

STATUS, TRENDS, AND IMPLICATIONS FOR THE CONSERVATION OF HERON AND EGRET NESTING COLONIES IN THE SAN FRANCISCO BAY AREA

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SUMMARY

The atlas of heronries summarizes continuing efforts by Audubon Canyon Ranch and the San Francisco Bay Bird Observatory to monitor colonially nesting herons and egrets in the central coastal region of California surrounding the San Francisco Estuary. The methods used provide for the intensive regional monitoring of nesting distributions, nest survivorship, productivity of successful nests, nesting habitat characteristics, and intraseasonal timing. The analysis focuses on comparisons of heron and egret nesting performance among nine major wetland subregions from 1991-2005.

We recorded an average of 73 active colony sites per year, supporting approximately 62 Great Blue Heron colonies, 25 Great Egret colonies, 13 Black-crowned Night-Heron colonies and 12 Snowy Egret colonies each year. Cattle Egret and Little Blue Heron each nested at a few sites. Regional nest abundances of all colonially nesting heron and egret species were stable or increasing. Annual changes in nest abundance within colony sites and subregions were consistent with shifts in colony site preferences 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 as well as to disturbance or predation events, suggesting that conspecific nest failure rather than disturbance or predation events alone may stimulate shifts in breeding distribution. Patterns of seasonal weather and annual reproductive performance suggested that a sharp decline in nest abundances may have resulted from reduced recruitment associated with increased juvenile mortality in winter, rather than from a decline in productivity. Persistence of colony site use increased substantially at sites that reached at least 20 active nests. Subregional increases in the nesting abundance coincided with the restoration of tidal marshes, suggesting that heron and egret nesting distributions may be useful in monitoring the landscape-scale effects of restoration projects in tidal landscapes.

Significant linear 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 American Crows and Common Ravens. 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 changes in nest survivorship were associated with processes such as nest predation, colony disturbance, and extreme weather events that operated at local or subregional scales.



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

INTRODUCTION

The slender, poised profiles of foraging herons and egrets are distinctive features of wetland and shoreline ecosystems. To many observers, these conspicuous birds signify the presence of potentially diverse and healthy wetlands worthy of protection. Consequently, herons and egrets are frequently used

as symbols of wetland conservation (Parnell et al. 1988, Kushlan and Hancock 2005). Such recognition is well substantiated by the ecologically important roles they play. As important predators, herons and egrets are sensitive to subtle changes in ecosystem productivity, hydrology, and vegetation, and (although their responses are not completely understood), they are recognized widely as indicators of processes that sustain or threaten wetland

ecosystems (Kushlan 1993, Erwin and Custer 2000). Although nesting herons and egrets at some sites may tolerate human activities at close range (Nisbet 2000; Hothem and Hatch 2004), their tolerance levels are highly variable and sensitive to differences in the timing, type, proximity, or intensity of human activity (Vos et al. 1985, Rodgers and Smith 1995, Kelly 2002; pers. observation). In addition, just as wetlands depend on watershed conditions that extend into upland areas, the use of wetlands by herons and egrets may depend on suitable nesting sites in upland habitats that do not qualify for wetland protection. The work presented here complements efforts to protect and restore wetland feeding areas by providing detailed information that could be used to protect heron and egret nesting colonies.

The atlas of heronries summarizes continuing efforts by Audubon Canyon Ranch (ACR) and the San Francisco Bay Bird Observatory to monitor colonially nesting herons and egrets in the central coastal region of California surrounding the San Francisco Estuary (Kelly et al. 1993). Prior to this work, information on populations of colonially nesting herons and egrets in the San Francisco Bay area was limited to local monitoring of a few large colony sites (Harvey et al. 1992, Kelly et al. 1993). Field studies contributing to the atlas began in 1967, when Helen Pratt initiated a long-term study of nesting herons and egrets at Bolinas Lagoon (Pratt and Winkler 1985) and began recording annually the number of active nests at several heronries in Marin County (Pratt 1983). In the 1980s, the San Francisco Bay Bird Observatory began monitoring a few heronries in South San Francisco Bay. In 1991 we initiated the current program to monitor annually the status of regional nesting populations (Kelly et al. 1993).

The goals of the atlas are to (1) provide a protocol for intensive regional monitoring of heronries, (2) develop current and historical perspectives on the regional, subregional, and local status of herons and egrets with regard to patterns and trends in their nesting abundance and reproductive performance, and (3) consider regional, subregional, and local implications for conservation. Specifically, we present information on regional distributions, nest survivorship, productivity, nesting habitat, intraseasonal timing, human disturbance, nest

predation, property ownership, and management concerns at all known heronries in the San Francisco Bay area. The results are based on field observations conducted over the last 15 years and additional data available for previous years as far back as 1967 (38 years).

The 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*). We also documented single nesting occurrences of Little Blue Heron (*Egretta caerulea*) in some years. The Green Heron (*Butorides virescens*) is a common breeder throughout the area that may form loose aggregations of a few nests, but it generally nests alone in hidden locations along wooded streams suitable for foraging (Davis and Kushlan 1994, Shuford 1993, Berner et al. 2003, Burrige 1995) and is therefore not included in this study.

NESTING BIOLOGY

Hérons and egrets nest in remote forested canyons, in tule marshes and swamps, on isolated islands, and along river banks and sloughs far from human activity (Kushlan and Hancock 2005). In California, they also nest in suburban neighborhoods, in non-native trees near ranch buildings and farm ponds, and in groves of introduced eucalyptus trees (*Eucalyptus* spp.). Their colonies may consist of several hundred nests or just a few pairs of breeders. Occasionally, herons and egrets breed as solitary pairs (Kushlan and Hancock 2005).

Nesting herons and egrets tend to feed within a few to several kilometers of their heronries (Custer and Osborn 1978, Bancroft et al. 1994, Custer and Galli 2002, Kelly et al. 2005b). They feed primarily in wetland (and some upland) habitats characterized by frequent shifts in suitability for foraging. These shifts in habitat quality are related to changes in prey availability, which are influenced by the dynamics of hydrology, tides, prey populations, and prey depletion by competing herons and egrets (Kushlan 1976, 2000, Gawlik 2002, Frederick 2002, Kushlan and Hancock 2005). The dependence of herons and egrets on finding food in patchy and changeable landscapes may account for the occurrence of nesting

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colonies in particular locations (Wittenberger and Hunt 1985). By providing efficient access to several productive feeding areas, the locations of heronries may be geographically important to nesting herons and egrets.

Hérons and egrets nest during seasonally high periods of prey availability (Butler 1993, Kushlan and Hancock 2005). A variable period of courtship precedes nest construction and clutch initiation. Nesting activity can be delayed by persistent rains, high winds, unusually cold temperatures, or other conditions that reduce their ability to capture enough prey to support the energy demands of breeding (Pratt 1970, McCrimmon et al. 2001, Butler 1993, and ACR unpubl. data). Nesting can also be delayed by human or predator disturbance to the colony (unpubl. data).

Great Blue Herons in the San Francisco Bay area generally begin to occupy colony sites in January or February, but sometimes as early as late December, with first clutches typically initiated in mid-to-late February (Pratt 1970, Pratt and Winkler 1985, and ACR unpubl. data). Great Egrets typically arrive at their nesting colonies between mid-February and early April, usually laying their first eggs in mid-March (Pratt 1970, Pratt and Winkler 1985, and ACR unpubl. data). The seasonal return of Snowy Egrets, Black-crowned Night-Hérons, and Cattle Egrets to previously established colony sites is more variable, ranging from March to late April (Hothem and Hatch 2004 and ACR unpubl. data). In the San Francisco Bay area, Great Blue Herons usually occupy colony sites through early to mid-June, and Great Egrets, Snowy Egrets, Black-crowned Night-Hérons and Cattle Egrets often occupy colony sites well into August. However, late nests in any species may remain active into mid-September (Pratt 1970, Hothem and Hatch 2004, and ACR unpubl. data).

The reproductive performance of herons and egrets is influenced by several processes that affect nest survivorship and productivity. Nest survivorship (proportion of nests that fledge at least one young) varies primarily with the risks of nest predation, severe weather, and colony site disturbance (Pratt and Winkler 1985, Frederick and Spalding 1994, Smith and Callopy 1995, Vennesland and Butler 2004, Kelly et al. 2005a). In contrast, the number of young produced in successful nests

depends on the amount of food available to produce eggs and provision nestlings (Frederick 2002, Kushlan and Hancock 2005). Herons and egrets typically reduce the sizes of each brood through asynchronous incubation and hatching, which leads to a competitive size hierarchy and differential survivorship among nestlings (Kushlan and Hancock 2005). One likely benefit of brood reduction is an ability to align their reproductive effort with the vagaries of prey availability in wetland systems (Lack 1947, 1954, Mock and Forbes 1994, Forbes and Mock 2000). By provisioning smaller broods in years when food is less available, herons and egrets improve the likelihood that some chicks will survive. Therefore, large changes in wetland productivity are likely to influence the extent of brood reduction and the number of young produced in successful nests.

STUDY AREA

The study area extends from the outer Pacific Coast eastward to the confluence of the Sacramento and San Joaquin rivers, Mount Diablo, and Mount Hamilton, and from the Russian River, Cloverdale, and Lake Berryessa southward through the Santa Clara Valley south of San Francisco Bay (Figure 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. We did not include heronries east of the Lower Sherman Island State Wildlife Area at the confluence of the Sacramento and San Joaquin Rivers. The extensive Sacramento-San Joaquin Delta, immediately beyond this eastern boundary of the study area, includes 1,792 km² of waterways and 1,417 km² of diked former marshland presently used for agriculture (California State Lands Commission 1991).

Within the study area, rolling hills and mountains of the Coast Range give way to coastal terraces and lagoons along the outer coast and alluvial shorelines and marshes of the San Francisco Estuary. Wetland systems associated with the Russian River and other freshwater streams in the north include a variety of lakes, marshes, creeks, and sloughs that provide freshwater feeding areas for herons and

egrets. Coast Redwood (*Sequoia sempervirens*), Douglas-Fir (*Pseudotsuga menziesii*), and mixed evergreen forests that dominate the outer coastal drainage open eastward into expanses of grassland, chaparral, and oak woodland that characterize the interior hills. Riparian zones along the outer parts of the Coast Range are dominated by willows (*Salix* spp.), alders (*Alnus* spp.), and coast redwoods, but in the interior riparian areas, willows, alders, and cottonwoods (*Populus fremontii*) predominate. Non-native eucalyptus trees (predominately *Eucalyptus globulus*) are the dominant trees associated with most of the wetland terraces surrounding the San Francisco Estuary and occur throughout the region as narrow windbreaks or small patches that cover generally less than 1 ha.

We analyzed breeding distributions by grouping colonies into nine major wetland subregions: (1) Outer Pacific Coast, divided into the outer coast north and south of San Francisco; (2) Russian River and Laguna de Santa Rosa; (3) Northern Napa County; four subregions of the San Francisco Estuary identified as (4) Suisun Bay, (5) San Pablo Bay, (6) Central San Francisco Bay, and (7) South San Francisco Bay; (8) Interior East Bay, including interior Contra Costa and Alameda counties; and (9) Santa Clara Valley (Figure 1).

