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LANDSCAPE INFLUENCE ON THE QUALITY OF HERON AND EGRET COLONY SITES

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Abstract: We evaluated landscape associations related to heron and egret colony site selection and the productivity of successful great blue heron (*Ardea herodias*) and great egret (*Ardea alba*) nests. The study was based on annual observations (1991–2005) at 45 colony sites known to be active within 10 km of historic tidal marshes of northern San Francisco Bay. The analyses focused on *a priori* models analyzed within 1, 3, 5, 7, and 10 km of colony sites, using the areal extents of several NOAA land cover types (Landsat images, 2000–2002), number of wetland patches, and total wetland edge as predictor variables. A comparison of landscape characteristics surrounding colony sites with those surrounding randomly selected, unoccupied sites revealed the primary importance of estuarine emergent wetland and open water within 1 km of colony sites. Increased productivity in successful great blue heron nests was associated with more estuarine emergent wetland, open water, and low-intensity development, and less grassland, but was not differentially related to the extent of habitat available within any particular distance from colony sites. The productivity in successful great egret nests was associated with variation in habitat extent at larger spatial scales, especially within 10 km of heronies, with nests producing more young at sites surrounded by more estuarine emergent wetland and low-intensity development, less open water and palustrine emergent wetland, and more patches of wetland habitat. To estimate landscape foraging patterns, we used aircraft to track the flights of great egrets departing from heronries and used the observed flight distances, colony sizes, and the regional distribution of wetland habitat to model regional foraging densities. Results suggested that increasing the extent of wetland feeding areas for herons and egrets might improve reproductive performance in colony sites up to 10 km away, increase foraging by herons and egrets in created or restored wetlands within 3–10 km of sites, and enhance nest abundance at colony sites within 1 km of restoration sites. Regional maps based on the distribution of colony-sites and predictions of landscape influences on colony site selection, nest productivity, and foraging dispersion, suggested areas potentially suitable for colonization.

Key Words: Ardeidae, coloniality, foraging, habitat selection, productivity, reproductive success, San Francisco Bay, wetland restoration

INTRODUCTION

Identifying habitat conditions needed for successful nesting is an essential part of protecting habitat to maintain populations of birds. Colonial nesting birds establish breeding territories that are spatially packed within a centralized colony site (heronry) from which they recurrently depart in search of food (Wittenberger and Hunt 1985). In herons and egrets, these foraging excursions may be limited to nearby feeding areas or may involve travel over considerably greater distances. For example, great blue herons (*Ardea herodias* (L.)) and great egrets (*Ardea alba* (L.)) often forage within a few km of their nesting colonies but may travel 20 km or more to hunt for food (Custer and Osborn 1978, Bancroft et. al 1994, Custer and Galli 2002). The costly expenditure of time and energy needed to conduct long flights is considered to be an important influence on the distances traveled by these birds (Wittenberger and Hunt 1985, Gibbs 1991, Smith 1995). If flight costs limit the ability of nesting herons and egrets to provision their young, any loss or degradation of foraging habitat that forces them to travel farther to find food might impose an additional burden that further limits their ability to feed young, leading to reduced reproductive success. The substantial ecological and economic values of wetlands and associated pressures resulting from changes in human land use have inspired continuing interest in the relationships between nesting distributions of herons and egrets and the extent or quality of their surrounding wetland feeding areas (Parnell et al. 1988).

Many authors have addressed the influences of foraging habitat within particular distances of heronries (Fasola and Alieri 1992a, Bancroft et al. 1994, Custer and Galli 2002, Tourenq et al. 2004) and the habitat preferences of foraging individuals (Custer and Osborn 1978, Hom 1983, Strong et al. 1997, Bancroft et al. 2002, Trocki and Paton 2006). Other investigators have measured the use or selection of nest-site or colony-site habitat (Gibbs et al. 1987, Fasola and Alieri 1992b, Kelly et al. 1993, 2007, Grüll and Ranner 1998). Studies in inland Maine (Gibbs 1991) and Illinois (Gibbs and Kinkel 1997) demonstrated that great blue herons established colonies near the center of available foraging habitat, potentially minimizing aggregate travel costs. Tourenq et al. (2004) found that annual variation in nesting abundance in colonies of tree-nesting herons was significantly related to changes in the spatial extent of rice fields within 1, 5, and 10 km of heronries. However the effects of habitat extent and configuration at multiple scales on the locations of colony sites, relative to available nesting habitat, has not been thoroughly investigated and has not been examined in an estuarine setting.

The productivity of heron and egret nests typically depends on the extent of brood reduction, which results from asynchronous incubation and hatching that leads to a hierarchy of competitiveness and survivorship among nestlings (Kushlan and Hancock 2005). One benefit of brood reduction is an ability to match the number of young produced in successful nests to unpredicted changes in prey availability, or variation in the quality or productivity of feeding areas (Lack 1947, 1954, Mock et al. 1987, Mock and Forbes 1994). Therefore, the productivity of successful nests is likely to be sensitive to the availability of suitable foraging habitat. A few studies have directly related the characteristics of foraging sites, nest sites, or colony sites to levels of reproductive success (Beaver et al. 1980, Powell 1983, Frederick and Collopy 1989, Frederick et al. 1992). However, information is lacking on the relative effects of available foraging habitat at multiple spatial scales on heron or egret reproductive performance.

The creation of wildlife habitat is often a principal goal in wetland restoration (Zedler 2001). Increasing interest in trophic connections as functional targets in ecological restoration recognizes the importance of top predators such as herons and egrets (Palmer et al. 1997, Vander Zanden et al. 2006). Herons and egrets exhibit patchy foraging distributions and respond closely to dynamic changes in prey abundance among wetland feeding sites (Kushlan and Hancock 2005). Measurements of foraging ranges further indicate that foraging densities of nesting herons and egrets decrease with increasing distance from heronries (Custer and Osborn 1978, Dowd and Flake 1985, Nemeth et al. 2005, but see Trocki and Paton 2006). Other evidence indicates that herons and egrets in many areas do not saturate available foraging habitat (Butler 1994, 1995, Gibbs and Kinkel 1997). Therefore, estimating foraging distributions and the spatial extent of habitat influences surrounding colony sites may help explain differences in foraging density or predation in particular areas such as wetland restoration sites.

The objectives of this study were to determine landscape-level habitat relationships of nesting great blue herons and great egrets in the northern San Francisco Bay region, based on 15 y of regional monitoring of colony sites. Specifically, we examined the relative extents of habitat types and the configuration of wetland patches, within multiple distances of nesting colonies, and modeled their influences on colony site selection and the productivity of successful nests. To evaluate regional implications, we used the resulting models to generate predictive maps of landscape quality with regard to colony site selection and the productivity of successful nests. To determine if the availability of suitable feeding and nesting areas was consistent with predicted patterns of space use by foraging great egrets, we modeled the distribution of flight distances from colony sites and used the results to predict the foraging distribution across northern San Francisco Bay wetlands.

STUDY AREA

The study encompassed all areas within 10 km of all heron and egret colony sites (1991–2005) within 10 km of the historic tidal-marsh boundary (ca. 1770–1820) of Suisun Bay and the Petaluma and Napa marshes of San Pablo Bay (Figure 1; San Francisco Estuary Institute 1999). The area includes extensive tidal marsh systems as well as historic wetlands that have been diked and drained or otherwise managed, although some areas have been restored to tidal action (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). The Petaluma Marsh consists primarily of fully tidal marshes; the Napa marsh is a matrix of former salt evaporation ponds and tidal marsh; and most of the wetlands in Suisun Marsh are impounded by water-control levees and managed for duck hunting. The salinities of wetlands within the study area range from 30 ppt in the southern part of San Pablo Bay to nearly fresh in parts of Suisun Marsh. Dominant wetland plants include perennial pickleweed (*Sali-*

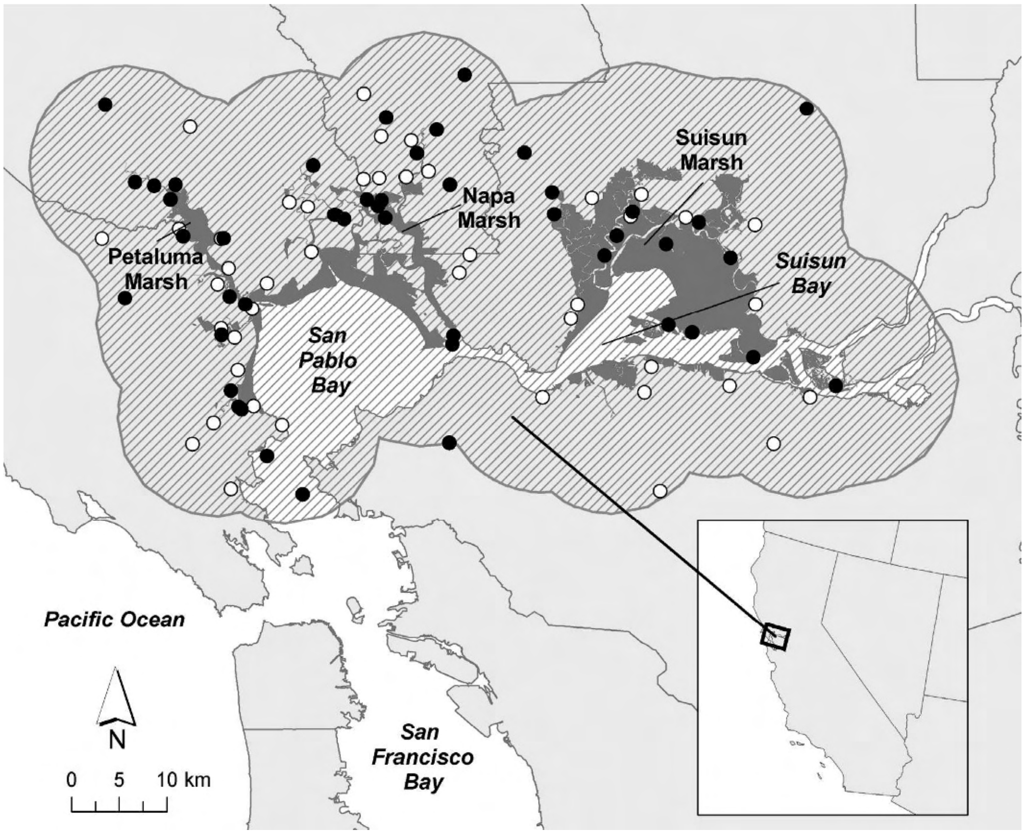

Figure 1. Heron and egret nesting colonies (solid circles) and randomly selected, unoccupied sites (open circles) within 10 km of historic tidal marsh in northern San Francisco Bay, 1991–2005. The study area is indicated by diagonal hatching.

cornia virginica (L.)) in the higher salinity marshes, bulrush species (*Bolboschoenus maritimus* (L.) *and Schoenoplectus americanus* (Pers.)) in brackish areas, and tule (*Schoenoplectus acutus* (Muhl. ex. Bigelow) and *S. californicus* (C. A. Mey.)), and cattail (*Typha* spp.) in the freshest marshes.

