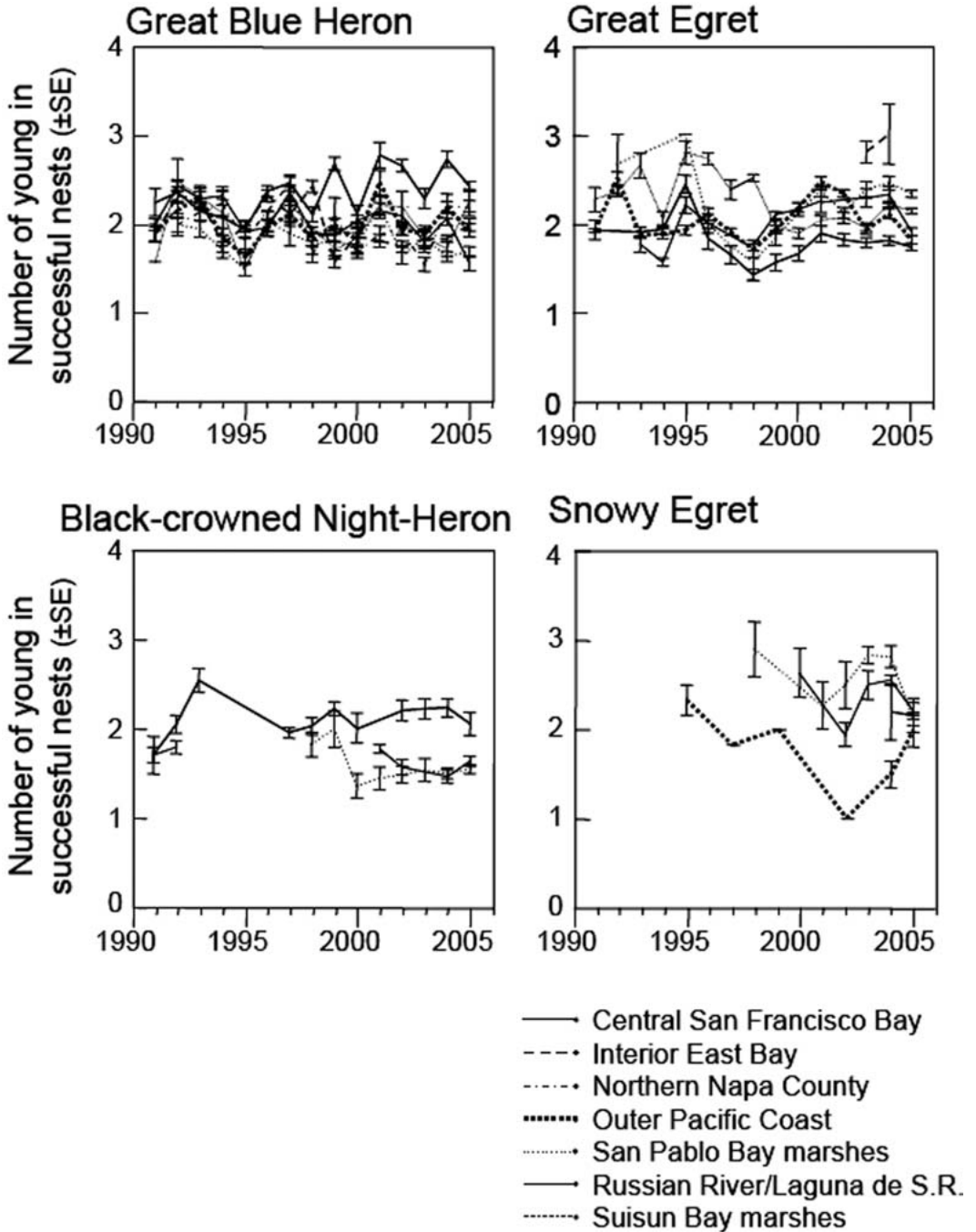


Figure 7. Annual mean number of young produced in successful Great Blue Heron, Great Egret, Black-crowned Night-Heron, and Snowy Egret nests (\pm SE), by subregion, in the northern San Francisco Bay area, 1991-2005.

um density residential use (Table 1). Fifty-four percent of the active heronries in 2003 were privately owned, and 46% were on publicly owned lands (N = 72).

Reproductive Success

Nest Survivorship. Percent nest survivorship based on all focal nests in the region

from 1993 to 2005 was $79 \pm 0.4\%$ for Great Blue Heron ($N = 3,227$ nests), $78 \pm 0.4\%$ for Great Egret ($N = 4,685$), $62 \pm 2.3\%$ for Black-crowned Night-Heron ($N = 1,940$), and $66 \pm 2.1\%$ for Snowy Egret ($N = 402$). Significant but weak linear declines in average regional nest survivorship were evident from 1993 to 2005 for Great Blue Heron ($b = -0.6 \pm 0.22\% \text{ y}^{-1}$, $F_{1,13} = 7.2$, $P < 0.02$), Great Egret ($b = -1.0 \pm 0.38\% \text{ y}^{-1}$, $F_{1,13} = 7.3$, $P < 0.02$), and Black-crowned Night-Heron ($b = -3.0 \pm 0.66\% \text{ y}^{-1}$, $F_{1,12} = 20.4$, $P < 0.001$; Fig. 8).

In general, annual changes in nest survivorship were not consistent among subregions (Fig. 6). The survivorship of Great Blue Heron nests was significantly greater in Northern Napa County than in Central San Francisco Bay, the Interior East Bay, or the Russian River/Laguna de Santa Rosa (Table 3). Although Great Blue Herons often nest in small colonies along rivers or streams, there was no evidence of a relationship between colony size and nest survivorship, either from inspection of scatter plots or from linear regression (controlling for year; $F_{1,410} = 0.01$, n.s.). Great Egret nests were significantly more likely to fledge young in Suisun Bay than in Central San Francisco Bay, the Outer Coast, or the Russian River and Laguna de Santa Rosa and were significantly more likely to fail on the Outer Coast than in all other subregions (Table 3). In 2005, Snowy Egret nest survivorship was significantly greater in Central San Francisco Bay than in San Pablo Bay or the Laguna de Santa Rosa (Table 3). Other subregional differences in nest survivorship were not detected for Snowy Egret or Black-crowned Night-Heron, but small sample sizes suggest the possibility of undetected differences (Table 3).