The Laguna de Santa Rosa is the southern-most tributary of the Russian River, with a 20,000-acre (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 Bay and the Petaluma and Napa marshes of San Pablo Bay. The Napa and Suisun marshes are characterized by extensive slough systems and extensive historic marshland that has been largely diked or drained, although some areas have been restored to tidal action (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). Most of the tidal marshland in South San Francisco Bay was also diked and drained for pasture in the early 1900s and eventually converted to salt evaporation ponds (Association of Bay Area Governments 1992). Planning efforts are currently under way to restore much of the South San Francisco Bay marshland to tidal action, although

some ponds will be managed as non-tidal wildlife areas (PWA et al. 2006). Freshwater discharges from South San Francisco Bay sewage treatment plants have converted additional salt marsh areas into brackish tule (*Scirpus* spp.) marsh. Estimated subregional losses of tidal wetlands since 1850 are 86% for South and Central San Francisco Bay (pooled), 70% for San Pablo Bay, and 86% for Suisun Bay (Association of Bay Area Governments 1992). Regional habitats are further described in Mayer and Laudenslayer (1988), Association of Bay Area Governments (1992), and the San Francisco Bay Area Wetlands Ecosystem Goals Project (1999).

PROTOCOL FOR MONITORING

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

Five, three-day regional observation periods were scheduled each year (Table 1). During each of these periods, we attempted to visit all colony sites to allow for comparisons of seasonal timing (Table 1). We defined a colony site or heronry as a group of active heron or egret nests within 500 m of each other. Whenever a group of nests in a heronry was isolated by more than 100 m from other nests within the site, it was considered to be a subcolony site and the associated data were recorded separately. However, the results presented in this report are pooled for each colony site.

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Table 1. Regional observation periods are used to monitor differences in intraseasonal timing among heronries and to structure the minimum number of annual monitoring visits in the San Francisco Bay area. All heronries are observed during each 3-day regional observation period each year, scheduled as closely as possible to the target dates for regional observations.

Target dates for regional observations	Monitoring objective
10-12 March	Number focal nests on a panoramic sketch. Monitor focal nests. Determine the total number of active nests in the colony, by species.
1-31 March	Unscheduled visit(s), as necessary, to identify "focal nests." Monitor focal nests. Determine the total number of active nests in the colony, by species.
10-12 April	Identify additional focal nests if the colony has not yet reached peak annual size. Monitor focal nests. Determine the total number of active nests in the colony, by species.
10-12 May	Monitor focal nests. Determine the total number of active nests in the colony, by species.
3-5 June	Monitor focal nests. Determine the total number of active nests in the colony, by species.
20-22 June	(Great Egrets, Snowy Egrets, and Black-crowned Night-Herons only) Monitor focal nests. Determine the total number of active nests in the colony, by species.

We observed all colonies from the ground or from boats using binoculars and telescopes. We used GPS or USGS 7.5-min topographic quads to record the geographic position of each heronry (NAD83). We were assisted at many sites by trained volunteer field observers. Observers visited most colony sites at least four times each breeding season, with an average of 6.8 ± 0.31 (standard error, SE) visits to each active colony site annually, 1991-2005. The annual percent of active colony sites visited only once was $19 \pm 1.4\%$ year⁻¹. Sites visited only once in a given year 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 $15 \pm 0.6\%$ year⁻¹.

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; Figure 1), colony site visits averaged 1.4 ± 0.04 hours each year. Longer periods of observation were required at larger colonies, especially in May and June when brood sizes were recorded (average hours = $1.25 + 0.004 \times$ peak annual nest abundance; $F_{1,801} = 54.9, P < 0.001$).

We used the peak number of active nests observed as an estimate of annual colony size. On visits 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. To avoid nest disturbance on islands where Snowy Egrets and Black-crowned Night-Herons nest in dense shrubs, we estimated the number of active nests from the perimeter of colonies by conducting multiple counts and mapping the locations of birds perched above, or visible through, the shrub canopy.

Table 2. Habitat variables used to evaluate differences among heron and egret colony sites in the San Francisco Bay area.

Land form: ridge, hillside, flood plain, wetland, island with bridge, island without bridge, or levee
Distance to nearest wetland by type (perennial stream or river, lake or pond, non-tidal marsh, tidal salt or brackish marsh, San Francisco Bay shore, Outer Pacific Coast shore; km)
Colony length x width (m ²)
Human land use within 200 m and 500 m: industrial, residential (<3, 3-10, and >10 houses per ha), farm, orchard, vineyard, grazing, natural area or park, and sports field
Nest height: mean, min, max (m)
Nest canopy height: mean, max (m)
Nest substrate structural types (presence of live branch on tree, dead branch on tree, snag, shrub (0.5-5 m tall), <i>Scirpus</i> or <i>Typha</i> spp., ground, other)
Nest substrate plant species composition
Tree dbh class: (1) 3-10 cm, (2) 11-50 cm, (3) 51-100 cm, (4) 101-150 cm, (5) ≥ 150 cm
Tree canopy cover (height > 5 m; %)
Shrub cover (height 0.5-5 m; %)
Ground vegetation cover (height < 0.5 m; %)

Occasionally, these estimates were confirmed or revised by clapping loudly to flush adults in the colony. 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, we estimated the number of nests from approximately 100 m away by boat. Because of the difficulty of counting Black-crowned Night-Heron nests at the Marin Islands, we multiplied nest counts 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. communication). These conversions were consistent with anecdotal observations, apparently related to disturbance events, of 115 night-herons standing along the shoreline of the colony in 1995 and 215 in 2005, relative to nest counts of 18 and 44 conducted in those years, respectively, by boat (Kelly et al. 2006).

NESTING HABITAT

We analyzed vegetation and other habitat characteristics at active heronries during the 2003 nesting season. To reduce the possibility of observer disturbance, colony site measurements were conducted only on days with favorable weather after most nesting pairs had begun to incubate eggs (Fredrick and Collopy 1989a, Tremblay and Ellison 1979). At each colony site, we recorded information on the geomorphology, distance to wetland habitats, size of the nesting area, human land uses, nest heights, nest canopy height, nest substrate type, nest substrate species, tree diameter at breast height (dbh; measured 1.3 m above ground), and vegetation cover (Table 2). We recorded human land uses 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 landscape conditions might affect the locations of colony sites (Watts and Bradshaw 1994).

We estimated the areal extent of each colony as the product of the length of the longest axis through the colony site and its longest perpendicular axis. We used the minimum convex polygon indicated by nest locations to determine colony site boundaries. Nest heights, canopy heights, and habitat patch area were measured with a range finder. Trees within the colony site boundaries were allocated into dbh classes using a reach stick (James and Shugart 1970). At large colony sites of more than 50 trees, we measured dbh based on a random sample of at least 50 trees. We estimated ground, shrub and canopy vegetation cover as the percent of perpendicular vegetation "hits" indicated by a cross-hair sighting viewed through an ocular tube at approximately 1 m intervals along each length and width transect (James and Shugart 1970). The minimum transect distance for these measurements was 10 m with at least 40 point

samples at each heronry. We determined distances (m) to wetland habitats, human land uses, and other heronries, using GIS (ArcGIS, ESRI, Redlands, CA, USA) or USGS topographic maps and field reconnaissance at each site.

REPRODUCTIVE SUCCESS

We measured reproductive success at colonies in the northern portion of the study area, including all subregions north of San Francisco, Central San Francisco Bay, the northern (Contra Costa County) portion of the Interior East Bay, and the northern portion (north of San Francisco) of the Outer Coast (Figure 1). We used focal nest samples at colony sites observed through the entire nesting season to measure nest survivorship. In colonies with fewer than 15 active nests, all nests initiated before the colony reached peak number of nests for the year were treated as focal nests. In colonies with more than 15 active nests, a random subset of 10-15 focal nests was selected and observers were encouraged to monitor as many focal nests as possible. In some larger colonies all observable nests were selected as focal nests.

In the northern portion of the study area indicated above, annual samples of focal nests (1993-2005) 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. At those colonies sampled, the number of nests that were treated as focal nests accounted for $90 \pm 1.1\%$ of the peak number of Great Blue Heron nests, $68 \pm 2.5\%$ of Great Egret nests, $50 \pm 6.0\%$ of Black-crowned Night-Heron nests, and $55 \pm 5.3\%$ of Snowy Egret nests.

On average, we sampled brood size in successful nests at $82 \pm 1.6\%$ of Great Blue Heron colonies, $71 \pm 2.8\%$ of Great Egret colonies, $40 \pm 4.6\%$ of Black-crowned Night-Heron colonies, and $51 \pm 4.9\%$ of Snowy Egret colonies in the northern portion of the study area. At those colonies sampled, brood size samples accounted for $66 \pm 1.2\%$ of the peak number of Great Blue Heron nests, $48 \pm 2.1\%$ of Great Egret nests, $32 \pm 3.4\%$ of Black-crowned Night-Heron nests, and $42 \pm 4.2\%$ of Snowy Egret nests.

Because the frequency of visits to most heronries was insufficient for measuring daily nest

survivorship (Mayfield 1961, 1975, Johnson 1979), we estimated the apparent survivorship of nests based on the success rates of focal nests. Focal nests were normally monitored from initiation or early in the incubation period, thus minimizing the potential for a (positive) survivorship bias related to undetected failures early in the nesting cycle. In addition, high daily survivorship during the incubation period for Great Egret nests and Great Blue Heron nests at Bolinas Lagoon Preserve of Audubon Canyon Ranch, 2003-2005 (pooled), indicated that the potential bias resulting from occasional selection of focal nests 1-2 wks into the 28-day incubation period was minor (daily nest survivorship for Great Egret: $99.8 \pm 0.1\%$ over 224 exposure days in the first 7 days of incubation, $99.7 \pm 0.1\%$ over 2617 exposure days in the first 14 days; daily nest survivorship for Great Blue Heron: $99.8 \pm 0.1\%$ over 189 exposure days in the first 7 days, $99.7 \pm 0.1\%$ over 371 exposure days in the first 14 days).

Great Egret and Great Blue Heron nests were considered successful if at least one chick survived to seven or eight weeks post-hatch, respectively (Pratt 1970, Pratt and Winkler 1985). Because Snowy Egret, Black-crowned Night-Heron and Cattle Egret nestlings begin to wander away from the nest when relatively young, we considered nests to be successful at 14 days after first hatch for Snowy Egret (Frederick and Callopy 1989a) and Cattle Egret (Telfair 1994) and 15 days after first hatch for Black-crowned Night-Heron (Custer et al. 1983). At most heronries, however, Snowy Egret, Black-crowned Night-Heron, and Cattle Egret nests were not observed frequently enough to determine survivorship.

We measured the productivity of successful nests based on the size of completely visible broods when Great Blue Heron nestlings were known to be 5-8 wks old and Great Egrets were known to be 5-7 wks old. During these periods, nestlings were too young to hop away from their nests and Great Egret and Great Blue Heron nestlings were old enough to have survived the period when most brood reduction occurs (Pratt 1970, Pratt and Winkler 1985). Because the nestlings of other species begin to wander away from nests at a younger age, we measured the productivity of successful Snowy Egret and Cattle Egret nests when the young were 7-14 days old (Frederick and Callopy 1989a, Telfair 1994, Parsons

and Master 2000), and the productivity of successful Black-crowned Night-Heron nests when the young were 7-15 days old (Custer et al. 1983, Davis 1993). We determined if nestlings had reached the appropriate ages indicated above by tracking the timing of nesting stages in nests followed through the nesting cycle (see Intra-seasonal Timing, below), or by nestling size. Therefore, 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.