The upper portions of the study area extend across the hillsides and lower slopes of the Coast Range, with freshwater streams, grazed grasslands, chaparral, oak and mixed evergreen forests, vineyards, and urban and suburban development. Broad alluvial terraces surrounding the tidal and non-tidal marshes include seasonal wetlands, rural roads and housing, and grazed or cultivated lands. Non-native eucalyptus trees (predominately *Eucalyptus globulus* (Labill.)) are the dominant trees associated with most of the wetland terraces surrounding the San Francisco Estuary and generally occur as narrow windbreaks or small patches of < 1 ha.

METHODS

We determined the locations of colony sites (heronries) through aerial searches in 1991, supplemented annually by communications with state, regional, and local natural resource managers, county breeding bird atlas project coordinators, and local bird watching networks, to identify new colony sites. In addition, we conducted annual, ground-based searches in May and June, when colony sites were relatively conspicuous because of adults actively feeding nestlings, nestlings large enough to be easily seen or heard, and guano accumulations beneath nests. Ground searches only rarely revealed newly established sites because new colonies were usually detected first through communications with other observers (3.3 ± 0.53 [SE] new sites yr^{-1}). Thus, we assumed that all active colony sites within the study area were included in our analysis. Colony sites in the region were generally established in trees, with a few exceptions in shrubs, snags, reeds, or artificial structures; the most common nesting substrates were *Eucalyptus* trees. Additional information on colony sites is available from previous papers (Kelly et al. 1993, 2006, 2007).

We used GPS or USGS 7.5-min topographic quads to record the geographic position of each heronry (NAD83). All colonies were observed from the ground or from boats using binoculars and telescopes. Observers visited most colony sites at least four times each breeding season, generally at monthly or more frequent intervals. Sites that could be visited only once in a given year were usually observed in May or early June when nests and broods were most conspicuous.

Colony Site Selection

To examine patterns of colony site use relative to the availability of potential nesting sites, we compared landscape conditions surrounding occupied colony sites ($n = 44$; species pooled, including great blue heron, great egret, snowy egret [*Egretta thula* (Molina)], and black-crowned night-heron [*Nycticorax nycticorax* (L.)]) to those surrounding a randomly selected set of unoccupied sites ($n = 44$). To identify unoccupied sites within the regional tidal marsh boundary, we first selected a set of random locations within the marsh area equal to the number of occupied sites. We then used aerial photographs to select the nearest edge of the nearest patch of mature trees from each random location as an unoccupied site. A patch was defined as a group of trees with a contiguous canopy of any areal extent (most patches < 1 ha), with height > 15 m. To generate a representative set of unoccupied sites outside the tidal marsh area, with regard to the proximity of wetlands, random locations beyond the regional tidal marsh boundary were selected with the constraint that they conformed to the distribution of distances from occupied colony sites to the tidal marsh boundary; as above, unoccupied sites were identified from aerial photographs as the nearest edge of the nearest unoccupied patch of mature trees from each of the randomly selected locations.

Nest Productivity

Overall nest productivity includes the combined effects of nest survivorship and the number of young produced in successful nests. Therefore, overall productivity is likely to vary with the extent of available foraging habitat needed to provide food for nestlings and with other processes, such as nest predation or disturbance, that affect nest survivorship and can vary with localized conditions (Kelly et al. 2007). Regional mean nest survivorship was 79 ± 0.4%, for great blue heron and 78 ± 0.4% for great egret. We used the number of young produced in successful nests as a response variable because it is potentially more sensitive than overall productivity to the availability of surrounding foraging areas needed to provide food for nestlings (Lack 1947, 1954, Mock et al. 1987, Mock and Forbes 1994).

We determined the productivity of successful nests based on prefledging brood size, determined when nestlings were 5–8 wks old, for great blue herons, or 5–7 wks old for great egrets. During these periods, nestlings were too young to hop away from their nests and old enough to have survived the period when most brood reduction occurs (Pratt 1970, Pratt and Winkler 1985). We determined nestling age by observing focal nests from initiation or early in the incubation period, by the onset of post-guardian parental behavior (nestlings 21–28 d old; Pratt 1970, McCrimmon et al. 2001), and by nestling size compared to known-age nestlings. Further detail on methods used to measure reproductive success is available in Kelly et al. (2007).

Landscape Variables

We analyzed landscape associations within 1, 3, 5, 7, and 10 km of colony sites, based on the areal extents (km^2) of land cover types (from 30-m pixel land cover classification of satellite imagery, NOAA 2000) and the configuration of wetland patches surrounding sites. These distances were selected to estimate a range of potential habitat associations related to foraging distances reported in other studies (e.g., Custer and Galli 2002, Smith 1995, Custer and Osborn 1978): adjacent to heronries (within 1 km), within a distance that could account for the majority of flights (3 km), within intermediate distances (5–7 km), and within a distance likely to account for most foraging flights (10 km).

We selected the five land cover variables as potentially important habitat associations related to colony site selection and foraging habitat preferences, based on experience with herons and egrets in this region and on published accounts of nesting and foraging behavior: 1) estuarine emergent wetland (km^2 of tidal and managed estuarine marsh; Hom 1983, McCrimmon et al. 2001, Trocki and Paton 2006), 2) open water (km^2; includes former salt ponds; Hom 1983, McCrimmon et al. 2001, Bancroft et al. 2002), 3) low-intensity development (km^2; includes small buildings, ditches, ponds, and substantial vegetated surface; Kushlan and Hancock 2005, Kelly et al. 2007), 4) grassland (km^2; Butler 1995, Smith 1995, Bancroft et al. 1994), and 5) palustrine emergent wetland (ha; Thompson 1978, Bancroft et al. 1994, McCrimmon et al. 2001). Land cover extents were calculated using ArcGIS 9.1 Spatial Analyst (ESRI 2005). We also hypothesized that colony site selection and the number of young in successful nests would be associated with two variables related to wetland configuration near heronries: 1) number of wetland patches (potentially associated with differences in hydrologic timing and water-level drawdowns that concentrate prey; Erwin

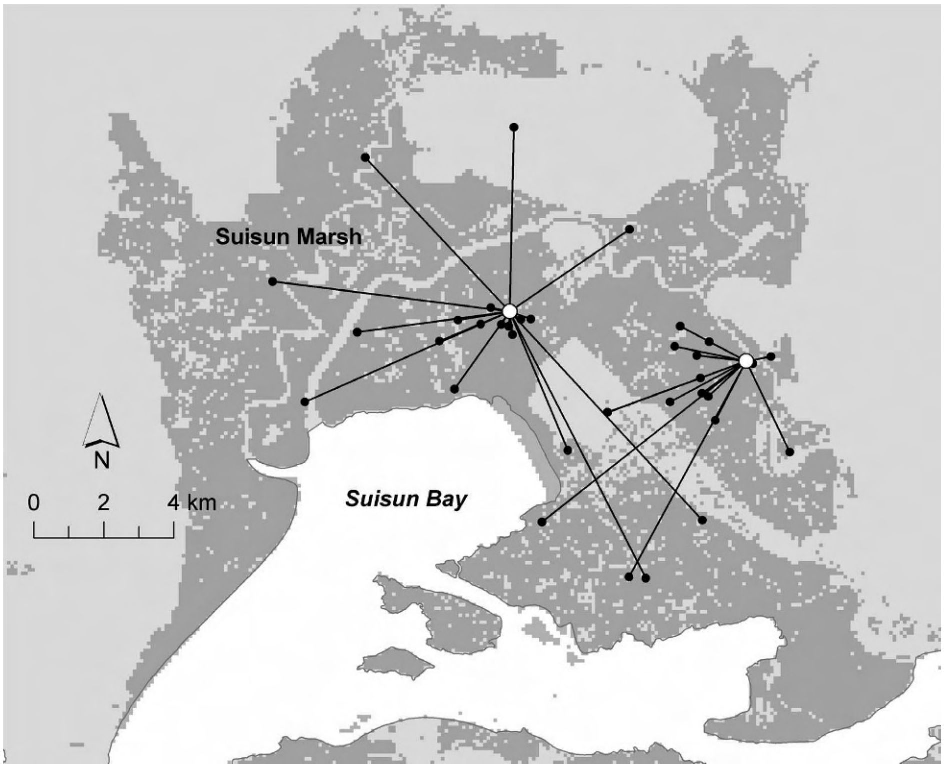

Figure 2. Foraging flight vectors and landing sites of great egrets from two nesting colonies in Suisun Marsh, California.

