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| **From:** | Jacob Patterson <jacob.patterson.esq@gmail.com> |
| **Sent:** | Wednesday, July 21, 2021 12:24 PM |
| **To:** | Lemos, June; Munoz, Cristal |
| **Cc:** | O'Neal, Chantell; Gurewitz, Heather |
| **Subject:** | Public Comment and Questions re staff report for Grocery Outlet appeal (7/26/21 CC Mtg. Item 7B) |
| **Attachments:** | Hard To Swallow_ Great Blue Herons Eating Gophers In Golden Gate Park.pdf; Hunting Herons at Point Reyes National Seashore - Exploring Nature by Sheila Newenham.pdf; Foraging Habitat Preferences of Herons and Egrets.pdf; Habitat utilization by great blue herons (Ardea herodias) in Elkh.pdf; kelly_etal_2008_wetlands.pdf |

City Council or Staff,

I have some questions about the following statements on page 8 of the staff report for the Grocery Outlet appeal:

"Herons have been observed eating gophers and other rodents on lawns and other open spaces, but this does not qualify the space as blue heron habitat."

"The site is far from secluded as it is right in the middle of a commercial district in town just one block east of a State Highway. The area where trees exist on site are frequented by transient human populations and is not suitable nesting habitat. There was no evidence of bird nesting as noted in the biological survey and the site, based on the wetlands survey cannot be considered Blue Heron habitat."

Is there a source for the allegation that "Herons have been observed eating gophers and other rodents on lawns and other open spaces, but this does not qualify the space as blue heron habitat"? I cannot recall or locate anything in the record that supports this assertion. In fact, this appears to be a likely incorrect assumption regarding the extent of the definition of "habitat" as being limited to nesting locations rather than also including foraging locations.

Is there a source for the allegation that "The area where trees exist on site are frequented by transient human populations"? I cannot recall or locate anything in the record that supports this otherwise unsupported assertion. Are there photos of the alleged transients under the trees? Are there police reports noting that particular activity? Are there documented site visits where someone observed the alleged transient activity or is this merely anecdotal or a staff assumption?

[As an aside, I find it ironic that the City appears to be basing the appeal analysis on assertions with no support in the record when staff's response to the majority of the objections raised in the public comments and testimony is to attempt to reject them as irrelevant for (allegedly) the exact same reason: a lack of supporting evidence. In my opinion, that is the primary underlying problem with the MND (as currently written) and the staff "analysis" that is frequently cited and being complete and sufficient. Moreover, contrary to the City staff's positions, a person need not introduce supporting evidence for the opposite conclusion than was was included in the City's entitlement review documents if the objection is that the initial positions recommended by staff and consultants are not supported by substantial evidence in the record and no such evidence actually exists because all positions need to be supported by facts and supported analysis in the record.]

Further, is there a source for the allegation that the alleged transient activity would make the area "not suitable for nesting habitat" or that the applicable definition of habitat is limited to nesting locations rather than foraging locations? I cannot recall or locate anything in the record that supports this assertion, including the biological study or any supplemental biological review to evaluate the documented observation of herons using the site as foraging habitat (not nesting habitat).

I understand that the definition of "habitat" in the context of biological studies scientific analysis of migratory bird includes both nesting locations as well as foraging locations. Since I am the person who submitted the photos based on personally visiting the site on numerous locations and observing/documenting the herons foraging under the subject trees and in the southern field on the project site, in that case hunting gophers for food--the extensive presence of gophers on the site was noted in the biological study as well--I thought it appropriate that I review and respond to how this was addressed in the staff report. Did staff not include foraging locations as within the definition of "habitat" for the documented migratory birds? If not, why was the biologist who authored the original study not contacted again to review their analysis and conclusions in light of the documented evidence of herons using the project site as foraging habitat? If there was a qualified biologist who opined that the nature of the site and the transient or other human activity made the site unsuitable to be considered heron habitat despite the documented observations of herons using the site for just that purpose, why was this not included in the packet or referenced in the staff report in a similar way to how the soil and hydrology study was updated by the subject matter expert?