Number of Young in Successful Nests. The regional average number of young fledged per successful nest was 2.04 ± 0.015 for Great Blue Heron ($N = 2,193$ nests), 2.15 ± 0.011 for Great Egret ($N = 3,124$), 1.82 ± 0.046 for Black-crowned Night-Heron ($N = 978$), and 2.50 ± 0.040 for Snowy Egret ($N = 343$). The only significant trend in the number of young produced by successful nests was in Black-crowned Night-Heron nests, which declined very slightly, but significantly, from

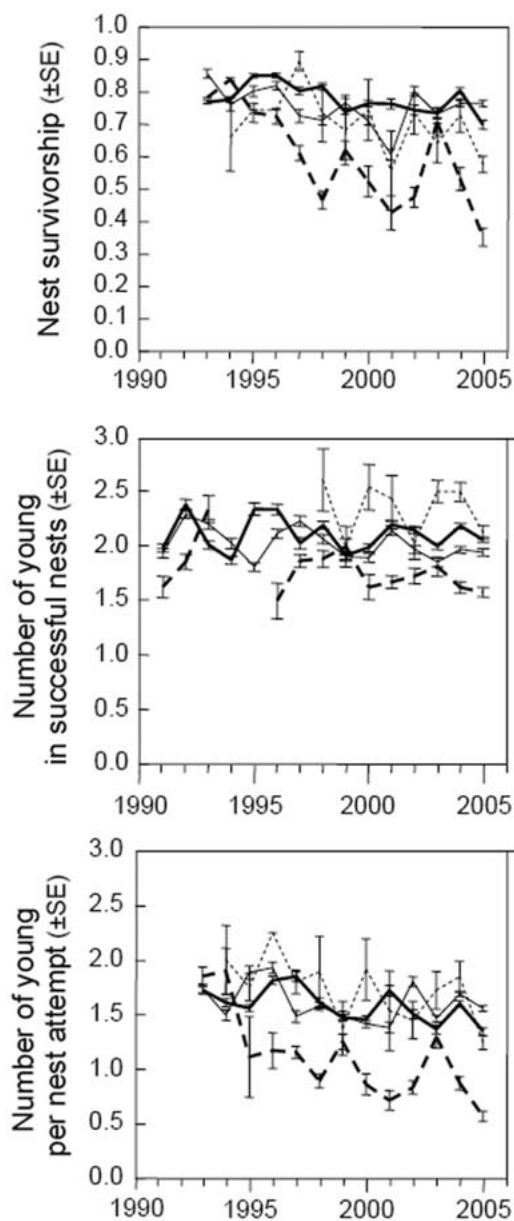


Figure 8. Annual mean (\pm SE) of nest survivorship, number of young in successful nests, and number of young produced per nest attempt by Great Blue Herons (bold, solid lines), Great Egrets (thin, solid lines), Black-crowned Night-Herons (bold, dashed lines), and Snowy Egrets (thin, dashed lines) in the northern San Francisco Bay area, 1991-2005.

1991 to 2005 ($b = -0.04 \pm 0.013 \text{ young y}^{-1}$; $F_{1,10} = 8.1$, $P < 0.02$; Fig. 8).

The productivity of successful nests appeared to covary annually across subregions (Fig. 7). Although only two of 21 (9.5%) cor-

Table 3. Nest survivorship \pm standard error (SE) for Great Blue Heron, Great Egret, and Black-crowned Night-Heron, by subregion in the San Francisco Bay area, weighted equally among years. Year span groups indicate (1) all years with adequate data (see Methods), 1993-2005, and (2) years with adequate data from all subregions (Great Blue Heron: 1993-2005; Great Egret: 1994-1998 and 2002-2005; Black-crowned Night-Heron: 1999-2005; Snowy Egret: 2002 and 2004-2005). Means with the same superscript capital letter within species and year span group are not significantly different (Bonferroni adjusted $P > 0.05$).

Subregion	Year span group	Great Blue Heron			Great Egret			Black-crowned Night-Heron			Snowy Egret		
		Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years
Central San Francisco Bay	1	0.77 \pm 0.006 ^B	349	13	0.78 \pm 0.010 ^C	872	13	0.62 \pm 0.012 ^A	1285	13	0.94 \pm 0.058 ^A	16	1
	2	— ^a	— ^a	— ^a	0.78 \pm 0.011 ^B	618	9	0.55 \pm 0.020 ^A	472	7	0.94 \pm 0.058 ^A	16	1 ^b
Interior East Bay ^c	1	0.72 \pm 0.023 ^B	251	13	0.88 \pm 0.026 ^A	28	6						
	2	— ^a	— ^a	— ^a	0.82 \pm 0.039 ^{AB}	22	4 ^d						
Northern Napa County	1	0.83 \pm 0.010 ^A	299	13									
	2	— ^a	— ^a	— ^a									
Outer Coast ^c	1	0.80 \pm 0.013 ^{AB}	431	13	0.70 \pm 0.007 ^D	1268	13				0.71 \pm 0.019 ^B	57	10
	2	— ^a	— ^a	— ^a	0.65 \pm 0.009 ^C	883	9				0.71 \pm 0.030 ^B	20	3
San Pablo Bay	1	0.79 \pm 0.010 ^{AB}	623	13	0.82 \pm 0.008 ^{AB}	147	9	0.54 \pm 0.028 ^A	259	11	0.78 \pm 0.032 ^{AB}	165	5
	2	— ^a	— ^a	— ^a	0.82 \pm 0.008 ^{AB}	147	9	0.58 \pm 0.033 ^A	194	7	0.71 \pm 0.009 ^B	124	3
Russian River and Laguna de Santa Rosa	1	0.78 \pm 0.010 ^B	739	13	0.79 \pm 0.012 ^{BC}	503	13	0.64 \pm 0.038 ^A	170	8	0.80 \pm 0.027 ^{AB}	71	4
	2	— ^a	— ^a	— ^a	0.76 \pm 0.016 ^B	372	9	0.59 \pm 0.043 ^A	165	7	0.74 \pm 0.035 ^B	67	3
Suisun Bay	1	0.77 \pm 0.018 ^{AB}	471	13	0.78 \pm 0.009 ^C	1673	13						
	2	— ^a	— ^a	— ^a	0.85 \pm 0.009 ^A	1275	9						

^aValue is same as line above; data were adequate from all subregions in all years.