1983, Dowd and Flake 1985) and 2) total length of wetland edge (m; Rodgers 1983, Hom 1983). Wetland patches (tidal marsh only) were determined by hand-delineation of wetland boundaries from the San Francisco Bay Area EcoAtlas (San Francisco Estuary Institute 1998). We used FRAGSTATS v. 3 to calculate the number of wetland patches and total edge (McGarigal and Marks 1995).

Following Flights

Using fixed-winged aircraft, we measured foraging dispersion by following the flights of great egrets departing from two colony sites in Suisun Marsh (n = 36; Figure 2). Observations of following flights were conducted by at least two observers, in addition to the pilot, during 2-h observation periods centered on low (0.01 m above mean lower-low water) or high (1.1–1.2 m above mean lower-low water) tides. Flights were conducted in the post-guardian period of the nesting season, when both parents at most nests conducted foraging excursions simultaneously (May 19 and June 6, 2004, June 13, 2005). For each following flight, the plane circled above a colony site and followed the first departing great egret, maintaining a distance of 300–350 m above and behind the bird to avoid disturbance to the bird's behavior (Custer and Osborn 1978, Smith 1995, Custer and Galli 2002). We recorded landing sites manually on USGS 7.5 min topographic maps and collected GPS coordinates as supplemental data. Nemeth et al. (2005) found that foraging great egrets did not choose areas farther from the colony site after their first landing, and Van Vessem et al. (1984) found that foraging Grey Herons (*Ardea cinerea* (L.)) did not move between sites before returning to the nesting colony. Therefore, the flight distances measured in this study are likely to be representative of foraging distances from colony sites. If a bird landed for less than one minute, we planned to follow the continuing flight path and record the subsequent landing location, but such continued movement did not occur.

Statistical Analysis

We used logistic regression to analyze differences between occupied and unoccupied sites in relation to *a priori* candidate models developed from nine combinations of the landscape variables described above (Table 1; see below). We considered colony sites that were occupied in one or more years of study (1991–2005) to be suitable sites for nesting and contrasted these with randomly selected sites for which regional communications and annual searches for new colonies provided no evidence of nesting.

Table 1. Combinations of independent variables used in *a priori* models of landscape effects on heron and egret colony site selection and productivity of successful nests in northern San Francisco Bay. Five models were generated from each combination of variables by measuring values within 1, 3, 5, 7, and 10 km of colony sites.[a]

Wetland area
Estuarine emergent wetland (km^2), open water (km^2), palustrine emergent wetland (ha)
Estuarine emergent wetland (km^2), open water (km^2)
Estuarine emergent wetland (km^2), palustrine emergent wetland (ha)
Wetland and upland area
Estuarine emergent wetland, grassland (km^2), low-intensity development (km^2)
Estuarine emergent wetland (km^2), open water (km^2), low-intensity development (km^2)
Estuarine emergent wetland (km^2), grassland (km^2)
Wetland area and configuration
Open water (km^2), number of wetland patches
Open water (km^2), total wetland edge (m)
Open water (km^2), palustrine emergent wetlands (ha), number of wetland patches

[a] Pairwise $|r| < 0.70$ between variables in each model; combinations of predictors did not include the following correlated pairs of variables: open water and grassland ($r < -0.70$ within 3, 5, 7, and 10 km), estuarine emergent wetland and number of wetland patches ($r > 0.70$ within 3, 5, 7, and 10 km); estuarine emergent wetland and total wetland edge ($r > 0.70$ within 5, 7, and 10 km); total wetland edge and number of wetland patches ($r > 0.70$ within 1, 7, and 10 km).

Occupied sites (n = 44) were weighted by average nest abundance (1991–2005; species pooled) and unoccupied sites (n = 44) were weighted equally. We used the peak number of active nests as an estimate of annual nest abundance. Before April 1, nests were assumed to be active if they contained two adults, an adult carrying nest material, nestlings, or an adult incubating or caring for eggs. After April 1 of each year, all occupied nests were assumed to be active.

We used the approach above to analyze colony site preferences, rather than accounting for possible differences between years, because 1) colony sites were generally active across most or all years, suggesting persistent site preferences, 2) traditional use of heronries (Simpson et al. 1987) suggests a potentially strong dependence in site selection between years, 3) local disturbance unrelated to differences in foraging habitat resulted in abandonment of colony sites in some years, 4) changes in the extent of tidal, nontidal (diked), and seasonal wetlands during the study period were minor (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999, The Bay Institute 2004, 2005), and 5) annual data for independent variables were not available.

We used multiple linear regression to analyze the effects of landscape variables on the productivity of successful nests. The analysis was organized around the same *a priori* combinations of predictor variables that were used in the colony site selection analysis (Table 1; see below). The dependent variable was mean prefledging brood size in each colony site (38 great blue heron colonies; 20 great egret colonies) each year (1991–2005; great blue heron: n = 255; great egret: n = 122), weighted by the number of nests measured (percent measured annually in each colony: 64 ± 1.7%, SE, for great blue heron; 31 ± 2.5% for great egret). Indicator variables for year were included in each model to control for annual differences in the productivity of successful nests.

The *a priori* candidate models used in logistic and multiple regression analyses were structured by identical combinations of independent variables (Table 1). These combinations were selected as simple groups of predictors that were most likely to account for variation in nesting or feeding behavior, based on our experience in this region and on published accounts of heron and egret habitat relationships. They represented general hypotheses related to wetland habitat area (three combinations of predictors), wetland and upland habitat area (three combinations), and wetland area and configuration (three combinations; Table 1). In each set of analyses, we used these general hypotheses to generate nine *a priori* models at each of five spatial scales, based on values measured within 1, 3, 5, 7, and 10 km of heronries. This resulted in 45 candidate models representing scale-specific hypotheses related to combinations of habitat influence. In developing the candidate models, we examined correlations between independent variables and excluded pairwise combinations that were highly correlated at one or more scales ($|r| > 0.70$, Table 1; Graham 2003). When choosing between highly correlated variables, we selected the predictor leading to a variable combination hypothesized to best account for nesting or foraging behavior.

We examined residuals to confirm that the assumption of linearity in the logit held for each independent variable in logistic regressions (Hosmer and Lemeshow 1989). Based on visual inspection of scatterplots and residual plots following multiple regressions, brood-size predictors were linearly related to response variables and assumptions of normality and equal variance were satisfied. To test for spatial autocorrelation of response variables, we calculated Geary's C for residuals from all brood size and colony site selection models, which was near

1.0 within distances of 10, 20, 30, and 40 km ($0.90 < \hat{C} < 1.02$, $P > 0.05$; Geary 1954, Schabenberger and Gotway 2005). Therefore, we assumed that response variables were not spatially correlated and that model assumptions of independence were satisfied. All statistical analyses were conducted using STATA (Statacorp 2005).

The best models were considered to be those with the lowest Akaike's Information Criterion corrected for small samples (AIC_c; Burnham and Anderson 2002). We calculated the differences between the AIC_c value for the top model and other candidate models (ΔAIC_c) and selected models with $\Delta AIC_c < 7$ as those with the greatest strength of evidence, given the data (Burnham and Anderson 2002). Because it is well established that foraging great blue herons and great egrets may fly farther than 10 km to feed (Smith 1995, Custer and Galli 2002, this study), we predicted that the relative strengths of candidate models in the analyses of colony site selection and brood size would be greatest when independent variables were measured within the largest radius around colony sites (10 km).

We evaluated the predictive information in each variable in the selected set of models by calculating its model-averaged coefficient as the sum across all models in which it occurred, multiplied by Akaike weights (w_i; relative measures of model support that sum to 1 across models), and calculated confidence intervals that incorporated model uncertainty (Burnham and Anderson 2002). We also evaluated the relative importance of each predictor variable present in the set of best models, by summing the relative Akaike weights across all models in which the variable occurred (Burnham and Anderson 2002). Because the logistic regression was based on case-control sampling of occupied vs. unoccupied sites, we interpreted the results in terms of odds ratios (Keating and Cherry 2004). To further evaluate the performance of important predictors across spatial scales, we calculated the model-averaged coefficients or odds ratios across all models, for all five scale-specific versions of each variable that occurred in the selected set of best models, and plotted the values across spatial extents of measurement. These predictors also accounted for all variables present in models with the most evidence of support within each scale ($\Delta AIC_c < 4.0$ within scales).

To examine regional patterns of landscape habitat influence, we created predictive maps based on model-averaged predictions from each selected set of best models. For each analysis, we mapped model-averaged predictions for all points in the study area across a 100-m resolution grid. Thus, we used the models to predict nest productivity and the odds of colony-site use expected at any point if suitable nest substrate and site-level conditions were present. To provide equations that produce estimates identical to averaging the predictions from the models in each set, we calculated averaged models based on model-averaged coefficients that incorporate values of zero for models in which they did not occur (Burnham and Anderson 2002: 152).

The observed foraging flight distances of great egrets did not differ significantly ($p > 0.05$) across days ($F_{2,31} = 0.03$), tides ($F_{1,31} = 1.14$), colony sites ($F_{1,31} = 0.34$), or interactions of these effects ($F_{1 \text{ or } 2,\, 30} < 0.77$). Because of limited sample sizes ($n = 36$), we pooled the observations to estimate the distribution of foraging distances, and thus flight distances predicted from this limited sample should be interpreted cautiously. We modeled foraging dispersion, based on 1,000 bootstrap samples of flight distances (Manly 1997), as a two parameter rise to a maximum proportion of landings with increases in habitat area accessible within foraging flight distances (radii):

$$y = 1 - e^{ax^b}, \tag{1}$$

where y is the cumultive proportion of foraging flights that terminate at locations within a given distance from the colony site, x is either the circular area (km^2) around the site within a radius equal to the foraging flight distance (distance model) or the area of wetland habitat (km^2 of estuarine emergent + palustrine emergent wetland) within a radius equal to the foraging flight distance (habitat model). The distance model estimates foraging densities that would be likely if foraging dispersion is determined solely by the time or energy costs of travel. The habitat model estimates foraging densities if dispersion varies with the extent of available habitat. The model parameters "a" and "b" elaborate slightly on the one-parameter model used by Nemeth et al. (2005), which estimates an exponential decline in landings that is proportional to flight distance. The parameter "a" is the proportional constant of exponential decline in cumulative landing rate and "b" scales landing rates to the extent of available habitat. Thus, area (x) should scale to near $b = 0.5$ to estimate the log-proportional decline in landing rate relative to flight distance or overall area (distance increases increases with $area^{0.5}$). If landing rate is estimated relative to available habitat, $b > 0.5$ because flight distance increases with $area^{> 0.5}$.