I have also attached several studies and supporting documents concerning heron foraging habitat that I believe are relevant to this issue (and so my positions have additional support in the record).

Regards,

--Jacob

J. Ecol. Field Biol. 30 (3): 237~244, 2007

# Foraging Habitat Preferences of Herons and Egrets

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**ABSTRACT**: We investigated the foraging habitat preferences of herons and egrets in an agricultural area in Asan city, Chungcheongnam-do, Korea. In the study area, rice fields were the most abundant habitat type (86.8%) and total suitable feeding habitat was greater in the northern area (59.0%) than the southern area (22.5%) of the colony. Most feeding herons and egrets were located in the northern area of the colony. The number of feeding individuals in a given area was related to the available feeding area (Pearson correlation, $r$=0.773, $p$<0.001 for field habitats; $r$=0.901, $p$<0.001 for freshwater habitats). Feeding habitat preferences differed among species. Grey herons (*Ardea cinerea*), great egrets (*Egretta alba*), and black-crowned night herons (*Nycticorax nycticorax*) used reservoirs and ditches. However, intermediate egrets (*E. intermedia*) and cattle egrets (*Bubulcus ibis*) were dependent on rice fields. The little egret (*E. garzetta*) was a habitat generalist using all types of habitats. The two largest species, grey herons and great egrets, fed at deeper site than little egrets and foraged in deeper sites in reservoirs than in ditches ($\chi^2$-test, $\chi^2_3$=26.6 and $p$<0.001 for grey herons, $\chi^2_3$ =17.5 and $p$<0.001 for great egrets). All species displayed seasonal changes in feeding habitat use and these changes were related with changes in availability of feeding habitats.

***Key words***: Ardeidae, Egrets, Feeding habitat, Foraging, Habitat preferences, Herons

## INTRODUCTION

Wetlands support several species of waterbirds and each species use available habitats and resources in different ways. The availability of feeding habitats is related to breeding success and population sizes (Hafner 1997). The choice of feeding habitat is particularly important in nesting seasons since energetic demands on adults are greater in the breeding season than the non-breeding season (Erwin 1985). In mixed-species colonies, inter-specific competition for food resources can occur, and therefore species may partition resources by using different prey types, feeding habitats, and foraging times (Smith 1997).

Bird species in the family Ardeidae (herons or egrets) are found in aquatic habitats worldwide (Kushlan and Hancock 2005). They are generally tall and slim, with long bills, a long neck, long legs, and long toes. They use a variety of habitats, including many human-altered landscapes. Most heron species are highly dependent on wetlands, but some also feed on dry land. They mainly feed on aquatic prey such as fishes, amphibians and aquatic insects, while some species also feed on terrestrial prey such as small mammals and insects (Kushlan and Hancock 2005). The choice of foraging habitats in heron species is influenced by several factors such as prey density (Hafner and Britton 1983, Draulans 1987, Kersten et al. 1991), habitat type (Erwin et al. 1985, Tojo 1996, Dimalexis et al. 1997, Wong et al. 2001), and water level fluctuations (Kushlan 1986, Smith 1995), etc. Moreover, the availability of food often varies both temporally and spatially. Therefore, the choice of foraging locations by feeding herons is also likely to vary across time and space (Hafner and Britton 1983, Maccarone and Parsons 1994).

Understanding ardeid feeding habitats and habits as well as nesting habitats is important for conservation. In Korea, there has been some research about ardeid breeding ecology (Yu and Hahm 1997, Kim et al. 1998, Kim and Koo 2007) and characteristics of nesting habitats (Lee et al. 2007), but species-specific feeding habitats and prey types are not fully understood. This study investigates the feeding habitat preferences of grey herons (*Ardea cinerea*), great egrets (*Egretta alba*), intermediate egrets (*E. intermedia*), little egrets (*E. garzetta*), cattle egrets (*Bubulcus ibis*), and black- crowned night herons (*Nycticorax nycticorax*), the most common Ardeidae species in Korea.