INTRASEASONAL TIMING

We measured the intraseasonal timing of nesting effort at colony sites in the northern portion of the study area (same area used to measure reproductive success, described above). We did not attempt to measure differences in the initial occupation of heronries at the onset of each nesting season. We examined differences in intraseasonal timing among colonies by comparing the proportions of nests among nesting stages during each regional observation period, scheduled as nearly as possible to target dates (Table 1). We used the following classifications: (1) egg-laying or incubation, adult lying down in nest for long periods, standing to turn eggs, defecate, or for nest relief; (2) hatching, small (downy) nestlings, or feeding observed low in the nest; (3) nestlings capable of standing, most or all of down replaced by juvenal plumage, parent(s) continuously at the nest; (4) adults not continuously at the nest but may be present for some time after feeding, nestlings usually on the nest platform; (5) young often off the nest on nearby branches. Occasionally, we were unable to visit colony sites within scheduled observation periods and therefore collected samples within a few days of the planned dates. To compare intraseasonal timing among subregions, we estimated differences in the average proportion of nests observed in the egg-laying and incubation period (Stage 1), the parental guardian period (Stages 2 and 3), and the post-guardian period (Stages 4 and 5), 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.

NEST PREDATION AND DISTURBANCE

At colony sites in the northern portion of the study area (see Reproductive Success above) we recorded evidence of nest predation and disturbance during each site visit. Because observations were generally conducted from remote positions, we rarely entered colony sites to search for or evaluate such evidence. We classified each occurrence of predation or disturbance by type (human, observer, avian, mammal, other predator, weather, or unknown) and level (colony abandonment, nest loss or nestling mortality, or behavioral response). These observations were summarized by converting them to the mean proportion of occurrences among colony sites and site visits per year within the region or wetland subregions. We summarized evidence of colony site abandonment, colonization or discovery, recolonization, and sources of disturbance over the entire study area. Disturbance notes for each heronry are included in the individual site accounts.

STATISTICAL ANALYSIS

Estimates of annual survivorship and productivity are based on the fates of individual heron and egret nests, which can be sampled only once each. Under these conditions, variance models based on sampling without replacement are more accurate than commonly used models that assume replacement, especially if a substantial proportion of the population is sampled (Thompson 1992). We sampled nest survivorship and productivity from a sampling universe equal to the number of nests (N) in a colony or group of colonies, with sample sizes (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. Therefore, we used unbiased variance estimators for sampling nests without replacement. Nest monitoring programs based on such models benefit from standard errors that are substantially and appropriately reduced. We calculated the variance of the estimated mean pre-fledging brood size (\hat{b}) by multiplying the estimator based on samples collected with replacement (s^2/n) by the finite population correction factor $1 - (n / N)$ (Thompson 1992):

$$\text{var}(\hat{b}) = (s^2/n) \cdot (1 - n/N).$$

Similarly, we estimated nest survivorship as the successful proportion (\hat{p}) of focal nests sampled without replacement (Thompson 1992), with an estimated variance of

$$\text{var}(\hat{p}) = (\hat{p} \cdot (1 - \hat{p}) / n) \cdot (n / (n-1)) \cdot (1 - n / N).$$

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, we used t-tests with Bonferroni adjustments for an experimentwise error of $P < 0.05$. 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). Unless indicated otherwise, pairwise comparisons of nest survivorship represented the years 1993-2005, and pairwise comparisons of the number of young in successful nests represented the years 1991-2005. When subregional data were incomplete across years, we conducted additional comparisons based on years with complete data from all subregions.

The proportions of focal nests or brood sizes sampled in each colony were not significantly related to colony size ($|r| < 0.1$, $P > 0.05$). However, because of differences in the difficulty of viewing colony sites, the proportions were not constant among sites, suggesting possible sampling biases within the region or subregions. To examine the influence of variation in sampling intensity among colony sites, we repeated 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 these weighted colony means did not differ from those based on pooled samples of individual nests, we considered the potential biases to be minor.

We estimated overall reproductive success (rs) as

the number of young produced per nest attempt, calculated as product of estimates of focal nest survivorship (\hat{p}) and pre fledging brood size in successful nests (\hat{b}):

$$\hat{rs} = \hat{p} \cdot \hat{b}$$

with a variance (Goodman 1960) of

$$\text{var}(\hat{rs}) = [(\hat{p})^2 \cdot \text{var}(\hat{b})] + [(\hat{b})^2 \cdot \text{var}(\hat{p})] - [\text{var}(\hat{b}) \cdot \text{var}(\hat{p})].$$

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

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

RESULTS

NEST ABUNDANCE AND DISTRIBUTION

In 1991-2005, we recorded an average of 73 ± 2.1 active colony sites per year ($n=15$ yrs; Figure 1). 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 in the study area. Active colony sites were separated by about 6 km (mean nearest-neighbor distance = 5.95 ± 4.8 km standard deviation; $n = 1116$ sites weighted equally among years; species pooled). Great Blue Heron colonies tended to be small and widely distributed in the region ($44 \pm 1.9\%$ of colonies had < 6 nests yr^{-1} and $65 \pm 1.4\%$ of those colonies occurred without other nesting species of herons or egrets). Great Egret nesting abundance was concentrated most strongly at several colony sites in the Suisun Bay subregion, with other important colony sites in Central and South

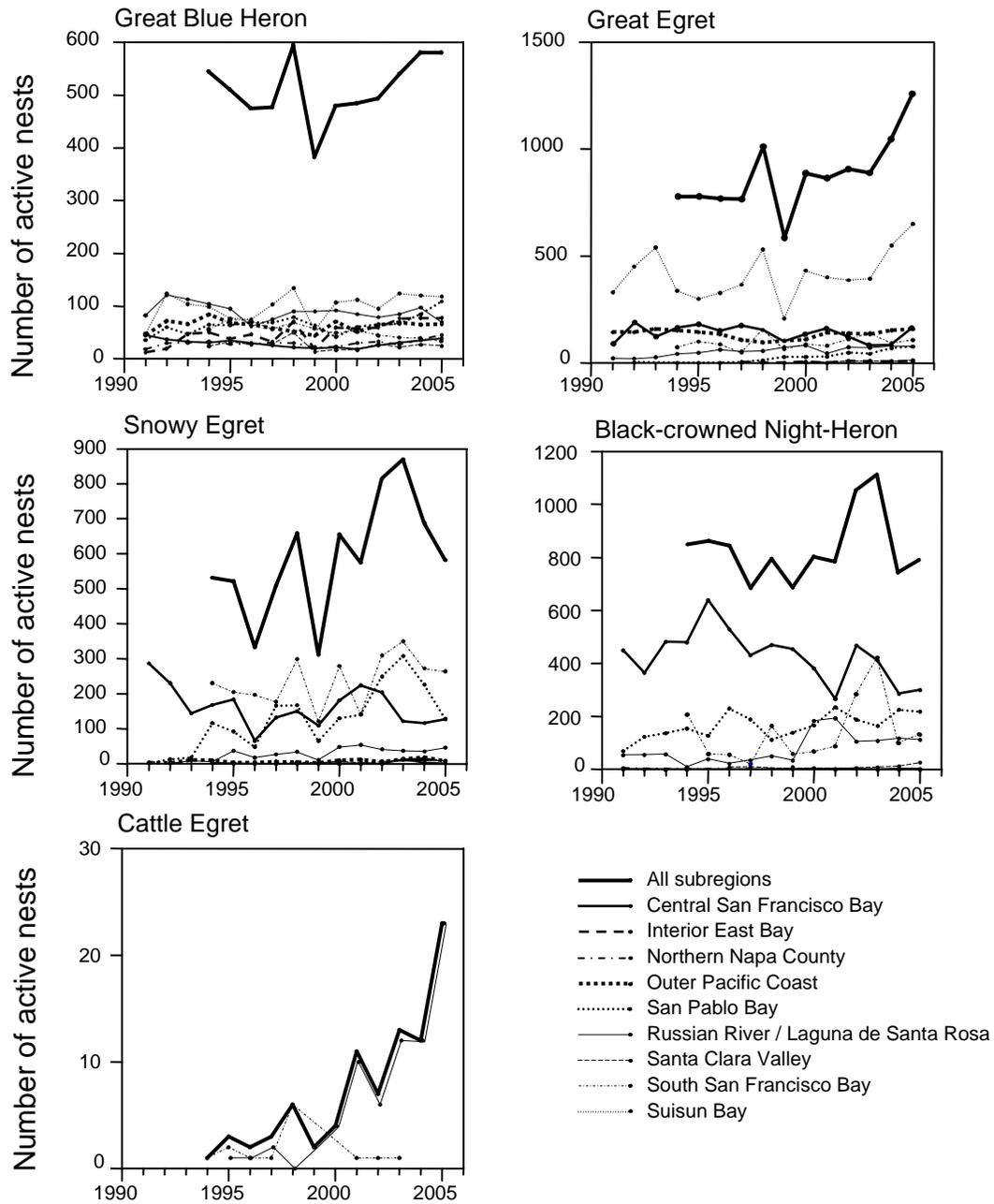


Figure 2. Peak number of active heron and egret nests observed annually within wetland subregions of the San Francisco Bay area. See Figure 1 for locations of heronries and subregions.

San Francisco Bay and along the Outer Pacific Coast. Cattle Egrets nested at one or two sites each year from 1994-2005 (along Santa Rosa Creek near the Laguna de Santa Rosa and at Mallard Slough, Hayward Shoreline, or Coyote Creek in South San Francisco Bay). Cattle Egrets also nested at Mallard Slough in 1985-1988 and 1990. Single pairs of Little

Blue Heron were observed nesting at Mallard Slough in South San Francisco Bay in 1990, 1993, and 1996.

The average annual number of nests in the region from 1994-2005 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. We emphasize that counts of Black-

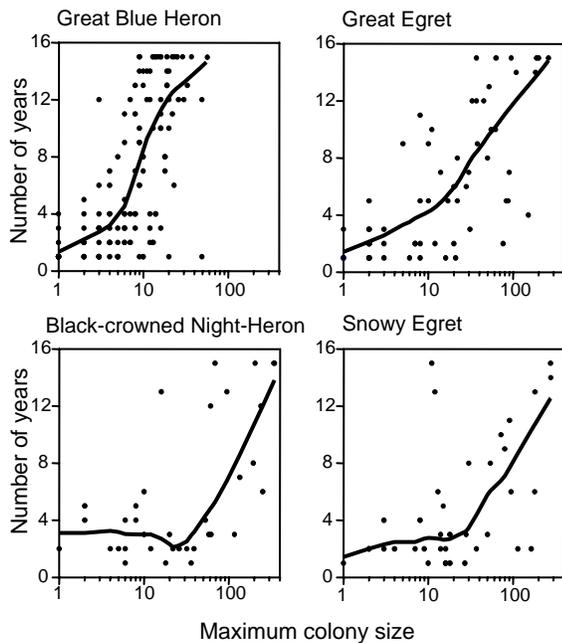


Figure 3. Relationships between persistence and maximum size of heron and egret nesting colonies (\log_{10} scale) in the San Francisco Bay area, 1991-2005. Lines represent LOWESS trends with smoothing parameter $f = 0.6$.

crowned Night-Heron and Snowy Egret nests may be lower than the actual number because of the difficulty of counting nests concealed in dense vegetation. Cattle Egrets nested in low numbers of 1-23 nests (Figure 2).