The derivative of Equation 1 predicts the proportional landing rate at any distance:

$$y' = -e^{ax^b} * a\, b\, x^{(b-1)}. \tag{2}$$

Table 2. Logistic regression models of occupied (n = 44) vs. unoccupied (n = 44) colony sites in northern San Francisco Bay, 1991–2005. The measurement scale (areal extent indicated by radius around colony site), number of parameters including constant (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in $AICc$ (ΔAIC_c), Akaike weights (w_i), and Hosmer-Lemeshow goodness-of-fit statistic ($\hat{C}$) are provided. Only models with $\Delta AIC_c < 7$ are presented, representing the 0.95 model confidence set ($\sum w_i$). The following predictors, each measured at the 1-km scale, were included in the averaged model (g(x)): estuarine emergent wetland (ESTUAR), open water (OPENW), palustrine emergent wetland (PALUSTR), low-intensity development (LOWINT), grassland (GRASSL), and number of wetland patches (NPATCH), and total wetland edge (TEDGE).

MODEL[a]	Scale (km radius)	K	AIC_c	ΔAIC_c	w_i	Hosmer-Lemeshow $\hat{C}$	Hosmer-Lemeshow p
ESTUAR, OPENW	1	3	107.47	0.00	0.422	11.27	0.187
ESTUAR, OPENW, PALUST	1	4	108.07	0.60	0.313	6.76	0.563
ESTUAR, OPENW, LOWINT	1	4	109.61	2.14	0.145	13.88	0.085
OPENW, NPATCH	1	3	112.47	4.99	0.035	8.16	0.418
OPENW, TEDGE	1	3	113.06	5.59	0.026	1.76	0.987
OPENW, PALUST, NPATCH	1	4	114.18	6.71	0.015	5.40	0.714
ESTUAR, GRASSL, LOWINT	1	4	114.41	6.93	0.013	9.14	0.331

$$g(x) = \exp[-1.017 + 0.642(ESTUAR) + 1.060(OPENW) + 0.017(PALUSTR) - 0.006(LOWINT) - 0.011(GRASSL) + 0.005(NPATCH) + 0.000001(TEDGE)] / [1+ \exp[-1.017 + 0.642(ESTUAR) + 1.060(OPENW) + 0.017(PALUSTR) - 0.006(LOWINT) - 0.011(GRASSL) + 0.005(NPATCH) + 0.000001(TEDGE)]]$$

Multiplying the proportion estimated by Equation 2 by twice the number of active nests predicts the density of birds at any distance when all nests are in the post-guarding stage (both parents foraging simultaneously). Because all observed foraging flights teminated in wetlands, we assumed in both models that all birds land in wetlands. To estimate the areal extent of wetlands within a given flight distance (radius) from each colony site, and thus the extent of foraging habitat assumed to be suitable for landing, we used quadratic models based on the extent of available wetland within 1, 3, 5, 7, and 10 km of each colony site. Because the data closely fit the quadratic models at all colony sites ($R^2 > 0.97$), we used the models to estimate the extent of wetlands accessible from each heronry at distances corresponding to each potential landing location, rather than measure actual wetland area for each distance from land cover data. The rate of increase in available wetland habitat relative to total area with increasing distance from each colony was measured as the derivative of each quadratic model divided by the derivative of the increase in total area (6.28 × distance). Thus, the distance model predicts the density of birds in wetlands (D) at any distance, based on observed flight distances, as

$$D_{\text{distance model}} = \left[2n * -e^{ax^b} * a\ b\ x^{(b-1)}\right] / \left[(H_A + 2H_B * \text{Dist})/(6.28 * \text{Dist})\right] \tag{3}$$

where the numerator is the number of adults in a colony (2n) times the proportional dispersion km^{-2} at a given distance (Equation 2), H_A and H_B are the linear and quadratic parameters, repectively, from the quadratic models for wetland area, and the denominator adjusts for the proportion of wetlands available within the foraging flight distance (Dist).

Table 3. Landscape variables in logistic regression models of occupied (n = 44) vs. unoccupied (n = 44) heron and egret colony sites in northern San Francisco Bay, 1991–2005. Scale indicates the radius around each colony site within which variables were measured. Model-averaged odds of predicted colony site use (based on all models in which each variable occurred, with 95% confidence interval), and relative importance ($\sum w_i$) of each variable are provided. Only variables in the selected best set of models ($\Delta AIC_c < 7$) are presented.

Variable	Scale (km radius)	Odds	95% CI	$\sum w_i^a$
Open water (km^2)	1	2.930	1.549–5.539	0.955
Estuarine emergent wetland (km^2)	1	2.008	1.075–3.724	0.899
Palustrine emergent wetland (ha)	1	1.050	0.969–1.138	0.328
Low-intensity development (km^2)	1	1.081	0.294–3.676	0.161
Number of wetland patches	1	1.106	0.872–1.401	0.054
Total wetland edge (m)	1	1.000	0.9999–1.0001	0.034
Grassland (km^2)	1	0.460	0.269–0.782	0.020

[a] Relative importance was calculated by summing Akaike weights (w_i) for all models in which the variable was present.

The habitat model predicts D with the simplifying assumption that foraging individuals disperse and land in relation to the areal extent of wetland habitat (x) around each colony site:

$$D_{\text{habitat model}} = 2n * -e^{ax^b} * a\ b\ x^{(b-1)}. \quad (4)$$

Both models assume that 1) all birds foraged in wetlands, 2) nesting distribution reflected long-term average distribution, 3) all nests were in the post-guardian stage with both adults foraging simultaneously, 4) all wetlands were equally suitable for foraging, 5) flight directions were random (Erwin 1983), 6) flight distances were not affected by colony size or density-dependent competition (Furness and Birkhead 1984, Marion 1989), and 7) flight distances were not affected by other unknown factors. To estimate landscape foraging density patterns we created predictive maps by summing model predictions for all colony sites at each point across a 100-m-resolution density grid. Unless indicated otherwise, precision of estimates is reported as ± SE.

RESULTS

Colony Site Selection

All of the selected best models of colony site selection represented habitat conditions within 1 km of heronries (Table 2). Hosmer-Lemeshow (1989) goodness-of-fit tests indicated that all of the best models statistically fit the data (Table 2). The resulting averaged model correctly classified 68% of the sites, which was 36% better than chance (kappa K = 0.36, Z = 3.7). Predictors of occupied vs. unoccupied (randomly selected) colony sites revealed the primary importance of estuarine emergent wetland and open water within 1 km, each of which occurred in the top three colony site models (Tables 2 and 3). The odds of landscape conditions being suitable for an occupied (vs. unoccupied) colony site increased by a factor of nearly three with each additional km^2 of open water within 1 km of the site and by a factor of two for each km^2 of estuarine emergent wetland within 1 km (Table 3). The odds of site use decreased by a half with each km^2 of grassland within 1 km, although grassland was a relatively unimportant predictor that did not occur in the most competitive models (Tables 2 and 3, Figure 3). The effects of surrounding habitat on the odds of colony site use declined dramatically when measured within distances >1 km from heronries (Figure 3). The predicted odds of colony site use across the study area suggested that landscape conditions suitable for heronries were more likely in areas immediately adjacent to the

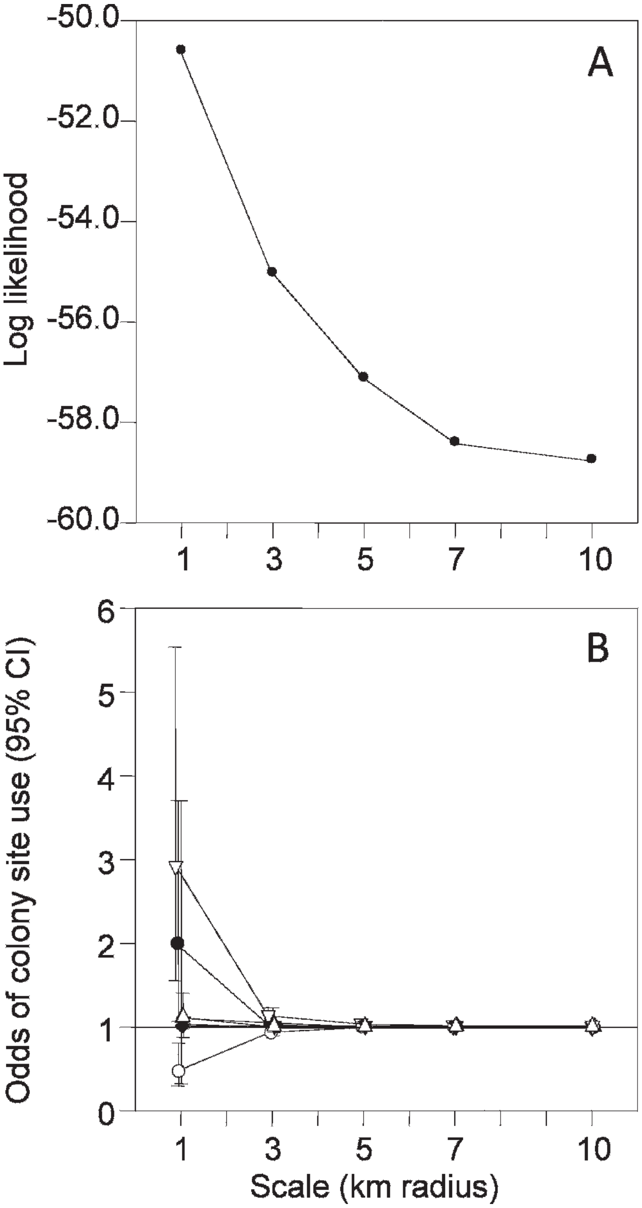

Figure 3. Logistic regression results from *a priori* models of landscape effects on heron and egret colony site selection in northern San Francisco Bay, 1991–2005, showing A) model-averaged log likelihood and B) odds of colony site use (95% confidence interval, CI) associated with landscape variables. All variables measured within a 1-km radius of sites were present in the selected set of best models: estuarine emergent wetland (solid circle), open water (open, downward-pointing triangle), low intensity development (solid, upward-pointing triangle), grassland (open circle), number of wetland patches (open, upward-pointing triangle), palustrine emergent wetland (solid, downward-pointing triangle), and total wetland edge (solid diamond).