## STUDY AREA AND METHODS

The study area included an area of about 5 km radius (a total of 8,800 ha) around a breeding colony (36° 52' 25" N, 127° 02' 02" E) in Asan city, Chungcheongnam-do in Korea (Fig. 1). Although herons and egrets may feed over a wider area, most individuals prefer feeding habitat within 5 km from their breeding colony (Hafner and Britton 1983, Hafner and Fasola 1992, Wong et al. 1999). Therefore, we assumed that all herons and egrets observed

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in the study area were from this colony. The breeding colony is located near a reservoir that many herons and egrets use as a feeding site and included about 600 nests of grey herons (16.1%), great egrets (4.8%), intermediate egrets (11.3%), little egrets (19.4%), cattle egrets (21.0%), and black-crowned night herons (27.4%).

The study area contains several types of feeding habitats, such as reservoirs, ditches, grasslands, and rice fields. Water conditions in rice fields changed seasonally. In spring and summer (from late April to September), all fields were filled with water. After the crop harvest in early autumn (normally in October), water levels were reduced and most rice fields either held only some patches of water or were dried out. Most reservoirs were constructed for agricultural purposes, and their water levels also fluctuate seasonally: normally water levels are high in winter and low from late May to October, except in late June and July, the rainy season in Korea.

Monthly counts of feeding individuals were conducted from April to October 2006, except that two counts were conducted in May. Feeding birds were distinguished from roosting individuals either by their activities or postures. Roosting individuals were not included in the data analysis. We observed each feeding individual for 2~3 minutes and recorded the foraging habitat type and water depth. We distinguished 5 foraging habitat types: 1) reservoirs, including small ponds; 2) ditches, including small streams and irrigation channels; 3) rice fields; 4) rice banks (levees), defined as levees or paths covered by grasses around rice fields; and 5) grass lands. Water depth was estimated in relation to the leg length of the birds. Water depth was divided into 4 categories: (1) 0-Ts1/2: water up to the half of length of the tarsus; (2) -Ts1: water up to the joint of tarsus and tibia; (3) -Tb1/2: water up to the half of the length of the tibia; (4) -Tb1: water up to the belly of birds. Also, in rice fields, we distinguished the location of feeding birds into two areas, inner parts and edges (<1 m of the bank), including rice banks.

The area of foraging habitat were measured using a point sampling technique (Farinha and Leitão 1996) from 1:25,000 maps with a grid containing 400 points per km$^2$ (1 point = 0.25 ha) and field surveys. Non-feeding habitats, including villages, industrial areas, forests, mountains, and roads, were not included in the feeding area. The study area was divided into five sections: the center, the north-east section, the north-west section, the south-east section, and the south-west section (Fig. 1). Because many herons (especially grey