^bIn 2005, Snowy Egret nest survivorship was significantly greater in Central San Francisco Bay than San Pablo Bay or the Russian River/Laguna de Santa Rosa but did not differ significantly from the Outer Coast.

^cNorthern portion only (Contra Costa County).

^dIn comparisons of subsets based on 1997 and 2003-2005 only, Great Egret nest survivorship in the Interior East Bay was significantly greater than in Central San Francisco Bay or the Russian River/Laguna de Santa Rosa but did not differ significantly from San Pablo Bay or Suisun Bay.

^eNorth of San Francisco only.

relations between subregions were significant for Great Blue Heron, three of 15 (20%) for Great Egret ($P < 0.05$), and none for Black-crowned Night-Heron or Snowy Egret, correlation coefficients were consistently positive ($r > 0$) between all pairs of subregions in all species.

Successful Great Blue Heron nests fledged significantly more young in Central San Francisco Bay than in all other subregions and significantly more in the Russian River/Laguna de Santa Rosa than all subregions except Central San Francisco Bay (Table 4). In contrast, successful Great Blue Heron nests in San Pablo Bay were significantly less productive than in all other subregions. Although Great Blue Herons often nest in small colonies along the Russian River and other parts of the region, there was no evidence of an effect of colony size on the productivity of successful nests, either from inspection of scatter plots or from linear regression (controlling for year; $F_{1,2922} = 2.5$, n.s.).

Successful Great Egret nests were dramatically more productive in the Interior East Bay than in other subregions and produced significantly more young in Suisun Bay and San Pablo Bay than in all subregions except the Interior East Bay (Table 4). Great Egrets were significantly less productive in Central San Francisco Bay than in other subregions. Successful Black-crowned Night-Heron nests were significantly more productive in Central San Francisco Bay than in heronries associated with San Pablo Bay or the Laguna de Santa Rosa (Table 4). Snowy Egret nests were significantly less productive on the Outer Coast than in other subregions (Table 4).

Number of Young per Nest Attempt. The number of young fledged per nest attempt was 1.61 ± 0.014 for Great Blue Heron, 1.68 ± 0.003 for Great Egret, 1.15 ± 0.037 for Black-crowned Night-Heron, and 1.76 ± 0.062 for Snowy Egret. Significant but weak linear declines in the regional average number of young produced per nest attempt were evident from 1993 to 2005 for Great Blue Heron ($b = -0.02 \pm 0.009 \text{ y}^{-1}$, $F_{1,11} = 6.2$, $P = 0.03$), Black-crowned Night-Heron ($b = -0.08 \pm 0.021 \text{ y}^{-1}$, $F_{1,11} = 14.1$, $P = 0.003$), and Snowy Egret ($b = -0.05 \pm 0.020 \text{ y}^{-1}$, $F_{1,10} = 5.4$, $P = 0.04$;

Fig. 8). These declines reflect primarily the effects of nest survivorship (Fig. 8).

Consistently positive correlations ($r > 0$) between all pairs of subregions suggested regionally consistent patterns in the overall reproductive success of Great Blue Herons and Great Egrets, although only two of 21 correlations (9.5%) were significant ($P < 0.05$) for Great Blue Heron and none for Great Egret. These patterns reflect primarily the regional-scale effects of productivity of successful nests (Figs. 7 and 9).

The overall reproductive performance of Great Blue Herons was significantly greater in Central San Francisco Bay, Northern Napa County, the Outer Coast, and the Russian River/Laguna de Santa Rosa than in other subregions (Table 5). The number of Great Egrets produced per nest attempt was significantly greater in Suisun Bay, San Pablo Bay, and the Interior East Bay than in other areas. Black-crowned Night-Herons produced significantly more young per nest attempt in Central San Francisco Bay (Alcatraz Island) than in San Pablo Bay or in the Laguna de Santa Rosa (Table 5).

Intraseasonal Timing

In early March, almost all active Great Blue Heron and Great Egret nests and all Black-crowned Night-Heron nests were in the egg-laying or incubation stage (Fig. 10). Snowy Egrets generally began nesting later in the season. By early April, $71 \pm 0.7\%$ of Great Blue Heron nests ($N = 2,723$) were in the egg-laying or incubation period. By early May, only $15 \pm 0.5\%$ of Great Blue Heron nests ($N = 3,845$), $44 \pm 0.5\%$ of Great Egret nests ($N = 5,268$), $56 \pm 1.9\%$ of Black-crowned Night-Heron nests ($N = 768$), and $67 \pm 2.3\%$ of Snowy Egret nests ($N = 360$), were still incubating or laying eggs (Fig. 10). At this time, $54 \pm 0.6\%$ of Great Blue Heron nests had reached the post-guardian period, while only $15 \pm 0.3\%$ of Great Egret nests, $23 \pm 1.5\%$ of Black-crowned Night-Heron nests, and $6 \pm 0.9\%$ of Snowy Egret nests were left unattended by adults.