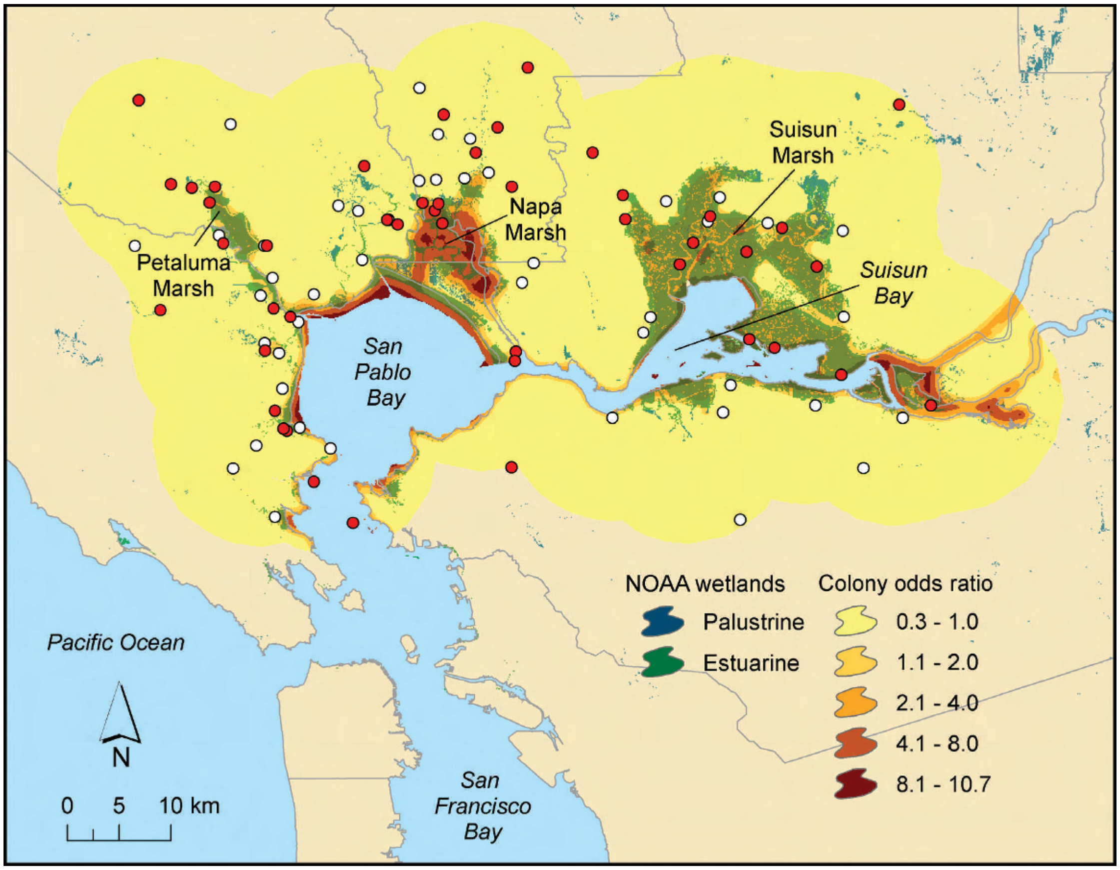

Figure 4. Odds of colony site use by herons and egrets relative to landscape conditions in northern San Francisco Bay, based on logistic regression (Table 2) of actual colony sites (solid circles), 1991–2005, vs. randomly selected, unoccupied sites (open circles).

shoreline of San Francisco Bay, near the upper (eastern) end of the estuary, and in the central portions of major tidal marsh areas, especially Napa and Suisun Marshes (Figure 4). Low odds of site use were predicted in surrounding areas in spite of the presence of several small great blue heron colonies, because weighting colony sites (species pooled) focused the models on conditions suitable for larger, mixed-species colonies.

Productivity of Successful Nests

The selected set of best models for predicting habitat effects on prefledging brood size in great blue herons included habitat influences measured within all spatial extents around colony sites (Table 4). However, none of the models acounted substantially for variation in nest productivity ($R^2 \leq 0.22$). The most important predictors, each associated with increases in prefledging brood size, were estuarine emergent wetland, open water, and low-intensity development, at all spatial scales of measurement (Figure 5). The number of young in successful nests declined with the extent of grassland within 3, 7, and 10 km, but grassland was a relatively unimportant predictor (Table 5). None of the spatial extents of habitat measurement resulted in models or variables that were substantially more predictive than others (Figure 5).

The number of young fledged in successful great egret nests was influenced primarily by habitat variation measured within the largest areas around colony sites (10 km radius; Table 4). As in great blue herons, the most important predictor variables were estuarine emergent wetland, open water, and low-intensity development, but in great egrets the effects were strongest when measured at the largest spatial scale (10 km; Tables 4 and 5). The negative influence of open water on great egret nest productivity contrasted with the positive effects of open water on great blue herons (Table 5). Other potentially important predictors of productivity in great egrets were the extent of palustrine emergent wetland (with effects similar to open water; Figure 6) and the number of wetland patches within 10 km (Table 5). Comparisons of predictors across spatial extents

Table 4. Multiple regression models predicting annual mean brood size of successful nests in colony sites, based on 38 great blue heron colonies (n = 255 sites × years) and 20 great egret colonies (n = 122 sites × years) in northern San Francisco Bay, 1991–2005. The measurement scale (areal extent indicated by radius around colony site), number of parameters including constant and indicator variables for year (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weights (w_i), and measures of model fit (R^2) are provided. Only models with ($\Delta AIC_c < 7$) are presented, representing the 0.95 model confidence set ($\sum w_i$) for each species. The following predictors were included in the averaged model for each species (g(x)): estuarine emergent wetland (ESTUAR), open water (OPENW), low-intensity development (LOWINT), grassland (GRASSL), palustrine emergent wetland (PALUSTR), and number of wetland patches (NPATCH), and year (to facilitate interpretation, indicator variables for year are removed from the model column). Suffixes on variable names in the averaged models indicate the scale of measurement (km radius).

Model	Scale (km radius)	K	AIC_c	ΔAIC_c	w_i	R^2
Great Blue Heron						
ESTUAR, OPENW, LOWINT	3	18	262.04	0.00	0.285	0.22
ESTUAR, OPENW, LOWINT	10	18	262.36	0.32	0.243	0.22
ESTUAR, OPENW, LOWINT	5	18	263.88	1.84	0.113	0.22
ESTUAR, OPENW, LOWINT	1	18	264.18	2.14	0.098	0.21
ESTUAR, OPENW, LOWINT	7	18	264.31	2.27	0.092	0.21
ESTUAR, GRASSL	10	17	266.13	4.09	0.037	0.20
ESTUAR, GRASSL, LOWINT	3	18	266.93	4.89	0.025	0.21
ESTUAR, GRASSL, LOWINT	10	18	267.05	5.01	0.023	0.20
ESTUAR, GRASSL	3	17	267.11	5.07	0.023	0.20
ESTUAR, GRASSL	7	17	267.55	5.51	0.018	0.20
$g(x) = 1.7649 + 0.0091(\mathrm{ESTUAR1}) + 0.0038(\mathrm{ESTUAR3}) + 0.0005(\mathrm{ESTUAR5}) + 0.0002(\mathrm{ESTUAR7}) + 0.0005(\mathrm{ESTUAR10}) + 0.0165(\mathrm{OPENW1}) + 0.0048(\mathrm{OPENW3}) + 0.0008(\mathrm{OPENW5}) + 0.0003(\mathrm{OPENW7}) + 0.0005(\mathrm{OPENW10}) + 0.0186(\mathrm{LOWINT1}) + 0.0132(\mathrm{LOWINT3}) + 0.0014(\mathrm{LOWINT5}) + 0.0005(\mathrm{LOWINT7}) + 0.0009(\mathrm{LOWINT10}) - 0.0006(\mathrm{GRASSL3}) - 0.0001(\mathrm{GRASSL7}) - 0.0001(\mathrm{GRASSL10})$						
Great Egret						
ESTUAR, OPENW, LOWINT	10	18	32.53	0.00	0.837	0.62
ESTUAR, OPENW, PALUST	10	18	36.64	4.11	0.107	0.60
OPENW, PALUST, NPATCH	10	18	39.25	6.71	0.029	0.59
$g(x) = 1.8755 + 0.0057(\mathrm{ESTUAR10}) - 0.0043(\mathrm{OPENW10}) - 0.0077(\mathrm{PALUSTR10}) + 0.0156(\mathrm{LOWINT10}) + 0.0002(\mathrm{NPATCH10})$						

showed relatively strong influences (both positive and negative) of habitat conditions measured within 10 km and relatively weak effects of habitats within 1 km (Figure 6).