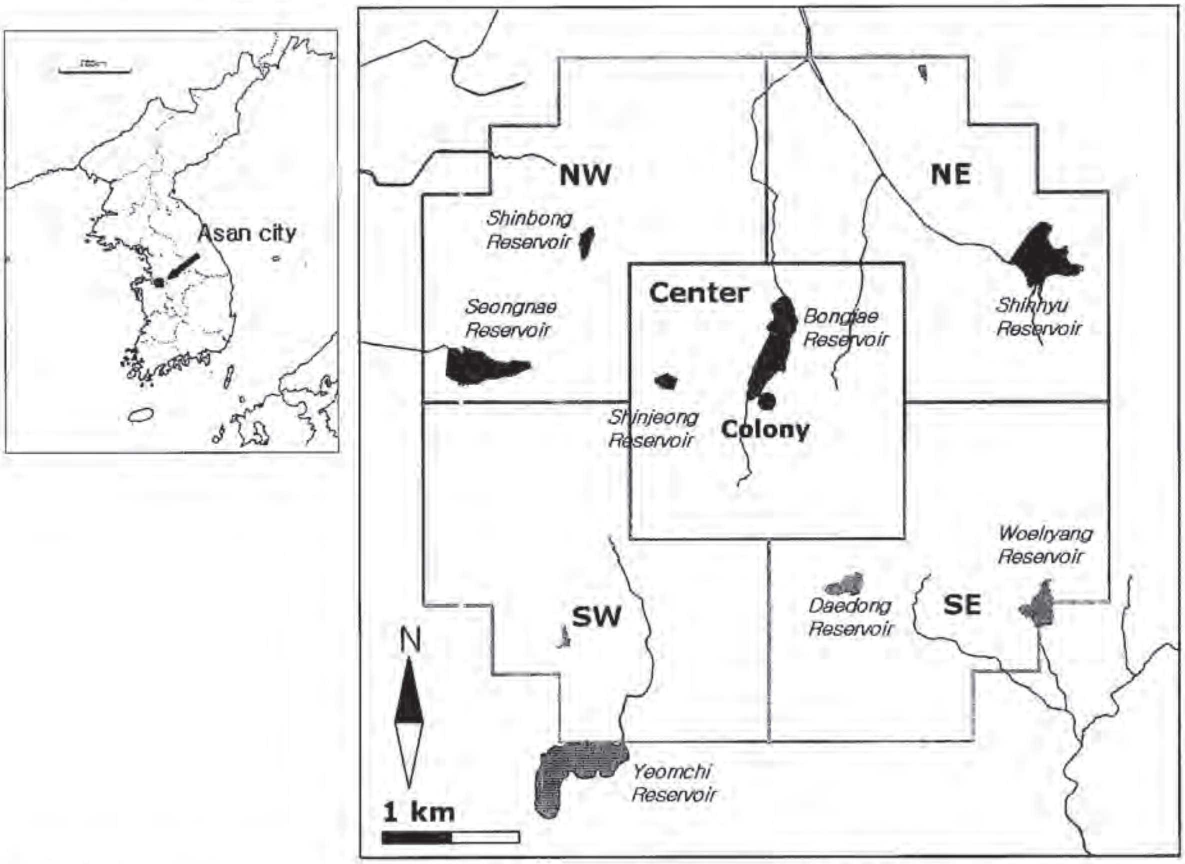

Fig. 1. Map of the study area showing main reservoirs and ditches around the breeding colony (solid circle at center). The study area is divided into five divisions or sections; center, north-east (NE), north-west (NW), south-west (SW), and south-east (SE).

herons) fed in the reservoir within 2 km from the breeding colony, we designated the area within 2 km from the colony as the center section (a total of 1,600 ha) and the remaining area was divided into four sections of equal size (each 1,800 ha). We examined relationships between the distribution of feeding herons or egrets and the area of feeding habitat. To evaluate the differences in foraging habitat selection among species, an ordination method, correspondence analysis (CA) was employed. The CA ordination was performed using the MVSP program (version 3.1) and all data were summarized on a monthly basis for each species. To compare the differences in water depth between habitat types for each species, we employed the $\chi^2$ test using SPSS software (version 11.2) and statistical methods described in Zar (1999).

## RESULTS

### Feeding Area and Number of Feeding Ardeidae

The total available feeding area was estimated at 2,105.2 ha (23.9% of the study area). The remaining area (6,694.8 ha, 76.1%) was considered to be unsuitable feeding habitat for Ardeidae and consisted of mountains, forests, villages, industrial factories and roads. Rice fields were the most abundant feeding habitat type (1,828.8 ha, 86.8% of total feeding area) within the study area, followed by reservoirs (173.4 ha, 8.2%), ditches (68.1 ha, 3.2%), and grasslands (34.9 ha, 1.7%) (Table 1). Feeding habitat was the most abundant in the north-east section (639.8 ha, 30.4% of the total feeding area), followed by the north-west section (601.6 ha, 28.6%), center (389.4 ha, 18.5%), the south-east section (287.6 ha, 13.6%), and the south-west section (186.8 ha, 8.9%). Most herons and egrets were located in the north-east section (Table 2 and Fig. 2). Fig. 2 shows that the number of birds related to the area of feeding habitat. The total number of feeding individuals was correlated with area of feeding habitat in both field (Pearson correlation, $r$= 0.773, $p$<0.001) and freshwater habitats ($r$=0.901, $p$<0.001).