In early June, $83 \pm 0.6\%$ of Great Blue Heron nests ($N = 2,519$), $57 \pm 0.6\%$ of Great Egret nests ($N = 4,427$), $45 \pm 2.1\%$ of Black-crowned Night-Heron nests ($N = 717$), and

Table 4. Mean number of young fledged \pm standard error (SE) in successful Great Blue Heron, Great Egret, Black-crowned Night-Heron, and Snowy Egret nests, by subregion, in the northern San Francisco Bay area, weighted equally among years. Year span groups indicate (1) all years with adequate data (see Methods), 1991-2005, and (2) years with adequate data from all subregions (Great Blue Heron: 1992, 1994-1995, 1997, and 1999-2005; Great Egret: 1992, 1995-1999 and 2001-2005; Black-crowned Night-Heron: 2001-2005; Snowy Egret: 2004-2005). Means with the same superscript capital letter within species and year span group are not significantly different (Bonferroni adjusted $P > 0.05$).

Subregion	Year span group	Great Blue Heron			Great Egret			Black-crowned Night-Heron			Snowy Egret		
		Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years	Mean \pm SE	Nests	Years
Central San Francisco Bay	1	2.38 \pm 0.028 ^A	278	15	1.82 \pm 0.022 ^D	513	14	2.03 \pm 0.033 ^A	485	11	2.18 \pm 0.135 ^{AB}	35	2
	2	2.42 \pm 0.033 ^A	204	11	1.81 \pm 0.025 ^D	408	11	2.09 \pm 0.061 ^A	150	5	2.18 \pm 0.135 ^{AB}	35	2
Interior East Bay ^a	1	2.01 \pm 0.036 ^B	224	13	2.93 \pm 0.133 ^A	13	3						
	2	2.04 \pm 0.041 ^C	188	11	2.93 \pm 0.133 ^A	13	3 ^b						
Northern Napa County	1	1.99 \pm 0.027 ^B	247	13									
	2	2.01 \pm 0.029 ^{BC}	211	11									
Outer Coast ^c	1	2.01 \pm 0.023 ^B	437	15	2.04 \pm 0.014 ^C	1007	15				1.82 \pm 0.076 ^B	38	9
	2	2.00 \pm 0.026 ^{BC}	335	11	2.01 \pm 0.018 ^C	674	11				1.75 \pm 0.086 ^B	15	2
San Pablo Bay	1	1.82 \pm 0.025 ^C	423	14	2.23 \pm 0.030 ^B	210	13	1.54 \pm 0.036 ^B	247	9	2.49 \pm 0.059 ^A	160	7
	2	1.79 \pm 0.026 ^D	346	11	2.18 \pm 0.027 ^B	207	11	1.42 \pm 0.029 ^B	199	5	2.46 \pm 0.046 ^A	103	2
Russian River and Laguna de Santa Rosa	1	2.06 \pm 0.023 ^B	631	15	2.04 \pm 0.026 ^C	350	13	1.51 \pm 0.028 ^B	284	8	2.37 \pm 0.060 ^A	97	5
	2	2.06 \pm 0.026 ^B	483	11	2.05 \pm 0.018 ^C	306	11	1.47 \pm 0.027 ^B	220	5	2.38 \pm 0.048 ^A	53	2
Suisun Bay	1	1.99 \pm 0.020 ^B	698	15	2.27 \pm 0.016 ^B	1733	15						
	2	1.90 \pm 0.022 ^C	526	11	2.26 \pm 0.016 ^B	1392	11						

^aNorthern portion only (Contra Costa County).

^bComparisons were based only on 2000 and 2003-2004 in all subregions; relative differences and significance among subregions did not change when limited to these years.

^cNorth of San Francisco only.