The number of years heron or egret colonies were active during the 15-year study period (1991-2005) was related to colony size and nesting species. New colonies were often initiated with a few nests and grew, either gradually or abruptly, into larger colonies in subsequent years. However, colonies tended to become inactive within 5 years unless nest abundance reached a threshold of increasing persistence (Figure 3). Great Blue Heron colonies that remained smaller than six nests generally became inactive within five years, but colonies persisted, on average, for 12 years or more if maximum abundance was greater than 20 nests (Figure 3). The persistence of Great Egret, Black-crowned Night-Heron, and Snowy Egret colonies began to increase 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, on average, within approximately eight years (Figure 4). These general patterns underestimate average

persistence because some colonies were active prior to discovery or may remain active beyond the 15-year monitoring period.

The nest abundances of all species were stable or increasing in the region from 1994-2005 (Figure 2). Great Blue Heron nest numbers showed no significant linear trend from 1994-2005 ($F_{1,10} = 1.1$, $P = 0.32$), but increased significantly by an average of 25 ± 2.8 nests per year from 1999-2005 ($F_{1,4} = 82.4$, $P < 0.001$; Figure 2). The number of Great Egret nests in the region increased significantly from 1994-2005 ($b = 32 \pm 11.2$ nests yr^{-1} , $F_{1,10} = 8.2$, $P = 0.02$), reflecting primarily a sharp increase in 2004 and 2005 (Figure 2). Black-crowned Night-Heron nest numbers did not increase significantly ($F_{1,10} = 0.4$, $P = 0.54$), but a marginally significant linear increase was evident in the number of Snowy Egret nests from 1994-2005 ($F_{1,10} = 4.5$, $P = 0.057$; Figure 2). Significant 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 ($F_{1,10} = 26.4$, $P < 0.001$).

We observed a consistent decline in the peak number of active nests by all species in 1999, particularly in Suisun Bay and South San Francisco Bay (Figure 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

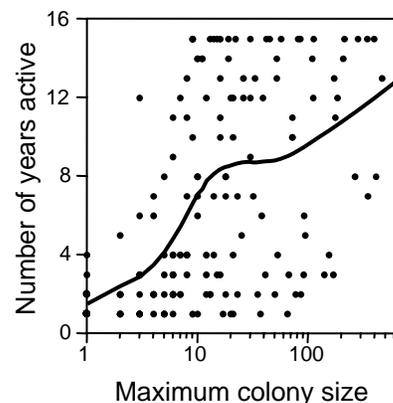


Figure 4. Relationship between persistence and maximum size of heronries (\log_{10} scale, all species combined) in the San Francisco Bay area, 1991-2005. Lines represent LOWESS trends with smoothing parameter $f = 0.6$.

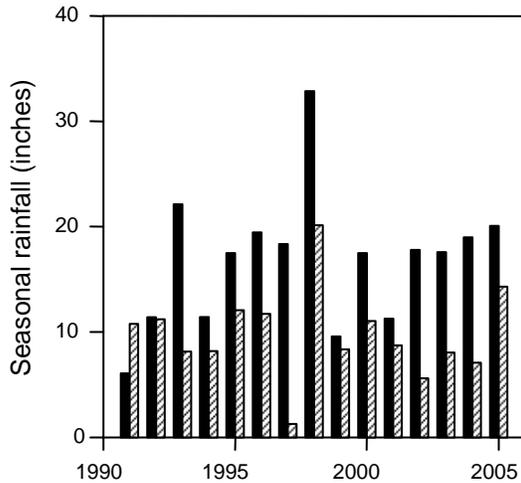


Figure 5. Cumulative rainfall in winter (November-February; solid bars) and the nesting season (February-June, striped bars), 1991-2005, recorded in San Francisco (California Data Exchange Center, Department of Water Resources).

and endured unusually heavy rainfall during their first winter (Figure 5). The dry breeding conditions in 1997 were associated with an unusual decline in nest survivorship only for Great Blue Heron in Suisun Bay (Figure 6) and were not associated with unusual declines in the productivity of successful nests (Figure 7). Therefore, if first time breeders normally represent a substantial portion of the nesting population and natal dispersal occurs primarily at intraregional scales, or within scales within the geographic extent of the harsh winter conditions from November 1997 to February 1998 (Figure 5), then the 1999 decline in regional nest abundance may have resulted from a decline in recruitment following reduced juvenile survival during harsh winter conditions. However, we did not measure juvenile survival.

NESTING HABITAT

Trees were used as nesting substrates in 90% of the active colony sites in 2003 (Table 3). Non-native eucalyptus trees were used as nesting substrate at 53% of sites and were the predominant tree species near wetland habitats (J. Kelly, pers. observation). In addition, Snowy Egrets and Black-crowned Night-Herons used sites with coast live oaks (*Quercus agrifolia*; 18% and 20% of sites, respectively), shrubs (24% and 40% of sites), and tule (*Scirpus* spp.) or cattail (*Typha* spp.) marshes (12% and 20% of sites).

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 ($n = 63$). Thirty-two (48%) of 66 sites with trees as nest substrates included one or more trees that were 1 m dbh or larger, and 13 sites with nesting trees (20%) included one or more trees larger than 1.5 m dbh.

Only 12% of colony sites were in wetland habitat (Table 3). 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 grazing, parks or natural areas and low-to-medium density residential use (Table 4). Low and medium density residential use occurred within 200 m of half of the sites used by Great Blue Herons, 40% of sites used by Black-crowned Night-Herons, and 38% of sites used by Snowy Egrets. Concentrated use of heronries in parks or natural areas by Snowy Egrets (47% of sites) and Black-crowned Night-Herons (40%; Table 4) was associated with their frequent use of protected islands (Table 3). 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. Overall nest survivorship in the region, using all focal nests weighted equally among years (1993-2005), was $79 \pm 0.4\%$ for Great Blue Heron ($n = 3227$ nests), $78 \pm 0.4\%$ for Great Egret ($n = 4685$), $62 \pm 2.3\%$ for Black-crowned Night-Heron ($n = 1940$), and $66 \pm 2.1\%$ for Snowy Egret ($n = 402$). In general, annual changes in nest survivorship were not consistent among subregions (Figure 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 and Laguna de Santa Rosa (Table 5). Although they often nest in small colonies along rivers or streams, we found no evidence of a relationship between Great Blue Heron colony size and nest survivorship, either from inspection of scatter plots or from linear regression (controlling for

Table 3. 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 (1113)	All species n = 73 (3332)
<u>Nesting substrate</u>					
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	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>Scirpus</i> or <i>Typha</i> spp.	0 (0)	3 (+)	12 (6)	20 (3)	4 (2)
<u>Land form</u>					
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)

year; $F_{1,410} = 0.01$, $P = 0.92$). 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 5).

The exclusion of small annual samples from subregional comparisons of Snowy Egret nest survivorship (see Methods) resulted in differences between the regional mean reported above and the subregional means in Table 5. However, 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 5). We did not detect other subregional differences in nest survivorship for Black-crowned Night-Heron or Snowy Egret, but small sample sizes suggest the possibility of undetected differences (Table 5).

Significant but weak linear declines in average regional nest survivorship were evident from 1993-2005 for Great Blue Heron ($b = -0.6 \pm 0.22\% \text{ yr}^{-1}$, $F_{1,13} = 7.2$, $P = 0.019$), Great Egret ($b = -1.0 \pm 0.38\% \text{ yr}^{-1}$, $F_{1,13} = 7.3$, $P = 0.018$), and Black-crowned Night-Heron ($b = -3.0 \pm 0.66\% \text{ yr}^{-1}$, $F_{1,12} = 20.4$, $P < 0.001$; Figure 8).

Number of young in successful nests. The

Table 4. 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 (1113)	All species n = 73 (3332)
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, 3-10 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)

estimated number of young fledged per successful nest in the northern San Francisco Bay area, weighted equally among years (1991-2005), was 2.04 ± 0.015 for Great Blue Heron ($n = 2193$ nests), 2.15 ± 0.011 for Great Egret ($n = 3124$), 1.82 ± 0.046 for Black-crowned Night-Heron ($n = 978$), and 2.50 ± 0.040 for Snowy Egret ($n = 343$).

The number of young fledged from successful heron and egret nests differed significantly among subregions (Table 6). Successful Great Blue Heron nests fledged significantly more young in Central San Francisco Bay than in all other subregions and significantly more young in the Russian River and Laguna de Santa Rosa than all subregions except Central San Francisco Bay. 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 rivers or streams in remote parts of the region, we found 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; $F_{1,2922} = 2.5$, $P = 0.11$).

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. 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

Table 5. 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	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{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	^{-b}	^{-b}	^{-b}	0.78 \pm 0.011 ^B	618	9	0.55 \pm 0.020 ^A	472	7	0.94 \pm 0.058 ^A	16	1 ^a
Interior East Bay ^c	1	0.72 \pm 0.023 ^B	251	13	0.88 \pm 0.026 ^A	28	6						
	2	^{-b}	^{-b}	^{-b}	0.82 \pm 0.039 ^{AB}	22	4 ^d						
Northern Napa County	1	0.83 \pm 0.010 ^A	299	13									
	2	^{-b}	^{-b}	^{-b}									
Outer Coast ^e	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	^{-b}	^{-b}	^{-b}	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	^{-b}	^{-b}	^{-b}	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	^{-b}	^{-b}	^{-b}	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	^{-b}	^{-b}	^{-b}	0.85 \pm 0.009 ^A	1275	9						

^aIn comparisons based on a single-year (2005), Snowy Egret nest survivorship in Central San Francisco Bay was significantly greater than San Pablo Bay or the Russian River/Laguna de Santa Rosa but did not differ significantly from the Outer Coast.