### Foraging Habitat Preferences

Correspondence analysis revealed differences in feeding habitat types among the six heron or egret species (Fig. 3). The first CA axis (CA1) expresses the gradient in foraging habitat from field habitats (rice fields and grasslands) to freshwater habitats (reservoirs and ditches). The second CA axis (CA2) expresses the gradient in the condition of field habitats from wet habitat types (rice fields) to dry habitat types (rice banks and grasslands). The grey heron and black-crowned night heron foraged mainly in reservoirs and the great egret selected both reservoirs and ditches, whereas the intermediate egret and cattle egret preferred rice field and grass habitats. The little egret was a generalist in its selection of feeding habitats; it fed in all habitat types except for grass habitats.

Seasonal changes in habitat selection were found for some species (Fig. 4). Most species foraged more frequently in rice fields early in the year (April~June) than late in the year (July~October). Early in the year, some grey herons and great egrets foraged on rice fields, but after July they did not use rice fields. Two rice-field-dependent species, intermediate egrets and cattle egrets, foraged more on rice banks or grass lands than rice fields themselves in the later

Table 1. Foraging habitat types found within a radius of 5 km of the breeding colony

| Area[1] | Area (ha) of habitat | | | | Total |
|---|---|---|---|---|---|
| | Ditch | Reservoir | Rice field[2] | Grass | |
| Center | 8.5 | 54.8 | 323.3 | 2.8 | 389.4 (18.5%) |
| NE | 39.0 | 41.5 | 546.5 | 12.8 | 639.8 (30.4%) |
| NW | 4.3 | 46.3 | 543.0 | 8.0 | 601.6 (28.6%) |
| SW | 8.5 | 3.8 | 168.0 | 6.5 | 186.8 ( 8.9%) |
| SE | 7.8 | 27.0 | 248.0 | 4.8 | 287.6 (13.6%) |
| Total | 68.1<br>(3.2%) | 173.4<br>(8.2%) | 1828.8<br>(86.9%) | 34.9<br>(1.7%) | 2105.2<br>(100.0%) |

[1] Area: NE, north-east; NW, north-west; SW, south-west; SE, south-east. See Fig. 1.

[2] Including rice banks.

Table 2. Mean numbers and percentages of feeding herons and egrets in each area

| Area[1] | Feeding herons or egrets[2] | | | | | | Total |
|---|---|---|---|---|---|---|---|
| | GH | GE | IE | LE | CE | NH | |
| Center | 27.3<br>(33.9%) | 7.3<br>(16.8%) | 2.0<br>(13.2%) | 7.0<br>(16.1%) | 5.6<br>(11.6%) | 3.5<br>(16.6%) | 52.6<br>(20.9%) |
| NE | 25.0<br>(31.1%) | 20.9<br>(48.4%) | 7.9<br>(52.1%) | 18.4<br>(42.2%) | 24.9<br>(51.3%) | 10.5<br>(49.7%) | 107.5<br>(42.7%) |
| NW | 12.6<br>(15.7%) | 8.9<br>(20.6%) | 2.5<br>(16.5%) | 10.1<br>(23.3%) | 12.3<br>(25.3%) | 4.0<br>(18.9%) | 50.4<br>(20.0%) |
| SW | 0.4<br>(0.5%) | 1.0<br>(2.3%) | 1.1<br>(7.4%) | 2.5<br>(5.8%) | 2.5<br>(5.1%) | 0.1<br>(0.6%) | 7.6<br>(3.0%) |
| SE | 15.1<br>(18.8%) | 5.1<br>(11.9%) | 1.6<br>(10.8%) | 5.5<br>(12.6%) | 3.3<br>(6.7%) | 3.0<br>(14.2%) | 33.6<br>(13.4%) |

[1] Area: NE, north-east; NW, north-west; SW, south-west; SE, south-east. See Fig. 1.