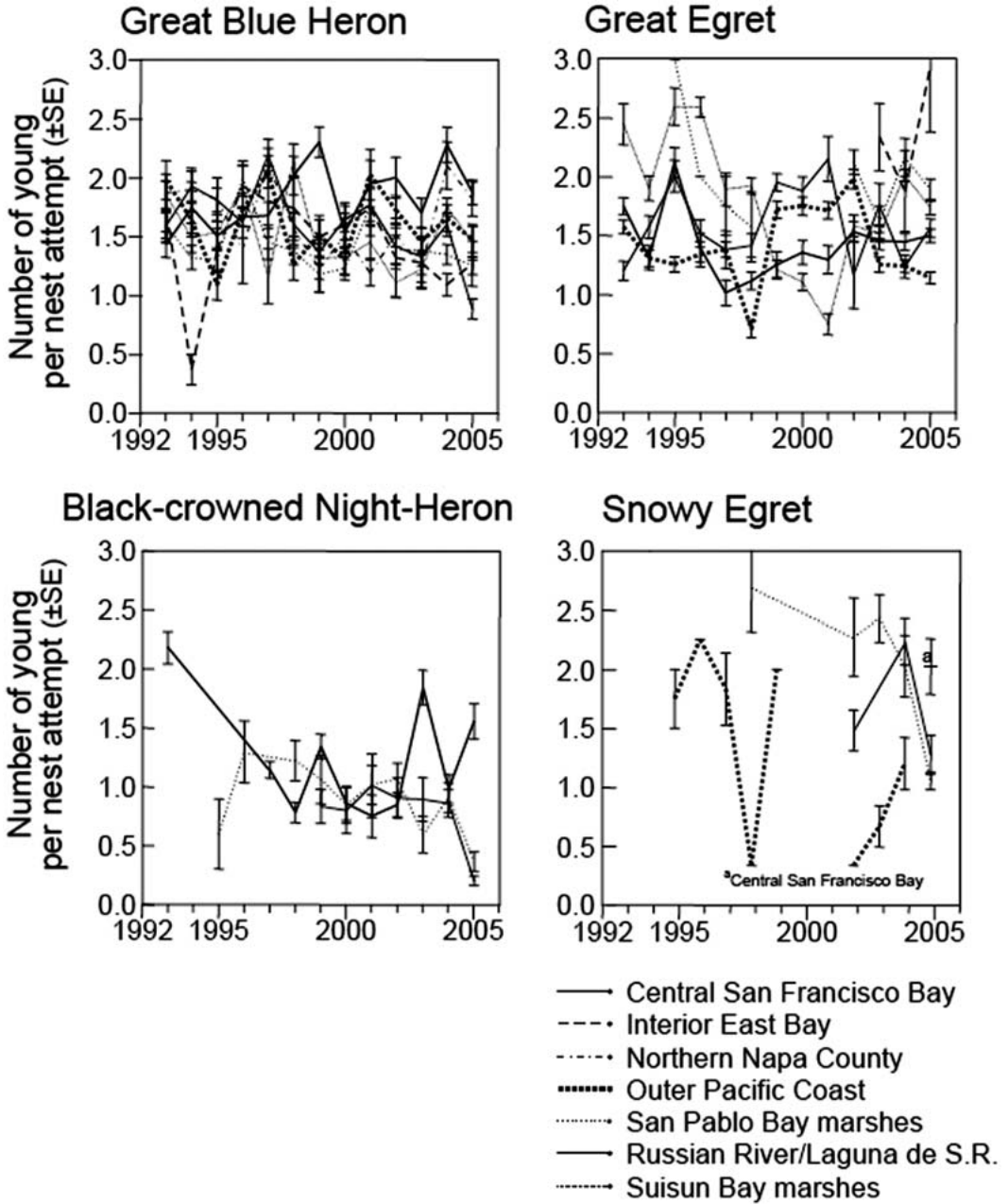


Figure 9. Annual number of young produced per nest attempt (\pm SE) by Great Blue Herons, Great Egrets, Black-crowned Night-Herons, and Snowy Egrets within subregions of the San Francisco Bay area, 1993-2005.

46 \pm 3.4% of Snowy Egret nests (N = 280) had reached the post-guardian period (Fig. 10). Fledging dates were not measured, but by late June nesting activity had declined at most colony sites, with 90 \pm 1.0% of Great Blue Heron nests (N = 730), 78 \pm 0.9% of Great Egret nests (N = 2,326), 41 \pm 2.8% of

Black-crowned Night-Heron nests (N = 413), and 73 \pm 2.8% of Snowy Egret nests in the post-guardian period (N = 195; Fig. 10).

Great Blue Herons tended to nest earlier in subregions characterized by freshwater conditions (Russian River/Laguna de Santa Rosa, Interior East Bay, Northern Napa County) or

Table 5. Mean number of young produced per nest attempt \pm standard error (SE) for Great Blue Heron, Great Egret, Black-crowned Night-Heron, and Snowy Egret, by subregion in the San Francisco Bay area, weighted equally among years. Year span groups indicate (1) all years with adequate data (see Methods) for both nest survivorship and number of young produced in successful nests, 1993-2005, and (2) years with adequate nest survivorship and productivity data from all subregions (Great Blue Heron: 1994-1995, 1997, and 1999-2005; Great Egret: 1995-1998 and 2002-2005; Black-crowned Night-Heron: 2000 and 2002-2005; Snowy Egret: 2004-2005). Means with the same superscript capital letter within species and year span group are not significantly different (Bonferroni adjusted $P > 0.05$).

Subregion	Year span group	Great Blue Heron		Great Egret		Black-crowned Night-Heron		Snowy Egret	
		Mean \pm SE	n _{years}	Mean \pm SE	n _{years}	Mean \pm SE	n _{years}	Mean \pm SE	n _{years}
Central San Francisco Bay	1	1.82 \pm 0.041 ^A	13	1.43 \pm 0.027 ^D	13	1.28 \pm 0.040 ^A	9	2.03 \pm 0.236 ^{AB}	1 ^a
	2	1.86 \pm 0.049 ^A	10	1.45 \pm 0.033 ^B	8	1.20 \pm 0.064 ^A	5	2.03 \pm 0.236 ^A	1 ^a
Interior East Bay ^b	1	1.39 \pm 0.065 ^{BC}	11	2.10 \pm 0.223 ^A	2 ^c				
	2	1.34 \pm 0.069 ^B	10	2.10 \pm 0.223 ^A	2 ^c				
Northern Napa County	1	1.66 \pm 0.045 ^A	12						
	2	1.65 \pm 0.050 ^A	10						
Outer Coast ^d	1	1.61 \pm 0.038 ^{AB}	13	1.41 \pm 0.020 ^D	13			1.27 \pm 0.073 ^C	8
	2	1.60 \pm 0.043 ^A	10	1.29 \pm 0.025 ^C	8			1.60 \pm 0.193 ^A	2
San Pablo Bay	1	1.43 \pm 0.034 ^C	13	2.01 \pm 0.058 ^A	8	0.79 \pm 0.048 ^B	9	2.09 \pm 0.119 ^A	5
	2	1.36 \pm 0.038 ^B	10	2.01 \pm 0.058 ^A	8	0.79 \pm 0.060 ^B	5	1.54 \pm 0.136 ^A	2
Russian River and Laguna de Santa Rosa	1	1.60 \pm 0.033 ^{AB}	13	1.60 \pm 0.040 ^C	13	0.78 \pm 0.073 ^B	6	1.66 \pm 0.103 ^B	3
	2	1.60 \pm 0.039 ^A	10	1.50 \pm 0.055 ^B	8	0.77 \pm 0.078 ^B	5	1.75 \pm 0.128 ^A	2
Suisun Bay	1	1.52 \pm 0.042 ^{ABC}	13	1.79 \pm 0.028 ^B	13				
	2	1.38 \pm 0.048 ^B	10	1.98 \pm 0.034 ^A	8				

^aComparisons were based only on 2005 in all subregions.

^bNorthern portion only (Contra Costa County).

^cComparisons were based only on 2003-2004 in all subregions.

^dNorth of San Francisco only.