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

^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

Table 6. 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	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{years}	Mean \pm SE	n _{nests}	n _{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

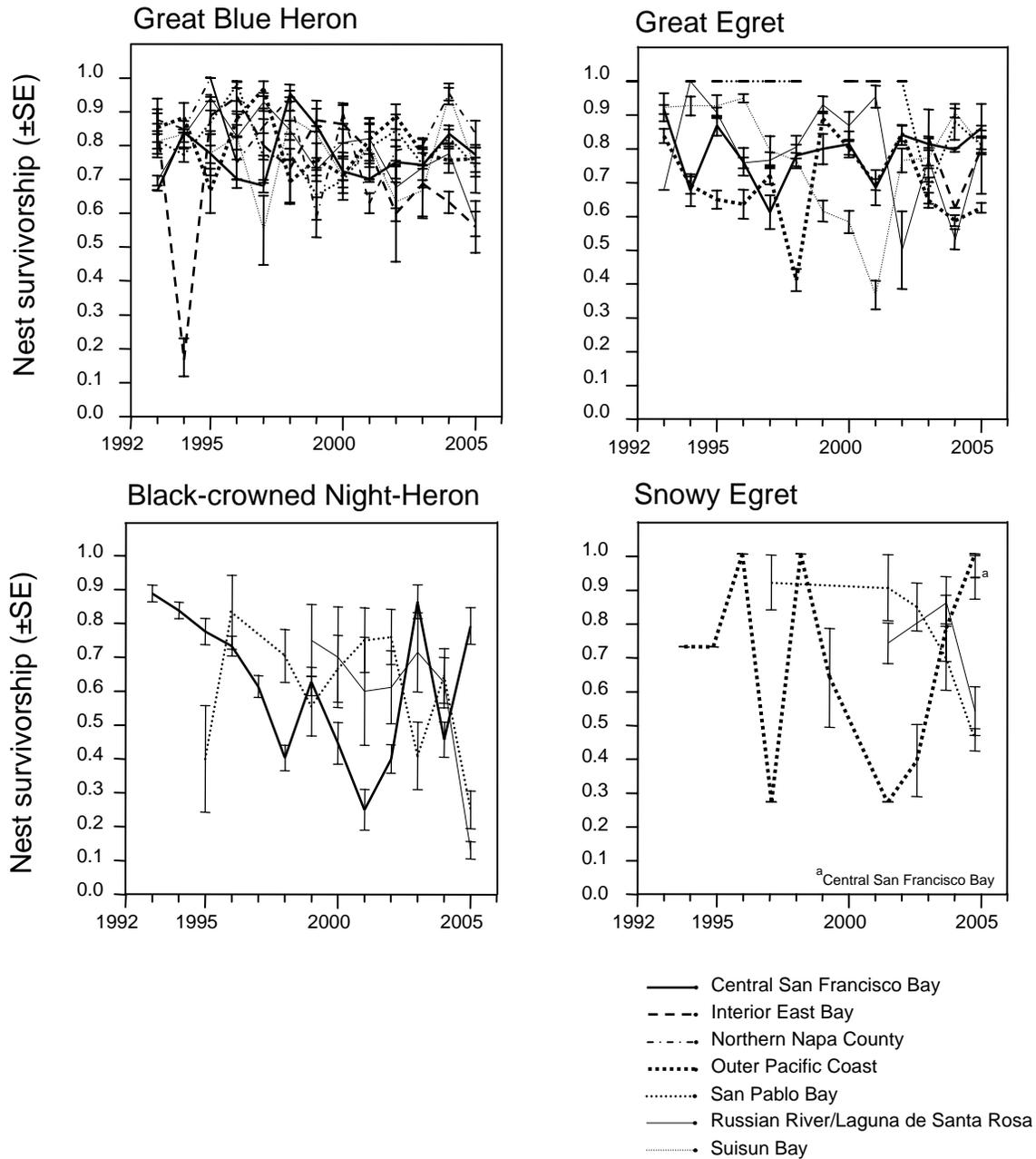


Figure 6. Mean survivorship (SE) of Great Blue Heron, Great Egret, and Black-crowned Night-Heron nests, by subregion, in the San Francisco Bay area, 1993-2005. Annual means with fewer than 10 focal nests are excluded unless samples represent at least half of the nests in the subregion.

Laguna de Santa Rosa (Table 6). As with nest survivorship, the exclusion of small annual samples from subregional comparisons of brood size in successful Snowy Egret nests resulted in differences between the regional mean above and subregional means (Table 6). Snowy Egret nests were significantly less productive on the Outer Coast

(Bollinas Lagoon Preserve of Audubon Canyon Ranch) than in other subregions (Table 6).

The number of young produced in successful nests appeared to covary annually among subregions (Figure 7). Although only two of 21 (9.5%) correlations between subregions were significant for Great Blue Heron, three of 15 (20%) for Great Egret

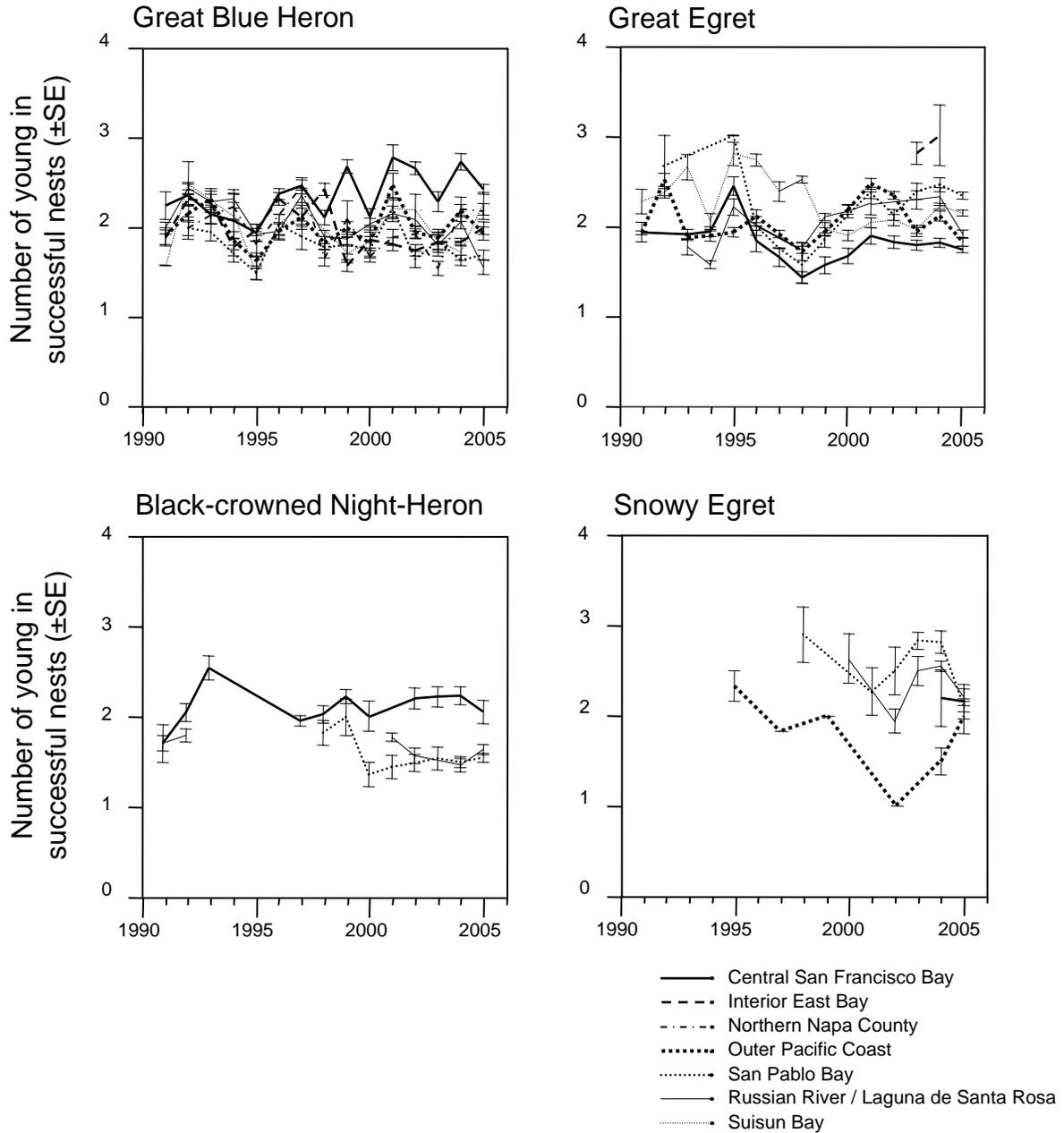


Figure 7. Mean number of young produced in successful Great Blue Heron, Great Egret, Black-crowned Night-Heron, and Snowy Egret nests, by subregion, in the northern San Francisco Bay area, 1991-2005. Annual means with fewer than 10 focal nests are excluded unless samples represent at least half of the nests in the subregion.

($P < 0.05$), and none for Black-crowned Night-Heron or Snowy Egret, the coefficients were consistently positive ($r > 0$) for all pairs of subregions in all species, suggesting that the average number of young produced by successful nests tended to increase or decrease each year across all subregions (Figure 7).

The average number of young produced by successful Black-crowned Night-Heron nests declined significantly from 1991-2005 but with a linear slope of only -0.04 ± 0.013 young yr^{-1} ($F_{1,10} = 8.1$, $P < 0.02$), and no significant trends occurred in other study species ($P > 0.05$; Figure 8).

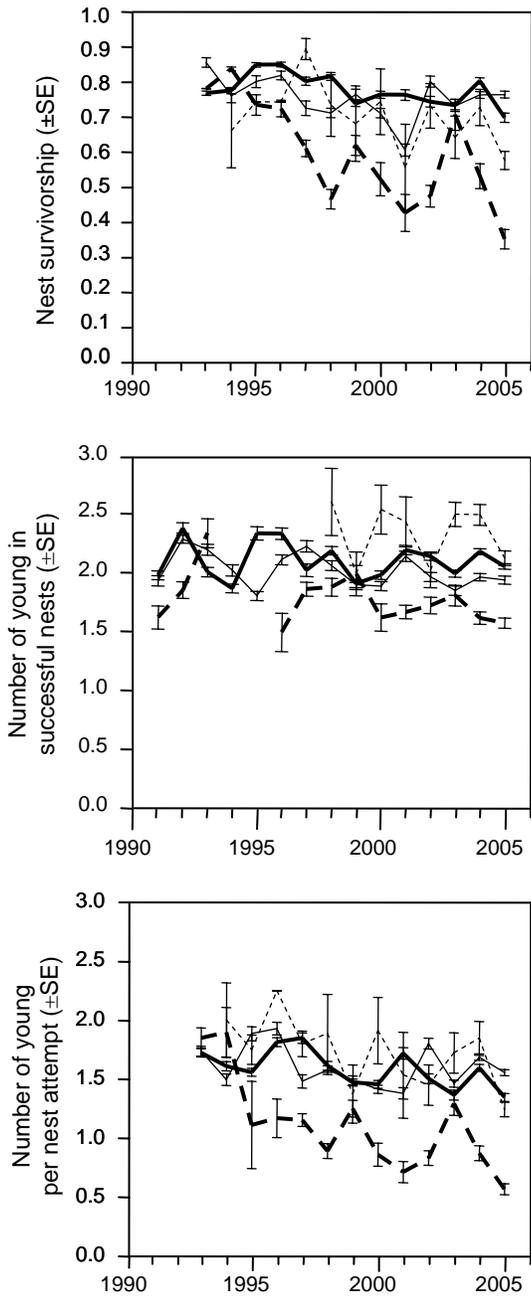


Figure 8. Annual mean \pm SE of nest survivorship, number of young in successful nests, and number of young produced per nest attempt by Great Blue Herons (bold, solid lines), Great Egrets (thin, solid lines), Black-crowned Night-Herons (bold, dashed lines), and Snowy Egrets (thin, dashed lines) in the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

The 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. Subregional

comparisons indicated that overall reproductive performance of Great Blue Herons, based on the number of young produced per nest attempt, 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 7). Overall reproductive success in Great Egrets was significantly greater in Suisun Bay, San Pablo Bay, and the Interior East Bay than in other areas. Black-crowned Night-Herons produce 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 7).

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 regional-scale effects on productivity of successful nests (Figures 7 and 9).