The predictive map of great blue heron nest productivity suggested higher productivity near bay shorelines and wetland areas (Figure 7). Patterns of landscape variation were broad, in spite of the multi-scale habitat associations in the selected set of models (Table 4, Figure 7). The map of predicted great egret brood size reflected the larger scale of landscape influences, with the greatest nest productivity in the vicinity of Suisun Marsh and in areas with low-intensity development adjacent to wetlands, and lower productivity in northern San Pablo Bay marshes (Figure 7). Model predictions for great egret nest productivity above 2.4 young per successful nest exceeded the maximum observed in colony sites. This may have resulted from a positive bias in areas where the extent of low-intensity development was considerably greater than the maximum extent in the data and unlikely to reflect the linear influence that occurred within the range of conditions around colony sites (max = 31%, 24%, 20%, 21%, and 17% low-intensity development, respectively, within 1, 3, 5, 7, and 10 km of colony sites).

Foraging Dispersion

Flight distances fitted to the dispersion models resulted in parameter values of a = −0.197 ± 0.001 and b = 0.472 ± 0.001 for the distance model and a = −0.120 ± 0.001 and b = 0.696 ± 0.002 for the habitat model (observed vs. predicted $r^2 > 0.92$ for both models). The distribution of flight distances indicated that approximately 60% of the great egrets foraged within 3 km of the colony site or within a radius that encompassed approximately 20 km^2 of estuarine/palustrine emergent wetland (Figure 8). These distances should be interpreted cautiously, however, because they were based on a small number of flights (n = 36).

The habitat model predicted a more even foraging distribution across regional wetlands than the

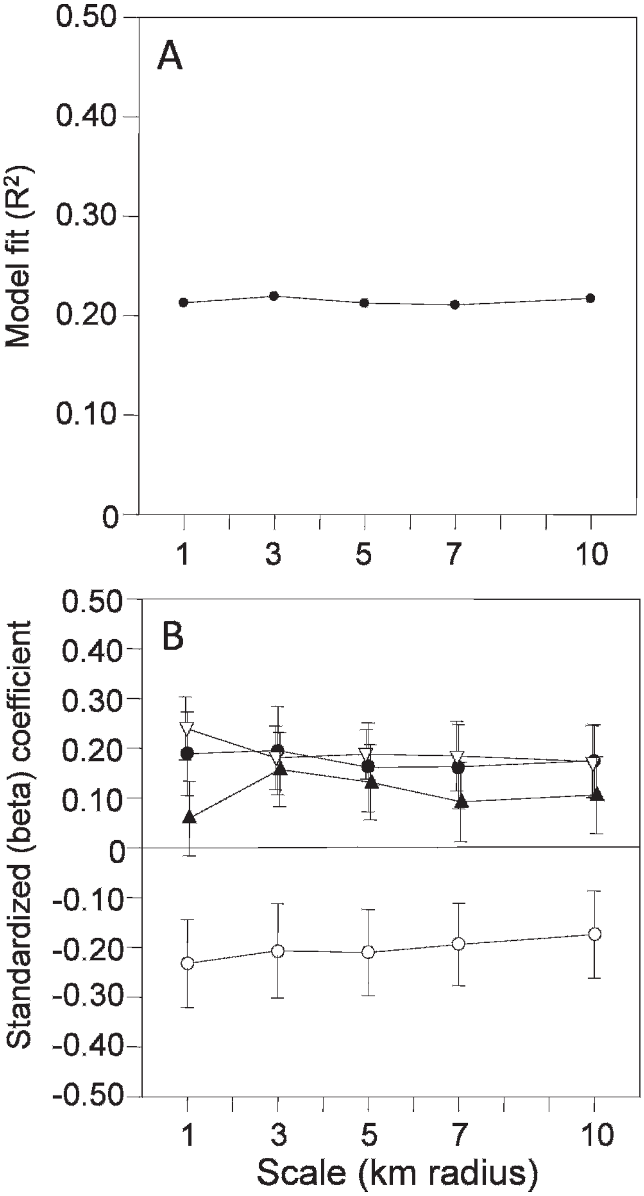

Figure 5. Multiple regression results from *a priori* models of landscape effects on mean prefledging brood size in great blue heron colonies in northern San Francisco Bay, 1991–2005, showing A) model-averaged fit (R^2) and B) standardized (beta) coefficients of landscape variables (± standard error). Only those variables present at one or more spatial scales in the selected set of best models are presented: estuarine emergent wetland (solid circle), open water (open, downward-pointing triangle), low intensity development (solid, upward-pointing triangle), and grassland (open circle).

distance model (Figure 9), but the predicted foraging densities of great egrets were still substantially concentrated near colony sites. Based on these predictions, regional foraging densities were highest in Suisun Marsh, the lower Petaluma Marsh, and along the western shoreline of San Pablo Bay southward to the northern shoreline marshes of Central San Francisco Bay (Figure 9B). Foraging concentrations were generally predicted in areas associated with higher predicted nest productivity and greater odds of colony site use (Figures 4, 7, and 9). Long flight distances required from great egret colonies to access the Napa Marsh resulted in relatively low predicted foraging densities (Figure 9B).

DISCUSSION

Our results showed that both the reproductive performance and the foraging distribution of a key group of wetland predators may depend on landscape patterns within distances of at least 10 km. The activities of wide-ranging predators such as herons and egrets that concentrate their nesting activities in particular areas may, in turn, influence other elements and processes in the tidal landscape through cascading effects on the populations or behavior of other species and through nutrient effects in the vicinity of nesting colonies (Master 1992, Frederick and Powell 1994, Frederick 2002, Batzer et al. 2006).

Our finding that colony-site selection is associated primarily with the extent of estuarine wetland and open water within 1 km suggests the importance of local foraging opportunities near heronries. The establishment of colony sites based on local conditions, combined with the predominance of foraging flights terminating within similarly localized areas and the relatively stable use of colony sites across years, suggests the long-term importance of nearby feeding habitat. The extent of low-intensity development was an important predictor of prefledging brood size but was not clearly important in predicting colony site use. This difference suggests that potential foraging benefits associated with greater productivity in successful nests may be offset by potentially negative effects (e.g., disturbance or predation) of locating colonies close to residential development. The spacing of colony sites at distances of approximately 6 km in the San Francisco Bay area (Kelly et al. 2007), and 5–7 km in northwest Italy (Fasola and Alieri 1992a), and the frequent formation of satellite colonies close to the original sites in the San Francisco Bay area (Kelly et al. 1993, 2007) and along the Atlantic Coast (Custer et al. 1980), further suggest smaller-scale processes affecting nesting distributions.

The lack of spatial differences in habitat effects on great blue heron nest productivity might be the result of the consistent use, by different individuals in a colony, of different feeding areas at different

Table 5. Landscape variables in multiple regression models predicting annual mean brood size of successful nests in colony sites, based on 38 great blue heron colonies (n = 255 sites × years) and 20 great egret colonies (n = 122 sites × years) in northern San Francisco Bay, 1991–2005. Scale indicates the radius around each colony site within which variables were measured. Standardized (beta) coefficients, based on all models in which each variable occurred, standard error (SE), and the relative importance ($\sum w_i$) of each variable are provided. Relative importance was calculated by summing Akaike weights (w_i) for all models in which the variable was present. Only variables in the selected best set of models ($\Delta AIC_c < 7$) are presented.

Variable	Scale (km radius)	Beta coefficient	SE	$\sum w_i$
Great Blue Heron				
Estuarine emergent wetland (km^2)	3	0.197	0.089	0.333
Low-intensity development (km^2)	3	0.157	0.075	0.310
Estuarine emergent wetland (km^2)	10	0.178	0.073	0.303
Open water (km^2)	3	0.181	0.064	0.285
Low-intensity development (km^2)	10	0.106	0.077	0.266
Open water (km^2)	10	0.173	0.072	0.243
Estuarine emergent wetland (km^2)	5	0.164	0.089	0.139
Low-intensity development (km^2)	5	0.131	0.076	0.123
Estuarine emergent wetland (km^2)	7	0.165	0.084	0.118
Open water (km^2)	5	0.188	0.050	0.113
Estuarine emergent wetland (km^2)	1	0.191	0.084	0.107
Low-intensity development (km^2)	1	0.059	0.075	0.102
Low-intensity development (km^2)	7	0.092	0.080	0.100
Open water (km^2)	1	0.240	0.063	0.098
Open water (km^2)	7	0.184	0.070	0.092
Grassland (km^2)	10	−0.171	0.088	0.060
Grassland (km^2)	3	−0.207	0.095	0.047
Grassland (km^2)	7	−0.194	0.083	0.026
Great Egret				
Open water (km^2)	10	−0.566	0.132	0.973
Estuarine emergent wetland (km^2)	10	0.920	0.103	0.956
Low-intensity development (km^2)	10	0.777	0.135	0.848
Palustrine emergent wetland (ha)	10	−0.511	0.139	0.137
Number of wetland patches	10	0.701	0.080	0.029

distances from the colony site (Dowd and Flake 1985, Simpson et al. 1987, Marion 1989). If so, nest productivity in great blue heron colonies may depend on the extent of foraging habitat at all scales, and models that specify habitat effects across several scales are likely to be more predictive than the scale-specific hypotheses used in our analysis. Simpson et al. (1987) found that great blue herons feeding near the colony site had nests that were more successful than herons feeding at distant sites. However, they determined that the number of young produced in successful nests was not significantly related to foraging distance.