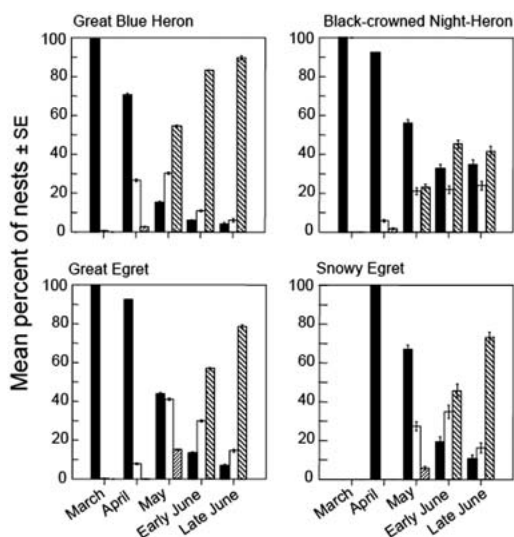


Figure 10. Intraseasonal timing of heron and egret nesting activity in the northern San Francisco Bay area, indexed by the mean percent (\pm SE) of nests in the egg-laying or incubation period (solid bars), parental guardian period (open bars), and post-guardian period (striped bars), during March (13 March \pm six d, SD), April (11 April \pm five d), May (13 May \pm six d), early June (7 June \pm four d), and late June (19 June \pm three d), weighted equally among years, 1992-2005.

low salinity marshes (Suisun Bay) than in subregions dominated by tidal wetlands (Fig. 11; multiple comparisons, $P < 0.05$). Great Egrets nested significantly earlier in Central San Francisco Bay and significantly later in the Interior East Bay than in other subregions (Fig. 11; multiple comparisons, $P < 0.05$).

Intraseasonal timing was less synchronous in Black-crowned Night-Heron and Snowy Egret nests than in the larger species (Fig. 10). Consequently, significant subregional differences in timing among night-heron nests were not detected. The percent of Snowy Egret nests in the post-guardian stage in early May indicated that they nested significantly earlier in the Laguna de Santa Rosa in 2001, and 2003-2005 ($32 \pm 4.1\%$, $N = 78$ nests) than in San Pablo Bay ($6 \pm 1.9\%$, $N = 119$ nests; $t_{195} = 6.7$, $P < 0.05$) and earlier in 2004-2005 ($60 \pm 7.3\%$, $N = 30$) than in Central San Francisco Bay ($16 \pm 5.8\%$, $N = 35$; $t_{64} < 4.8$, $P < 0.05$).

Nest Predation and Disturbance

Evidence of one or more nest failures associated with colony site disturbance, weath-

er, or nest predation, at $13 \pm 1.0\%$ of sites y^{-1} ($N = 15$) was found. Colony size was significantly more likely to decline in the subsequent year at these sites than at sites where there was no detection of such disturbance or predation (Yates' corrected $\chi^2_1 = 4.8$, $P < 0.05$). In addition, colony sites that subsequently declined in size had significantly greater rates of nest failure than sites that did not, at all sites ($F_{1,438} = 13.7$, $P < 0.001$) as well as at sites where disturbance was not detected ($F_{1,364} = 4.41$, $P < 0.04$). Annual changes in colony size were not significantly related to the productivity of successful nests for any species. The percent of colony sites abandoned annually was $7.4 \pm 0.99\%$ in the northern portion of the region (1992-2005) and $2.5 \pm 0.49\%$ in the southern portion of the area (1995-2005). Some abandoned sites in the region were recolonized ($2.5 \pm 0.83\%$ annually), but these often represented only a few pairs at sites that previously supported much larger numbers of nests.

Colony site disturbances associated with nest failure were detected on $1.7 \pm 0.02\%$ of site visits ($N = 1,073$ visits of 1.8 ± 0.03 h per visit; hourly disturbance rates were not measured). Disturbances leading to nest failure were associated with avian predators at $6.2 \pm 0.93\%$ of sites y^{-1} , weather (primarily wind) at $2.7 \pm 0.53\%$ y^{-1} , human disturbance at $2.0 \pm 0.35\%$ y^{-1} (none by observers), mammalian predators at $0.1 \pm 0.13\%$ y^{-1} , unidentified nest predators at $0.8 \pm 0.25\%$ y^{-1} , and unknown sources at $2.7 \pm 0.58\%$ y^{-1} ($N = 15$). Disturbances associated with one or more nest failures occurred at a significantly greater percent of colony sites each year, on average, in Central San Francisco Bay ($34 \pm 3.5\%$ of 6.7 ± 0.29 sites y^{-1}) than in any other subregion except the Outer Coast ($20 \pm 3.5\%$ of 8.2 ± 0.37 sites y^{-1} ; multiple comparisons, $P < 0.05$).

DISCUSSION

Regional Status and Trends

Nest abundances of all colonially nesting heron and egret species are stable or increasing in the San Francisco Bay area. The stable