Significant but weak linear declines in the regional average number of young produced per nest attempt were evident from 1993-2005 for Great Blue Heron ($b = -0.02 \pm 0.009 \text{ yr}^{-1}$, $F_{1,11} = 6.2$, $P = 0.03$), Black-crowned Night-Heron ($b = -0.08 \pm 0.021 \text{ yr}^{-1}$, $F_{1,11} = 14.1$, $P = 0.003$), and Snowy Egret ($b = -0.05 \pm 0.020 \text{ yr}^{-1}$, $F_{1,10} = 5.4$, $P = 0.04$; Figure 8). These declines reflect primarily the effects of declines in nest survivorship described above (Figure 8).

INTRASEASONAL TIMING

The proportions of nests in the egg-laying or incubation stage, guardian stage, and post-guardian stage during each regional observation period provide a summary of intraseasonal timing in the region (Figure 10). In early March, almost all active Great Blue Heron nests ($99.3 \pm 0.18\%$, $n = 1539$ nests over 14 years) and Great Egret nests ($99.8 \pm 0.17\%$, $n = 594$ over 10 years), and all active Black-crowned Night-Heron nests (100%, $n = 235$ over 4 years) were in the egg-laying or incubation stage (Figure 10). Snowy Egrets generally began nesting later in the season.

In early April, $71 \pm 0.7\%$ of Great Blue Heron nests ($n = 2723$ over 14 years), $92 \pm 0.3\%$ of Great Egret nests ($n = 3900$ over 14 years), $92 \pm 0.7\%$ of

Table 7. 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. Values represent the product of nest survivorship (Figure 8) and the number of young produced in successful nests (Figure 9). 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

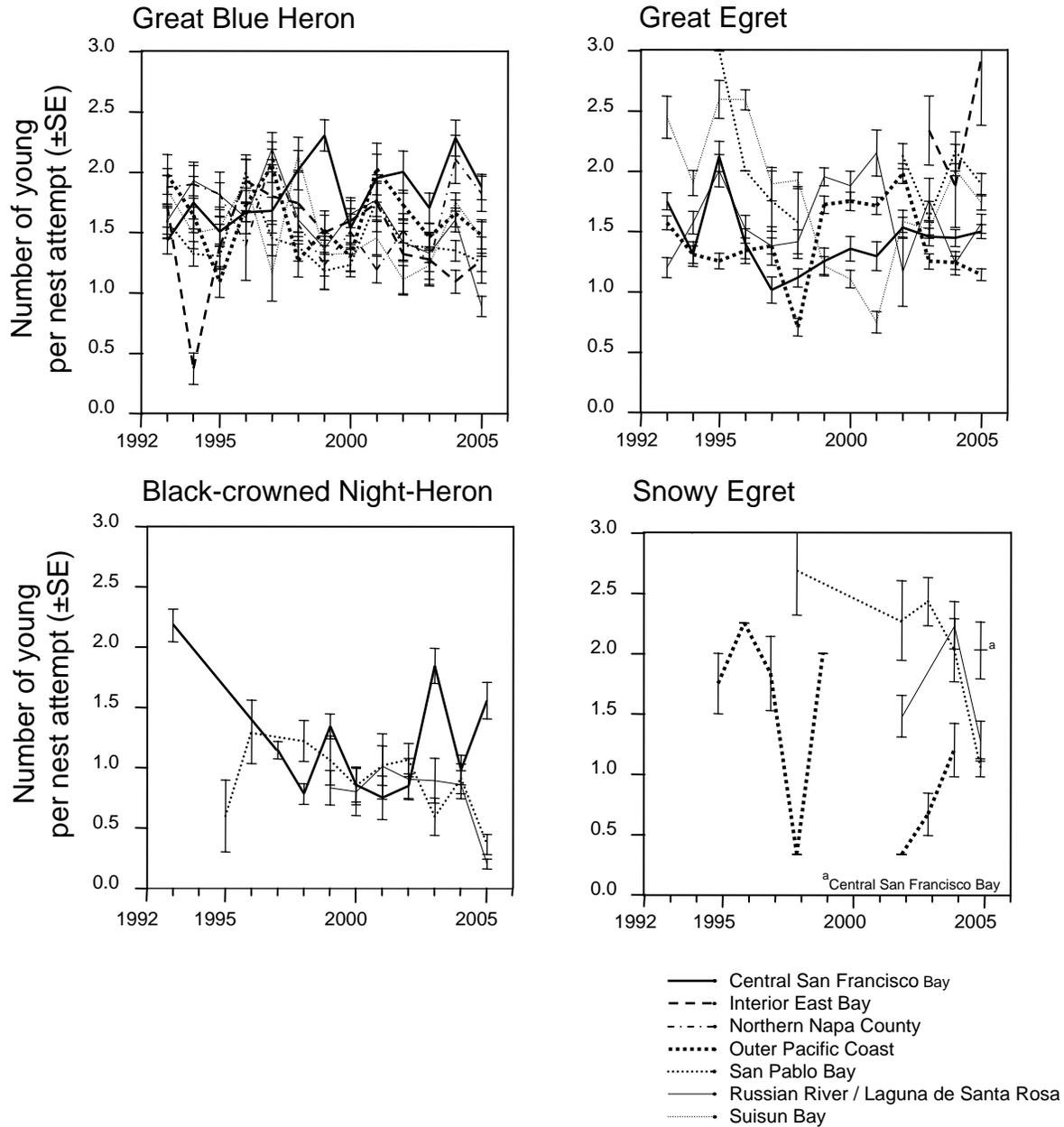


Figure 9. Number of young produced per nest attempt by Great Blue Herons, Great Egrets, Black-crowned Night-Herons, and Snowy Egrets within subregions of the San Francisco Bay area, 1993-2005. Values represent the product of nest survivorship (Figure 4) and number of young produced in successful nests (Figure 5).

Black-crowned Night-Heron nests ($n = 1016$ over 7 years), and all (100%) of Snowy Egret nests ($n = 326$ over 8 years) were in the egg-laying or incubation period (Figure 10).

By early May, only $15 \pm 0.5\%$ of Great Blue Heron nests ($n = 3845$ over 14 years), $44 \pm 0.5\%$ of

Great Egret nests ($n = 5268$ over 14 years), $56 \pm 1.9\%$ of Black-crowned Night-Heron nests ($n = 768$ over 10 years), and $67 \pm 2.3\%$ of Snowy Egret nests ($n = 360$ over 10 years), were still incubating or laying eggs (Figure 10). At this time, $54 \pm 0.6\%$ of Great Blue Heron nests had reached the post-guardian period,

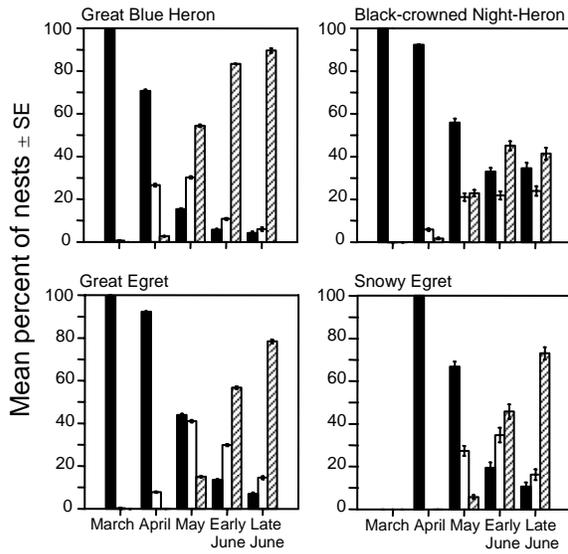


Figure 10. Intraseasonal timing of heron and egret nesting activity in the northern San Francisco Bay area, indexed by the mean percent \pm SE of nests in the egg-laying or incubation period (solid bars), parental guardian period (open bars), and post-guardian period (striped bars), during March (13 March \pm 6 days, std. dev.), April (11 April \pm 5 days), May (13 May \pm 6 days), early June (7 June \pm 4 days), and late June (19 June \pm 3 days), weighted equally among years, 1992-2005.

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 ($n = 2519$ over 14 years), $57 \pm 0.6\%$ of Great Egret nests ($n = 4427$ over 14 years), $45 \pm 2.1\%$ of Black-crowned Night-Heron nests ($n = 717$ over 10 years), and $46 \pm 3.4\%$ of Snowy Egret nests ($n = 280$ over 9 years) had reached the post-guardian period.

We did not measure fledging dates, but by late June nesting activity had declined at most colony sites, with $90 \pm 1.0\%$ of Great Blue Heron nests ($n = 730$ over 9 years), $78 \pm 0.9\%$ of Great Egret nests ($n = 2326$ over 12 years), $41 \pm 2.8\%$ of Black-crowned Night-Heron nests ($n = 413$ over 7 years), and $73 \pm 2.8\%$ of Snowy Egret nests in the post-guardian period (Figure 10).

Differences in intraseasonal timing among subregions were most apparent during May for Great Blue Heron (Figure 11). 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 low salinity marshes (Suisun Bay) than in subregions dominated by tidal wetlands (Figure 11). In May, significantly greater percentages of Great Blue Heron nests reached the post-guardian period in Suisun Bay ($72 \pm 1.1\%$, $n = 1258$) and the Interior East Bay ($72 \pm 1.7\%$, $n = 271$) than in other subregions, whereas significantly smaller percentages of nests reached the post-guardian period in Central San Francisco Bay ($28 \pm 1.4\%$, $n = 291$ over 14 years) and along the Outer Coast ($29 \pm 1.5\%$, $n = 416$ over 14 years, multiple comparisons with Bonferroni adjusted $P < 0.05$; Figure 11).

Subregional differences in the intraseasonal timing of Great Egret nests were most apparent during early June (Figure 11). A significantly greater percentage of Great Egret nests reached the post-guardian stage in early June in Central San Francisco Bay ($77 \pm 1.3\%$, $n = 587$ over 12 years) than in other subregions (Figure 11; multiple comparisons with Bonferroni adjusted $P < 0.05$). Great Egrets nested later in the Interior East Bay (San Pablo Reservoir) than in other subregions, based on a significantly smaller percent of nests in the post-guardian period in early June ($37 \pm 1.3\%$, $n = 32$ over 6 years: 1997, 1999, 2000, 2003-2005; multiple comparisons with Bonferroni adjusted $P < 0.05$).