The negative effect of grassland extent on great blue heron nest productivity might be related to the inverse correlation between grassland and open water, which was associated with increased productivity. In contrast, the extent of open water was negatively related to the number of young in successful great egret nests. This difference was consistent with 1) the positive effect of estuarine emergent vegetation on great egret productivity, 2) the inverse correlation between open water and grassland areas which may provide suitable foraging habitat for great egrets (McCrimmon et al. 2001), 3) Custer and Galli's (2002) finding that great egrets foraged preferentially in small ponds whereas great blue herons chose larger bodies of water for foraging, and 4) the possibility that open water areas often exceed the shallow foraging depths (< 19 cm) preferred by great egrets but may provide more extensive feeding areas for great blue herons, which are less sensitive to water depth than great egrets (Gawlik 2002). The positive effect of low-intensity development on productivity in both species suggested an association with small, undetected ponds, ditches, and other manipulated water sources, although we have not verified this possibility. The spatially extensive habitat influences on great egret reproductive success suggested by our results were consistent with shifts in nesting distribution of 10 km or more in response to periods of localized drought in the Everglades (Bancroft et al. 1994).

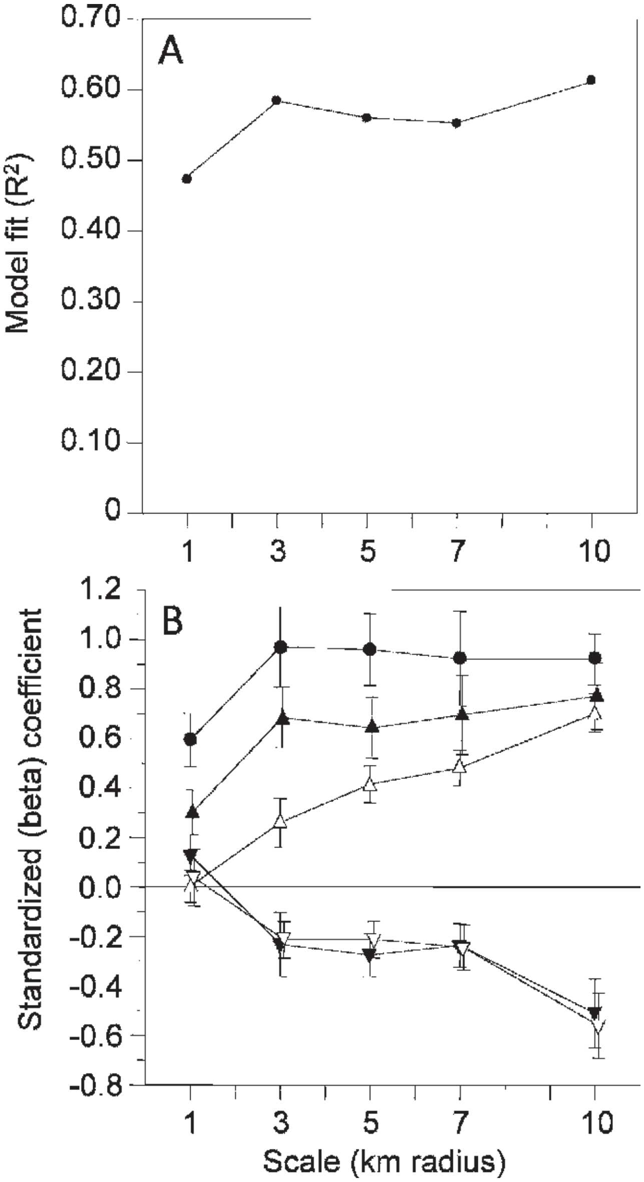

Figure 6. Multiple regression results from *a priori* models of landscape effects on mean prefledging brood size in great egret colonies in northern San Francisco Bay, 1991–2005, showing A) model-averaged fit (R^2) and B) standardized (beta) coefficients of landscape variables (± standard error). Only those variables present at one or more spatial scales in the selected set of best models are presented: estuarine emergent wetland (solid circle), low intensity development (solid, upward-pointing triangle), number of wetland patches (open, upward-pointing triangle), palustrine emergent wetland (solid, downward-pointing triangle), and open water (open, downward-pointing triangle).

The great egret dispersion models provided evidence of concentrated foraging near heronries that was consistent with the importance of nearby wetlands suggested by the colony site analysis. The reasonable expectation that habitat selectivity is greater than distinguished by the models (violation of assumptions 4, if wetland habitat quality is variable, and 5, if flight directions are not random) suggests greater variability in foraging densities and some limitations of the predicted patterns. Predictions are likely to be lower than actual densities in high quality habitat because predicted densities were calculated over all areas of wetland habitat, some of which may be low quality. The possibility that flight distances might increase with colony size (violation of assumption 6) suggests a bias in the flight distance models toward greater foraging dispersion because distances were based on flights from colonies that were larger than most in the region. This possibility strengthens the prediction of concentrated foraging near colony sites.

The habitat model of foraging dispersion assumed that the costs of accessing wetlands from all sites were similar to those in Suisun Marsh where foraging flights were measured (landing rate was log-proportional to wetland area$^{0.696}$). However, at sites that are farther from surrounding wetlands than those in Suisun Marsh, the costs of extended travel might reduce the extent of accessible foraging habitat. If so, birds may be forced to forage closer to the colony, relative to the extent of surrounding wetland area, than we predicted. Because more wetland habitat was available near colony sites in Suisun Marsh, the habitat model was likely to underestimate the effects of travel costs from more isolated sites, overestimating foraging dispersion. This bias also strengthens the prediction of concentrated foraging near colony sites. However, Parris and Grau (1978) found that great blue herons nesting at island and mainland sites in southwestern Lake Erie used the same amount of foraging habitat even though they differed greatly in the distance traveled to find food, suggesting that differences in travel costs did not affect foraging dispersion. If so, foraging dispersion might vary substantially among colony sites with different amounts of surrounding foraging habitat. In addition, foraging distances might vary with interannual differences in foraging habitat quality.

If foraging great egrets actually fly farther relative to the extent of available wetlands than we predicted, foraging dispersion would be less concentrated near colony sites. The flight distances we used to predict landscape foraging patterns were comparable to those reported in other geographic areas. The average great egret foraging distance of 3.0 ± 0.40 km was near the lower end of the range of average distances of 2.8–8.6 km reported in other geographic areas (Custer and Osborn 1978, Thompson 1978, Bancroft et al.

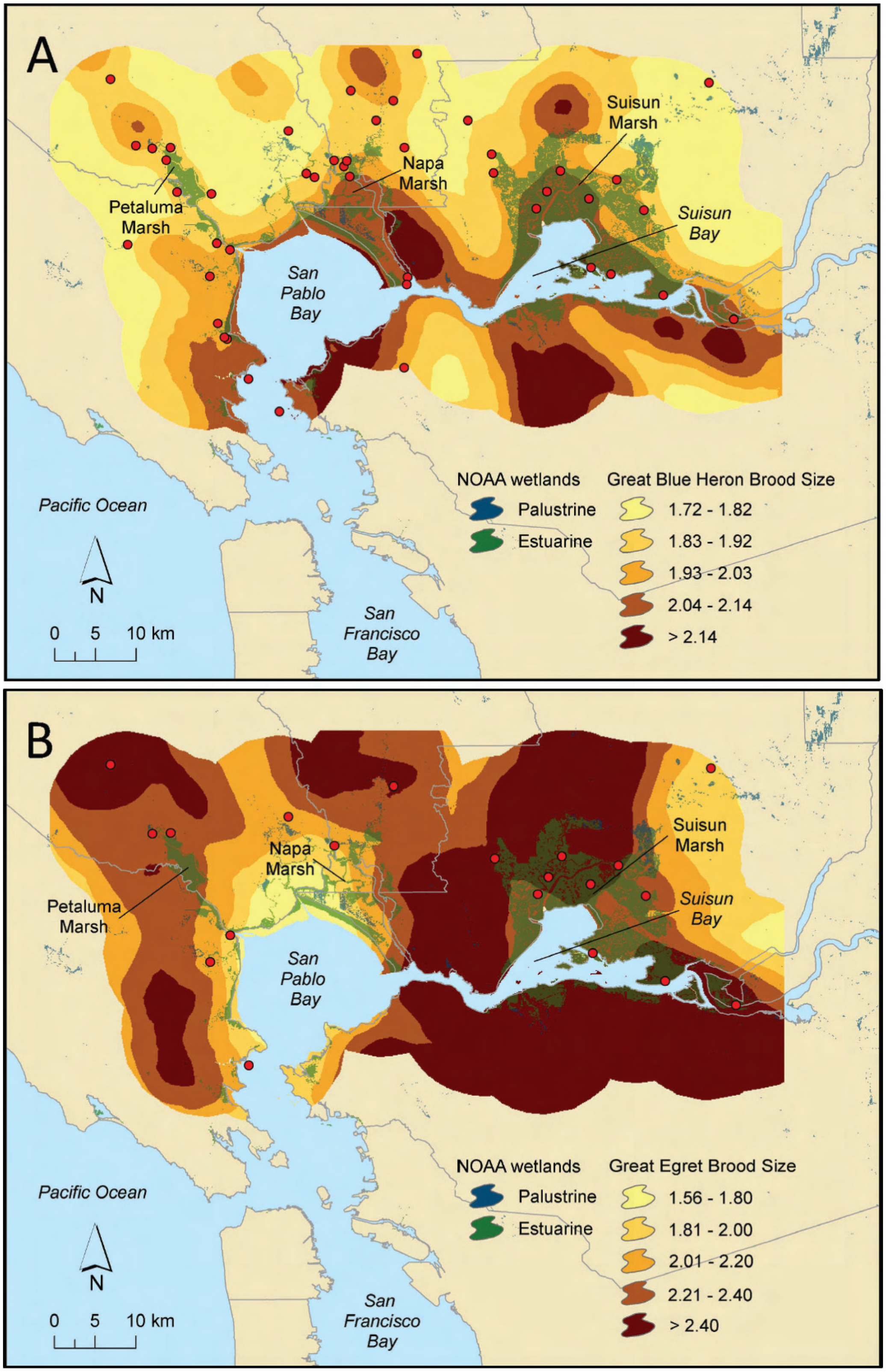

Figure 7. Prefledging brood size in successful A) great blue heron and B) great egret nests, as predicted by landscape influences in northern San Francisco Bay, based on model-averaged multiple regressions of mean colony brood sizes, 1991–2005, against land cover and wetland patch variables (Table 4). Solid circles indicate colony sites.