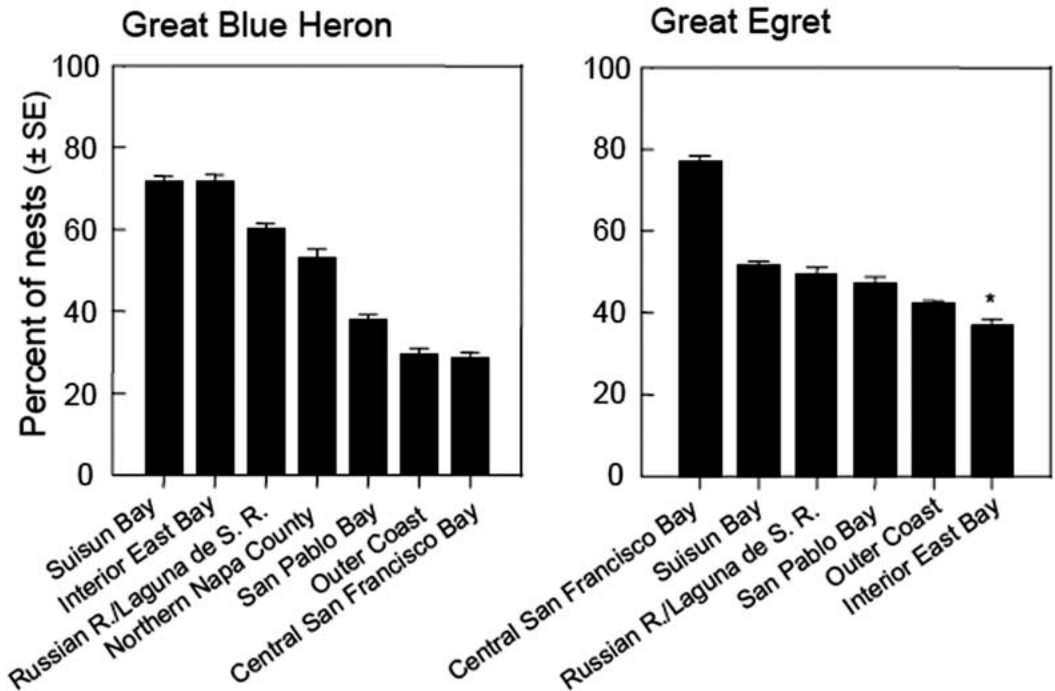


Figure 11. Mean percent (\pm SE) of Great Blue Heron nests in the post-guardian period in May, 1992-2005 (13 May \pm six d, SD) and Great Egret nests in the post-guardian period in early June, 1994-2005 (7 June \pm seven d), in wetland subregions of the northern San Francisco Bay area. *The percent of Great Egret nests in the Interior East Bay represents 1997, 1999, 2000, and 2003-2005 only.

or increasing numbers of Great Blue Herons are consistent with other regions of North America, but intensive count data are not available from most regions because this species often nests solitarily or in small colonies over vast areas (Butler 1992; Butler *et al.* 2000; this study).

The significant increase in the number of Great Egret nests observed in this study was associated with recent counts of over 1,000 nests. These counts contrast with a statewide survey in 1982 that detected only 347 nests in the San Francisco Bay area and central California coastal counties from San Luis Obispo to Mendocino (Schlorff 1982). General increases in the number of nesting Great Egrets have been observed across North America north of Mexico (McCrimmon *et al.* 2001).

Recent increases in the number of Snowy Egret and Black-crowned Night-Heron nests observed in the San Francisco Bay area are associated with large annual fluctuations in nest abundance that prevent the detection

of underlying trends. Annual variation in Snowy Egret nest abundance has also been substantial at the Salton Sea (Molina and Sturm 2004), and breeding populations across North America have been subject to considerable flux since the mid-twentieth century (Parsons and Master 2000). Adequate data are not available to assess continental population trends for Black-crowned Night-Heron (Davis 1993).

Annual changes in nest abundance within colony sites and subregions in the San Francisco Bay area were consistent with shifts in colony site preferences, which are likely to occur across years and over space with fluctuations in the proximity of suitable foraging areas (Fasola and Alieri 1992; Bancroft *et al.* 1994; Gibbs and Kinkel 1997; Frederick 2002), competition for food or foraging areas (Gibbs *et al.* 1987; Gibbs and Kinkel 1997), or risk of nest predation or disturbance (Tremblay and Ellison 1979; Simpson *et al.* 1987; Smith and Collopy 1995). In the

San Francisco Estuary, herons and egrets prefer sites with more estuarine-emergent habitat and open water within one km than is available at other potential sites in the wetland landscape (Kelly *et al.* 2005b). The importance of local feeding areas has also been suggested by declining habitat use with increasing distance from the colony (Gibbs *et al.* 1987; Simpson *et al.* 1987; Fasola and Alieri 1992) and by the frequent initiation of subcolonies or new colony sites near heronries that are subjected to heavy nest predation or disturbance (Custer *et al.* 1980; JPK, unpubl. data). The concentration of Great Egret nests in Suisun Bay was associated with the zone of greatest estuarine circulation in the San Francisco Estuary, where the maximum abundances of larval or juvenile fish, or other prey, are most likely to occur (Nichols *et al.* 1986; Kelly *et al.* 1993).

In contrast to the importance of local feeding areas, larger scale influences on habitat use are also evident. The abundances of nesting herons and egrets within major wetland subregions in the San Francisco Bay area are not related clearly to the extent of tidal marshland in those areas (Kelly *et al.* 1993). For example, concentrations of Great Egrets and Black-crowned Night-Herons nest in Central San Francisco Bay where the extent of tidal marsh habitat is relatively limited. An explanation for this is implied by the angular distribution of arrival and departure flights of Great Egrets and Snowy Egrets nesting on the Marin Islands in Central San Francisco Bay (Kelly *et al.* 2007), which strongly suggests that they forage primarily in the marshes of San Pablo Bay to the north. Therefore, the benefits of nesting at sites that are relatively safe from terrestrial predators (e.g., islands) may offset the costs of traveling to more distant feeding areas.

With the exception of a colony site near the freshwater wetlands of the Laguna de Santa Rosa, Snowy Egret and Black-crowned Night-Heron nest distributions were consistent with a preference for tidal feeding areas (Willard 1977; Custer and Osborn 1978; Davis 1993; Parsons and Master 2000). These species also nested at relatively few sites, several of which were close to roads and buildings

that suggest a tolerance of human activity. However, Snowy Egrets in other regions have abandoned coastal sites in favor of isolated islands, suggesting the importance of safe nesting sites within profitable commuting distances to estuarine feeding areas (Parsons and Master 2000), and Black-crowned Night-Herons are especially sensitive to nest predation and disturbance and may abandon nests when disturbed (Tremblay and Ellison 1979; Blus *et al.* 1997; Hothem and Hatch 2004).

Reproductive Success

Significant regional declines in reproductive success of Great Blue Herons, Black-crowned Night-Herons, and Snowy Egrets resulted primarily from declining nest survivorship. These declines coincided with regional increases in abundances of Common Ravens (*Corvus corax*) and American Crows (*Corvus brachyrhynchos*) (Kelly *et al.* 2002), and increases in nest predation by Common Ravens in heronries along the Outer Coast and in Central San Francisco Bay (Hothem and Hatch 2004; Kelly *et al.* 2005a), although the declines could have resulted from other, unknown processes.

The subregional productivity of successful Great Blue Heron and Great Egret nests fluctuated with larger-scale variation across the region. This regional variation may be influenced by annual differences in rainfall, weather, or other processes that broadly affect foraging conditions or the regional dynamics of prey populations. In contrast, annual changes in nest survivorship were not consistent among subregions, suggesting that processes associated with nest failure, such as nest predation, colony disturbance, and extreme weather events, operate primarily at local or subregional scales.