Intraseasonal timing was less synchronous in Black-crowned Night-Heron and Snowy Egret nests,

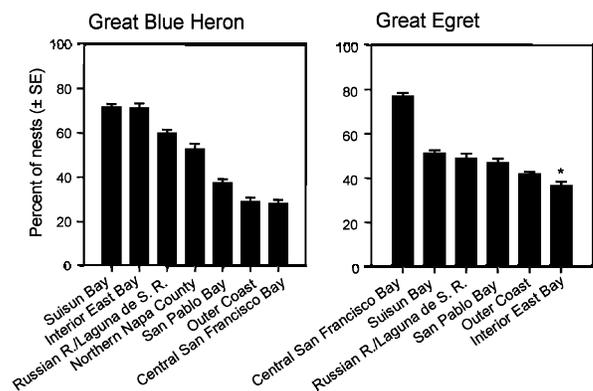


Figure 11. Mean percent \pm SE of Great Blue Heron nests that reached the post-guardian period in May, 1992-2005 (13 May \pm 6 days, std. dev.) and Great Egret nests that reached the post-guardian period in early June, 1994-2005 (7 June \pm 7 days), in wetland subregions of the northern San Francisco Bay area, weighted equally among years. *The percent of Great Egret nests in the Interior East Bay represents 1997, 1999, 2000, and 2003-2005 only and is significantly less than other subregions during these years (see text).

showing greater variation in the number of nests at each nesting stage than evident in the larger species (Figure 10). Consequently, we did not detect significant subregional differences in timing among night-heron nests ($P > 0.05$). However, the average proportion of Snowy Egret nests that reached the post-guardian stage by early May, 2001 and 2003-2005, was significantly greater in the Laguna de Santa Rosa ($32 \pm 4.1\%$, $n = 78$ nests) than in the San Pablo marshes ($6 \pm 1.9\%$, $n = 119$ nests; $t_{195} = 6.7$, Bonferroni adjusted $P < 0.05$). In addition, the percent of Snowy Egret nests at the Laguna de Santa Rosa that reached the post-guardian period by early May in 2004-2005 ($60 \pm 7.3\%$, $n = 30$) was greater than at Alcatraz Island in Central San Francisco Bay ($16 \pm 5.8\%$, $n = 35$; $t_{64} < 4.8$; Bonferroni adjusted $P < 0.05$). Therefore, Snowy Egrets appear to have nested earlier, on average, in the Laguna de Santa Rosa than at heronries in San Pablo Bay or Central San Francisco Bay.

NEST PREDATION AND DISTURBANCE

An average of 4.1 ± 0.60 sites ($7.4 \pm 0.99\%$) were abandoned annually in the northern portion of the region after the first year (1991) of region-wide monitoring ($n = 14$ years). Only 0.7 ± 0.20 sites ($2.5 \pm 0.49\%$) were abandoned annually in the southern portion of the area ($n = 11$ years, 1995-2005). Over the entire study area, 1.5 ± 0.51 sites ($2.5 \pm 0.83\%$) known to be active previously were recolonized, but many of these represented only a few pairs returning to sites that previously supported much larger numbers of nests.

We found evidence of one or more nest failures associated with colony site disturbance, weather, or nest predation, at $13 \pm 1.0\%$ of colony sites each year (55 ± 1.3 sites yr^{-1} , $n = 15$ years). Colony size was significantly more likely to decline in the subsequent year at sites where we detected these disturbances than at sites where we did not (Yates' corrected $\chi^2_1 = 4.8$, $P < 0.05$). In addition, rates of nest failure were significantly greater at colony sites that subsequently declined in size than at those that did not (all sites: $F_{1,438} = 13.7$, $P < 0.001$; sites where disturbance was not detected: $F_{1,364} = 4.41$, $P < 0.04$). The productivity of successful nests was not significantly related to between-year changes in colony size ($P > 0.05$; Great Blue Heron: $F_{1,356} = 0.74$, Great Egret:

$F_{1,121} = 0.06$, Snowy Egret: $F_{1,23} = 0.19$, Black-crowned Night-Heron: $F_{1,17} = 2.97$, all species: $F_{1, 412} = 0.49$).

Disturbances leading to nest failure were associated with avian predators at $6.2 \pm 0.93\%$ of sites yr^{-1} ($n=15$), weather (primarily wind) at $2.7 \pm 0.53\%$ yr^{-1} , human disturbance (not caused by observers in this study) at $2.0 \pm 0.35\%$ yr^{-1} , mammalian predators at $0.1 \pm 0.13\%$ yr^{-1} , unidentified nest predators at $0.8 \pm 0.25\%$ yr^{-1} , and unknown sources at $2.7 \pm 0.58\%$ yr^{-1} . We did not detect any nest failure associated with observer disturbance in this study, although some nest failure may have occurred during nest monitoring and egg collecting for a contaminant study at six heronries in Central and South San Francisco Bay in 1989-1991 (Hothem et al. 1995). We did not measure the rate of colony site disturbances detected per hour of observation, but one or more colony site disturbances associated with nest failure were detected on 1.7 ± 0.02 percent of site visits ($n = 1073$ visits), with an average of 1.8 ± 0.03 hours per visit.

Within the northern portion of the study area, 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 yr^{-1} , $n = 15$ yrs) and the Outer Coast ($20 \pm 3.5\%$ of 8.2 ± 0.37 sites yr^{-1}) than in any other subregion (multiple comparisons, Bonferroni adjusted $P < 0.05$). Colony site disturbance leading to nest failure was significantly less likely in Suisun Bay ($5 \pm 3.5\%$ of 9.2 ± 0.26 sites yr^{-1}) and Northern Napa County ($4 \pm 3.5\%$ of 4.9 ± 0.36 sites yr^{-1}) than in the Central San Francisco Bay or along the Outer Coast (multiple comparisons, Bonferroni adjusted $P < 0.05$).

DISCUSSION

REGIONAL STATUS AND TRENDS

Heron and egret nesting colonies occur throughout the wetland landscapes of the San Francisco Bay. The locations of heronries may be influenced by the proximity of suitable foraging areas (Fasola and Alieri 1992, 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 Callopy 1995). 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 as wetland suitability and disturbance patterns fluctuate across years and over space (Bancroft et al. 1994, Fasola and Alieri 1992).

The value of nesting near productive feeding areas may involve energetic benefits associated with the costs of travel to and from multiple feeding sites that fluctuate in suitability over time (Wittenberger and Hunt 1985, Gibbs 1991). In the San Francisco Estuary, herons and egrets establish colony sites in relation to landscape conditions within 1 km and prefer sites with more estuarine-emergent habitat and open water within this distance than is available at other potential colony sites in the wetland landscape (Kelly et al. 2005b). The importance of local feeding areas has also been suggested by declining habitat exploitation with increasing distance from the colony (Gibbs et al. 1987, Simpson et al., 1987, Fasola and Alieri 1992) and by the frequent initiation of sub-colonies or new colony sites near heronries that are subjected to heavy nest predation or disturbance (Custer et al. 1980; ACR unpubl. data).

In contrast to the importance of local feeding areas, larger scale patterns of habitat use also occur. Nesting abundances of herons and egrets near 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, relatively few Great Egrets and Black-crowned Night-Herons nested near San Pablo Bay, where most of the tidal marshland occurs, but concentrated their nesting activity in Central San Francisco Bay, where the extent of tidal marshes is relatively limited. An explanation for these differences 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. 2006), which strongly suggests that the nesting birds foraged primarily in the San Pablo Bay marshes. Therefore, the benefits of nesting on islands that are relatively safe from terrestrial predators may offset the costs of traveling to more distant feeding areas.

Nest abundances of all colonially nesting heron and egret species are stable or increasing in the San

Francisco Bay area. The stable 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, and this study).

The significant increase in the number of Great Egret nests observed in this study was associated with recent counts of over 1000 nests. These counts compare with a statewide count of 1245 nests in 1982, of which only 347 nests were from the central California coast (San Francisco Bay area counties and 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). Nest counts in Oregon indicated an increasing number of nesting Great Egrets in the mid-1980s, with a peak of 755 pairs in the vicinity of Malheur National Wildlife Refuge, 140 pairs in the Warner Basin, and 100-200 pairs in the Klamath Basin (McCrimmon et al. 2001, Marshall et al. 2003).

Recent increases in the number of Snowy Egret and Black-crowned Night-Heron nests in the San Francisco Bay area are associated with large annual fluctuations in nest abundance that prevent the detection of underlying trends. Substantial annual variation in Snowy Egret nest abundance has also been evident in 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).

The formation of small colonies of less than ten nests by Great Blue Herons along the Russian River and throughout other watersheds in the region is consistent with their breeding distributions in other areas, their generalist feeding behavior, and their ability to exploit a wide range of habitats (Butler 1992, Butler et al. 2000, Gawlik 2002, Kushlan and Hancock 2005). In addition, the reduced extent of wetland feeding areas in higher portions of watersheds may limit the sizes of colonies (Farinha and Leitao 1996, Gibbs 1991). Alternatively, if food supplies along perennial rivers and streams are more

stable than feeding sites in marshes or tidal wetlands, herons might exploit these areas by forming smaller colonies near local food sources (Wittenberger and Hunt 1985). We found no differences in reproductive performance related to variation in Great Blue Heron colony size.

In contrast to the broad nesting distribution of Great Blue Herons, other species of herons and egrets nested in fewer but larger heronries. The nesting distribution of Great Egrets was consistent with a preference for tidal feeding areas, although their use of tidal wetlands varies among regions in North America (McCrimmon et al. 2001). 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).

With the possible 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 also consistent with a preference for tidal feeding areas (Willard 1977, Custer and Osborn 1978, Davis 1993, Parsons and Master 2000). In other parts of their breeding range, Snowy Egrets have abandoned coastal nesting sites in favor of more completely isolated sites on islands, and their populations may be limited by the availability of safe nesting sites within profitable commuting distances to estuarine feeding areas (Parsons and Master 2000). Consistent with the possibility that the availability of suitable colony sites was limiting, Snowy Egrets in the San Francisco Bay area nested at relatively few sites. The nesting distribution of Black-crowned Night-Herons was similarly restricted, primarily to the same sites used by Snowy Egrets. Although their colony sites in the San Francisco Bay area are often close to human activity, Black-crowned Night-Herons are especially sensitive to nest predation and disturbance, including human disturbance, and readily abandon nesting attempts when disturbed (Tremblay and Ellison 1979, Blus et al. 1997, Hothem and Hatch 2004).

REPRODUCTIVE SUCCESS

Significant linear declines in regional reproductive success of Great Blue Herons, Black-crowned Night-

Hérons, and Snowy Egrets resulted primarily from declining nest survivorship. These declines in nest survivorship coincided with regional increases in abundances of American Crows and Common Ravens (Kelly et al. 2002), and increases in nest predation by Common Ravens 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. Conflicts with human activities or land development near heronries did not increase noticeably during the study period (ACR unpubl. data). However, we did not precisely measure these occurrences, and the cumulative effects of urban and suburban development on rates of colony disturbance, or on nest predation by other animals associated with human-altered landscapes, is unknown.

Our results indicate that the local and subregional productivity of successful Great Blue Heron and Great Egret nests fluctuates within 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.

We found small but significant subregional differences in nest survivorship, productivity, and overall reproductive success. Subregional differences in reproductive success of wading birds have been reported among freshwater, estuarine and marine habitats in Florida (Frederick et al. 1992), but reproductive success in the San Francisco Bay area was not clearly related to the predominance of tidal or non-tidal habitats. Although herons and egrets seem to move freely among colony sites as nesting distributions shift between years (Bancroft et al. 1994, this study), subregional differences in nest productivity were not precluded by the possibility that such movement might lead to 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 potential fitness

among nesting areas.

Although the inherent intraseasonal predictability of declining water levels may be important to nesting wading birds (Kushlan 1986), the difficulty of predicting changes in the availability of food over a relatively long nesting period is a fundamental aspect of heron and egret nesting biology (Lack 1947, 1954, Mock and Forbes 1994) that may account for subregional differences in nesting performance. In addition, significant subregional differences in both nest survivorship and productivity suggest that colony site choices may be complicated by uncertainties related to tradeoffs between the risk of nest predation and the suitability of feeding areas. Alternatively, the subregional differences in reproductive success might result from (1) individuals forcing others to nest or feed in suboptimal areas (despotic distribution; Fretwell and Lucas 1970), (2) long-term benefits of mate- or colony-site fidelity, (3) unpredicted costs of long-distance foraging, or (4) other potential fitness considerations.