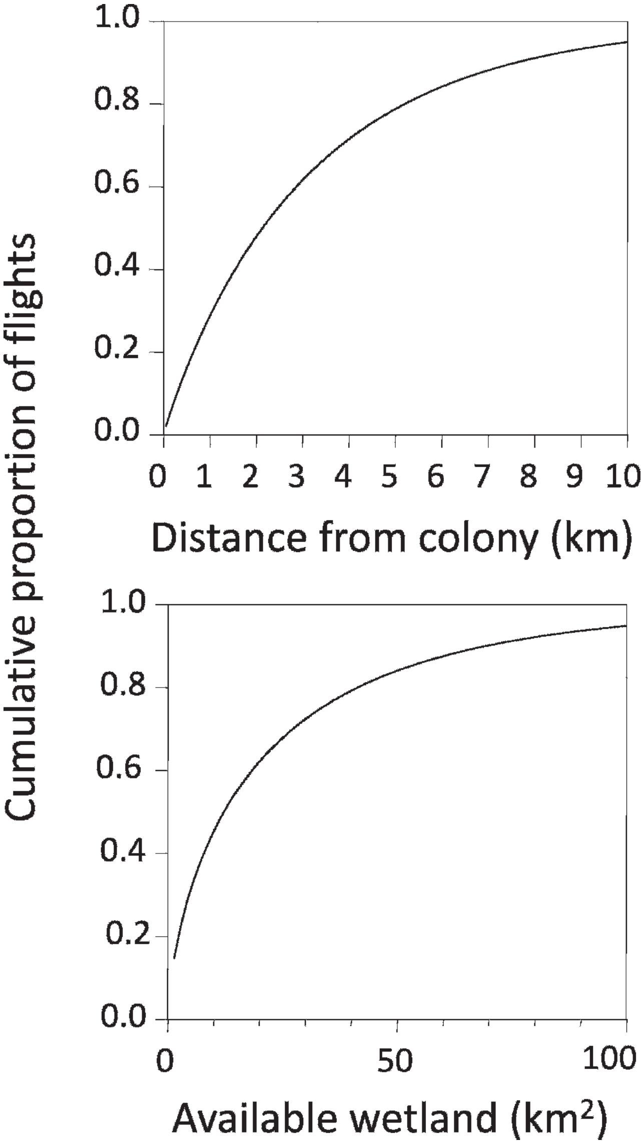

Figure 8. Estimated cumulative foraging dispersion of great egrets, based on 1,000 bootstrap samples of departure flights (n = 36) from colony sites in Suisun Marsh, modeled as a function of A) flight distance and B) areal extent of estuarine and palustrine emergent wetland accessible within flight distances (see text).

1994, Smith 1995, Custer and Galli 2002). Similarly, the distance model estimated that 1% of flights exceeded 28.2 km, which was near the lower end of maximum distances of 28–40 km reported by the same studies.

The predicted dispersion patterns suggested extensive areas with relatively low rates of foraging by nesting great egrets in the marshes of northern San Pablo Bay and more intensive foraging in marshes along the western shore of San Pablo Bay and in Suisun Marsh. These patterns, functions of nesting distribution and foraging dispersion, could be related either to large-scale variation in foraging or nesting habitat quality, trade-offs related to the costs of travel (Gibbs 1991, Gibbs and Kinkel 1997) or, alternatively, underestimation of foraging dispersion. However, information is lacking on the extent to which areas far from colony sites might be subject to foraging by non-breeding individuals not limited by the need to return to nest sites (Bancroft et al. 1994). Trocki and Paton (2006) found no significant relationship between the number of foraging great egrets or snowy egrets using marshes in Rhode Island and the distance to the nearest colony site.

The restoration of wetland habitat can result in increased use by herons and egrets and the establishment of new colony sites (Mauchamp et al. 2002, Kelly et al. 2007). Spatial predictions suggested that landscape values responsible for relatively low odds of colony site use in northern San Pablo Bay marshes were also associated with reduced nest productivity. This suggests that increasing the extent of suitable foraging habitat in this area might lead to an increase in breeding densities, with an associated increase in foraging activity. The broad influence of landscape habitat conditions on great blue heron and great egret nest productivity further suggests the importance of regional wetland management and collaborative planning. Regional planners could enhance the value of wetland landscapes to nesting herons and egrets by promoting clusters of habitat protection or restoration projects within a few to several km of colony sites. Based on our results, we hypothesize that restoring the extent or suitability of wetland foraging habitat (both vegetated and unvegetated) for herons and egrets may 1) influence reproductive performance in colony sites up to 10 km away, 2) lead to increased foraging by herons and egrets at sites within 10 km of colony sites, and especially within 3 km, and 3) increase nest abundance at colony sites within 3 km of restoration sites.

We recommend prioritizing the protection, restoration, or creation of potential nesting sites in areas of wetland landscapes that are more than 6 km from active colony sites and have landscape features associated with both higher reproductive performance and preferred colony sites. Such features include more extensive areas of emergent wetland interspersed with open water channels and ponds, within 1 km and 10 km. Similar criteria should be used to create or protect a viable wetland patch matrix in areas surrounding existing colony sites.

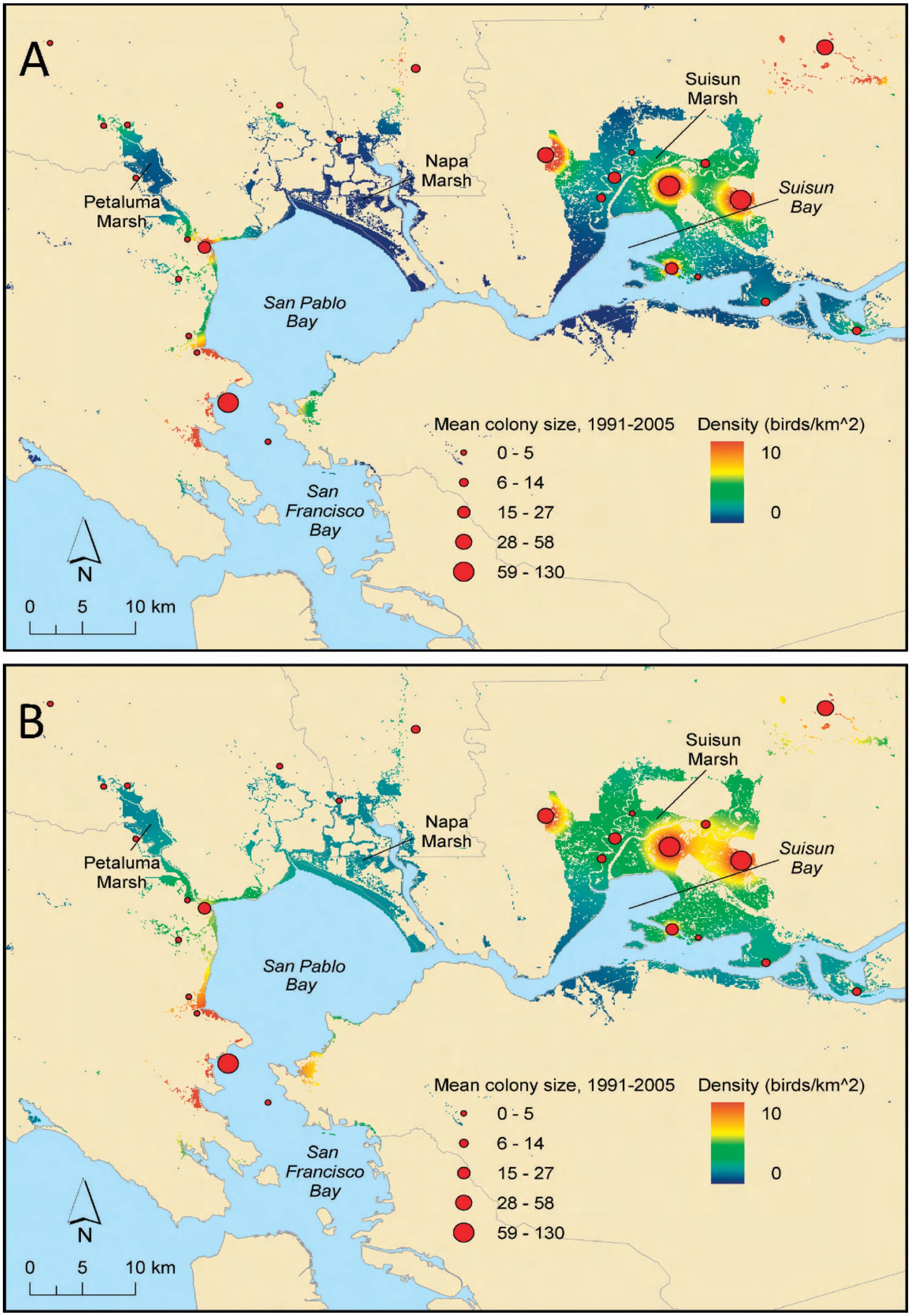

Figure 9. Predicted great egret foraging densities in estuarine and palustrine emergent wetlands in northern San Francisco Bay, based on average nesting distribution, 1991–2005, and foraging dispersion from colony sites (solid circles) relative to A) flight distance and B) the areal extent of wetland accessible within flight distance (see text).

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