Subregional differences in reproductive success of wading birds have been reported among freshwater, estuarine and marine habitats in Florida (Frederick *et al.* 1992), but variation in reproductive success in the San Francisco Bay area was not related to the predominance of tidal or non-tidal habitats. Although herons and egrets seem to move freely among colony sites as nesting distribu-

tions shift between years (Bancroft *et al.* 1994; this study), subregional differences in nest productivity were not precluded by possible density-dependent effects on foraging, as predicted by an ideal free distribution (Fretwell and Lucas 1970). Therefore, annual shifts in nesting distribution may not reflect "ideal" knowledge of differences in foraging habitat quality and associated fitness potential among nesting areas.

Subregional differences in reproductive performance may reflect the difficulty of predicting changes in food availability over a relatively long nesting period (Lack 1947, 1954; Mock and Forbes 1994). Subregional differences in both nest survivorship and productivity suggest that colony site choices may be further complicated by tradeoffs between the risk of nest predation and the suitability of feeding areas. Alternatively, the subregional differences in reproductive success might result (1) if some individuals force others to nest or feed in suboptimal areas (despotic distribution; Fretwell and Lucas 1970), (2) if the value of mate- or colony-site fidelity outweighs potential benefits of moving to a new site, or (3) from other potential fitness considerations.

Higher rates of nest mortality led to significant decreases in colony size, even at sites where nest predation or disturbance was not detected. Therefore, declines in colony size and associated shifts in breeding distribution might be stimulated by declines in conspecific nest success (Boulinier 1996; Danchin *et al.* 1998) as well as by repeated or catastrophic disturbance detectable by observers. Alternatively, colony sizes may have declined in response to undetected disturbance.

Intraseasonal Timing

The intraseasonal timing of food availability is a strong stimulus for the initiation of nest attempts by herons and egrets (Kushlan 1986; Frederick and Collopy 1989), especially prior to or during the time of egg formation (Butler 1993; Bancroft *et al.* 1994). In the San Francisco Bay area, Great Blue Herons and Snowy Egrets nested earlier in subregions dominated by freshwater wetlands. This is

consistent with the early availability of seasonally flooded marshes, ephemeral creeks, and receding ponds after normal periods of winter rainfall. The general pattern of nesting later near tidal areas suggests the importance of estuarine prey as spring salinities rise and fish abundances increase with the seasonal influxes and productivity of estuarine breeders from marine habitats (Day *et al.* 1989).

Implications for Conservation

The relative stability of larger colonies in the San Francisco Bay area suggest that conservation efforts should prioritize the protection of colony sites with 20 or more active nests and provide long-term protection for colony sites with more than 100 nests. Values related to the expected longevity of mixed-species heronries increase more rapidly as numbers increase above six Great Blue Heron nests, 20 Great Egret nests, 30 Snowy Egret nests, or 30 Black-crowned Night-Heron nests. Efforts to protect or manage smaller heronries should consider that they may be more sensitive to disturbance and more prone to abandonment than larger heronries.

Sharp declines in nest abundance of heron and egret species in 1999 were consistent with the hypothesis that winter foraging conditions and juvenile survival are primary influences on annual nesting abundance and the dynamics of heron and egret populations (North 1979; Butler 1994; Cezilly 1997). In areas where water systems are controlled by dikes or managed discharges, starvation risk in juveniles during their first winter is likely to be reduced by practices that (1) maintain shallow (5 to 25 cm) water depths across flooded wetlands and in the mouths of creeks or channels that connect wetland patches (Frederick 2002; Gawlik 2002; Maccarone and Brzozard 2005), (2) improve the ability of seasonal marshes to support fish and amphibians (Kushlan 2000a; Gawlik 2002), or (3) minimize areal extent or duration of heavy turbidity (Cezilly 1992) related to the movement of water, land uses, and watershed erosion.

The substantial use of sites associated with low or medium housing suggests a tolerance of human activity and the potential val-

ue of tall trees near houses in rural and suburban areas adjacent to wetlands. However, nest success in such areas could be limited by chronic human intrusion (Thompson 1977) or nest predation by human commensals such as raccoons or ravens (Pratt and Winkler 1985; Parsons and Master 2000; Kelly *et al.* 2005a). If severe nest losses are caused by one or a few individual predators (Rodgers 1987), it may be feasible to protect disturbance-prone colonies by removing or deterring particular individuals.

Regional changes in the structure or availability of planted eucalyptus groves, which provide most of the alternative colony sites in the San Francisco Bay area, might alter the distribution of heronries. If nesting herons and egrets are forced to relocate substantial distances to find suitable nest trees, they might have to increase the amount of time or energy spent on foraging or reduce their use of some wetlands (Gibbs *et al.* 1987; Simpson *et al.* 1987; Fasola and Alieri 1992). The spacing of heronries at intervals of approximately six km in the San Francisco Bay area was similar to distances of 5 to 7 km between heronries in northwest Italy (Fasola and Alieri 1992), suggesting a suitable scale for managing networks of active colony sites and the availability of alternative sites.

Restoration of wetland habitat and prey abundances can result in increased use by herons and the initiation of new heronries (Mau-champ *et al.* 2002). Increases in the number of herons and egrets nesting in San Pablo Bay since the late 1990s coincided with increases in the extent of restored tidal marshes (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999; Featherston *et al.* 2006), suggesting that distributional shifts may partly reflect increases in the availability of suitable wetland feeding areas (Frederick and Collopy 1989; Bryan *et al.* 2003). In the absence of active habitat restoration or enhancement, annual shifts in nesting distribution related to changes in habitat suitability are likely to be relatively small in tidal landscapes because hydrologic conditions are more stable between years than in wetlands that vary primarily with seasonal rainfall or runoff (Kushlan 1977; Frederick 2002). Therefore, shifts in heron and

egret distributions may be particularly useful in monitoring the effects of restoration projects in tidal landscapes.

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