We did not find a significant relationship between nest productivity and changes in colony size. However, higher rates of nest mortality led to significant decreases in colony size, even at sites where nest predation or disturbance was not detected. Observers were likely to find evidence of nest predation or disturbance at sites where such events occurred frequently or where colony site disturbance was catastrophic. Therefore, declines in colony size and associated shifts in breeding distribution may be stimulated not only by repeated or catastrophic disturbance but also by declines in conspecific nest success (Boulinier 1996, Danchin et al. 1998) or, alternatively, undetected instances of colony 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 Callopy 1989a, Frederick 2002). The availability of food early in the season, immediately prior to and during the time of egg formation, may be particularly important (Butler 1993, Bancroft et al. 1994). In the San Francisco Bay area, earlier nesting by Great Blue Herons and Snowy Egrets in subregions dominated by freshwater wetlands is consistent with the

relatively early availability of seasonally flooded marshes, ephemeral creeks, and receding ponds after normal periods of winter rainfall. In contrast, later nesting 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). The relatively early nesting by Great Egrets in Central San Francisco Bay is unclear, but could involve longer flights to feed in other areas (Kelly et al. 2006) or to exploit unknown sources of food available early in the season.

IMPLICATIONS FOR CONSERVATION

The dynamic nature of heron and egret nesting distributions and the relative stability of the 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. However, efforts to protect or manage smaller heronries should consider that they may be more sensitive to disturbance and more prone to abandonment than larger sites. While the importance of mixed species heronries is enhanced by the presence of additional nesting species, the values associated with the expected longevity of any heronry increase more rapidly as numbers increase above 6 Great Blue Heron nests, 20 Great Egret nests, 30 Snowy Egret nests, or 30 Black-crowned Night-Heron nests.

We observed sharp declines in nest abundance of heron and egret species in 1999. We do not know if natal dispersal occurs primarily at intraregional scales or within the geographic extent of harsh winter conditions that occurred from November 1997 to February 1998 (and continued into the following spring). However, if juveniles disperse within these scales prior to their first breeding attempts, the declines in nest abundance in 1999 may have resulted from reduced recruitment associated with increased juvenile mortality, rather than from reduced reproductive success. These results are 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 (5-25 cm) water depths across flooded wetlands and in the mouths of creeks or channels that connect wetland patches (Gawlik 2002, Frederick 2002, Maccarone and Brzorad 2005), (2) improve the ability of seasonal marshes to support fish and amphibians (Kushlan 2000, Gawlik 2002), or (3) minimize areal extent or duration or heavy turbidity (Cezilly 1992) related to the movement of water, land uses, and watershed erosion.

Our measurements of nesting habitat illustrate the range of nesting conditions used by herons and egrets (Kushlan and Hancock 2005), but they do not include measures of habitat availability and therefore do not necessarily describe habitat preferences. However, the substantial use of sites associated with low or medium housing suggests a tolerance of human activity and the potential value of tall trees near houses in rural and suburban areas adjacent to wetlands, as alternative nesting sites for herons and egrets. Alternatively, 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 (Parsons and Master 2000, Pratt and Winkler 1985, Kelly et al. 2005a). Because severe nest losses can be 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.

Non-native eucalyptus trees (*Eucalyptus* spp.) are widely planted in California and achieve their best growth on alluvial soils in the coastal fog belt of the San Francisco Bay area (Esser 1993, Bossard et al. 2000). The predominant use of eucalyptus trees (primarily, *Eucalyptus globulus*) for nesting substrate by herons and egrets is associated with an apparent scarcity of other potential nesting substrates in the vicinity of tidal marshes of the San Francisco Estuary (JPK, pers. observation), although we did not measure substrate availability. With planted eucalyptus groves providing most of the alternative colony sites, regional changes in their structure or availability without increases in other nesting substrates might alter the distribution of heronries. If nesting herons and egrets that depend on the close

proximity of suitable wetland feeding areas are forced to relocate substantial distances to find suitable nest trees, they might have to increase the amount of time or energy they spend on foraging or reduce their use of some wetlands (Gibbs et al. 1987, Simpson et al. 1987, Fasola and Alieri 1992). Therefore, regional management to maintain the availability of alternative colony sites may be important in sustaining the use of wetlands by herons and egrets.

In addition, our results indicated that annual shifts in colony locations and the relative use of colony sites were influenced by nest failures associated with localized disturbance and predation events. Such events further suggest the value of alternative nesting habitat near existing sites (Custer et al. 1980) to provide continued nesting opportunities within profitable distances of preferred feeding areas. The spacing of heronries at intervals of approximately 6 km in the San Francisco Bay area was similar to distances of 5-7 km between heronries in northwest Italy (Fasola and Alieri 1992). Thus, regional management for tree-nesting herons and egrets should not only protect existing colony sites but should also protect patches of tall trees near active colony sites and at intervals of approximately 6 km near wetland feeding areas, to provide alternative nesting sites in case of disturbance or loss of trees at existing heronries.

Restoration of wetland habitat and prey abundances can result in increased use by herons and the development of heron nesting colonies (Mauchamp 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 (Bryan et al. 2003, Frederick and Callopy 1989a). Such distributional shifts may occur gradually with incremental restoration or enhancement of the wetland landscape. In the absence of active habitat restoration or enhancement, annual shifts in nesting distribution related to large-scale 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, long-term shifts in heron and egret nesting distributions may be particularly useful in monitoring the cumulative, landscape-scale effects of tidal marsh restoration or enhancement projects. Given the value of suitable feeding areas near heronries, regional planners could enhance the value of wetland landscapes to nesting herons and egrets by promoting clusters of smaller restoration or enhancement projects within several km of colony sites.

RECOMMENDED BUFFER ZONES

Nesting herons and egrets can be easily disturbed by human activity and may respond by abandoning their nests or colony sites (Dusi and Dusi 1987, Hafner 2000). At some sites, nesting herons and egrets tolerate human activity at close range (Nisbet 2000; Hothem and Hatch 2004). However, tolerance levels are highly variable over time and among heronries, and unpredictable changes in the type, proximity, or intensity of human activity at any site may adversely affect the nesting birds (Tremblay and Ellison 1979, Vos et al. 1985, Rodgers and Smith 1995, Hafner 2000, Kelly 2002; pers. observation). Adverse effects of human disturbance include egg and nestling mortality, premature fledging, reduced body mass or slower growth of nestlings, and reduced settlement of breeders in the colony (Rodgers and Smith 1995, Hafner 2000, Frederick 2002). Even temporary abandonment can lead to nest failure during unfavorable weather or in the presence of opportunistic predators such as crows or ravens (Burger and Hahn 1977, Tremblay and Ellison 1979, Hafner 2000).

The responses of herons and egrets to disturbance can vary substantially among the stages of the breeding season (Figure 9; Butler 1992, Hafner 2000, Kelly 2002). Colonies are most easily disturbed when some individuals are still in the pre-laying or courtship phase (January-March). As birds settle into the incubation phase, they become more site-tenacious (March-April). As nestlings grow larger and are able to thermoregulate, adults may temporarily alter their behavior or flee without neglecting their young (May-June). Near the end of

the nesting season (June-August or later), adults are rarely present at their nests, returning only to feed their young. At this time, nestlings are large and alert to disturbance but reluctant to flee from their nests. Nestlings forced to flee before they are mature enough to find their way back into their nests may not survive.

The responses of nesting herons and egrets to disturbance by humans also vary with differences in the structure of the nesting habitat and types of human activity (Kelly 2002). Herons and egrets nesting in very tall trees or very dense vegetation may be less sensitive to disturbance, whereas herons and egrets nesting in open habitat or isolated trees tend to react earlier and more intensely to approaching humans. Fledging success may be greater in heronries that are isolated by moat-like water barriers or fencing than at sites isolated only by greater distances to human activity (Carlson and McLean 1996).

Erwin (1989) recommended 200-m buffer distances to protect heronries from human disturbance. This was based on 100-m flush distances plus an additional 100 m to protect colony sites early in the season before all nests are established. Butler (1992) suggested buffer zones of 300 m from Great Blue Heron colonies, but indicated that the most easily disturbed herons in a colony in British Columbia remained in their nests until he approached within 200 m. Rodgers and Smith (1995) recommended a 100 m buffer around wading bird colonies in Florida, based on upper 95th percentile of standard normal flush distances, i.e., the distance beyond the average disturbance distance at which disturbance is not expected 95% of the time. Their estimate incorporated flush distances plus 40 m for other (unmeasured) responses, such as intraseasonal differences, alert/agonistic responses prior to flushing, differences in vegetation cover etc. Disturbance trials conducted at 23 heronries in the San Francisco Bay Area in 1994 indicated substantial tolerance of approaching humans at some heronries but considerable variation in responses, both among heronries and among stages of nesting (Kelly 2002). The results were consistent with buffer zones of 100-200-m based on the responses of nesting birds to a single person approaching on foot.

An important consideration in determining appropriate buffer zones around heronries is that the

distances recommended by scientific investigators are generally based only on one or two humans approaching on foot. Larger groups of people or other types of human activity are likely to disturb heronries at greater distances. Boats tend to be less disturbing to nesting herons and egrets than some other types of human intrusion. Vos et al. (1985) found that boat disturbance distances average only about 50-85 m, but they did not measure the distance that is likely to prevent disturbance 95% of the time. Disturbance by groups of boats rather than single boats might increase the width of the disturbance zone. In general, the size of buffer zones should be increased with increases in the expected frequency, duration, or extent of human activity.

Nisbet (2000) argued that, where appropriate, waterbird colonies could be managed for multiple uses including research, education, and recreation, to promote habituation of nesting birds to human activity and thereby reduce adverse impacts of disturbance. Such habituation may contribute to the variability among heronries in their tolerances to human activity, although the actual reasons for such differences are unknown. Although some investigators have suggested that habituation may be possible (Nisbet 2000, Frederick 2002), this has not been clearly demonstrated with regard to a capacity of behavioral change in nesting adults. In contrast, other investigators have presented evidence indicating increasingly adverse effects of repeated or prolonged disturbance (Tremblay and Ellison 1979, Rodgers and Smith 1995). Any attempts to promote or rely on habituation should be implemented very cautiously because (1) serious adverse effects of human disturbance on heronries are well-documented, (2) the sensitivity of nesting birds to human activity is highly variable and difficult to assess, (3) the potential for habituation is unknown, (4) any disturbance by humans could result in opportunistic nest predation by diurnal avian predators such as gulls or ravens, and (5) the behaviors of humans can be unpredictable (Carney and Sydeman 1999, 2000, Nisbet 2000). Therefore, even at sites where birds appear to be relatively tolerant of human activity, managers should consider the use of appropriate barriers and buffer distances, with careful attention to nesting behaviors and the timing of nesting stages (Parnell et al. 1988, Hafner 2000).

Because heronries vary widely in their responses to human disturbance, we recommend establishing buffer zones of at least 200 m around heronries to minimize the potential adverse effects of human intrusion during the nesting season. These buffer zones should be established from 1 January to 30 June for Great Blue Herons, and 1 March to 31 August for other species. However, because late nesting attempts may extend beyond these dates, a qualified biological observer should confirm that herons and egrets are no longer occupying the colony site at the end of the nesting period before increases in human activity are allowed.

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