[2] Species: GH, grey herons; GE, great egrets; IE, intermediate egrets; LE, little egrets; CE, cattle egrets; NH, black-crowned night herons. Data presented as the monthly mean value of all observations.

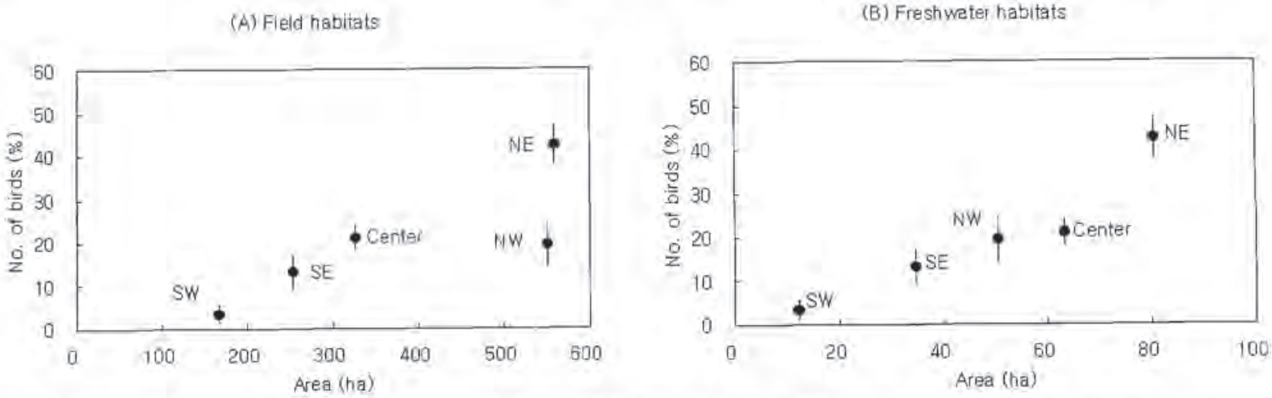

Fig. 2. Number of feeding herons and egrets in relation to the area of habitat: (A) field habitats and (B) freshwater habitats. Field habitats included rice fields and grasslands, and freshwater habitats included reservoirs and ditches. All data are presented as mean±SD. NE: north-east, NW: north-west, SW: south-west, SE: south-east.

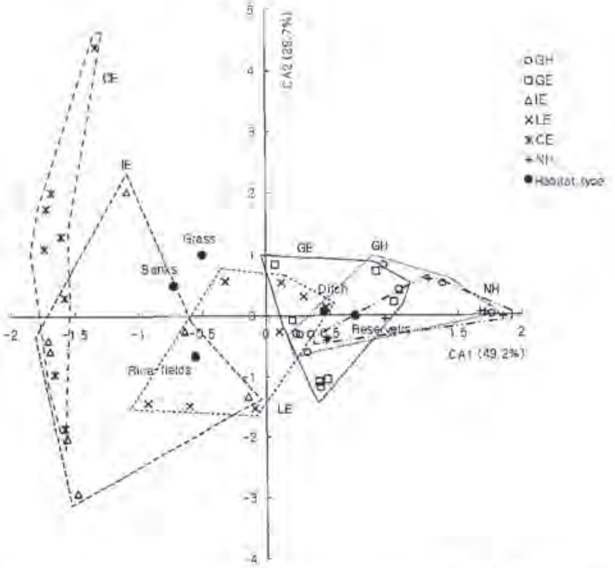

Fig. 3. Ordination plot of foraging habitat of six heron species on the first two axes from correspondence analysis (CA). GH: grey herons, GE: great egrets, IE: intermediate egrets, LE: little egrets, CE: cattle egrets, NH: black-crowned night herons.

part of the year. Most little egrets fed in rice fields in from April～June, but they used various habitat types later in the year. Black-crowned night herons fed mainly in reservoirs; a few individuals fed in rice fields from April～June.

### Feeding Water Depth

Fig. 5 shows the depths of water in which three species foraged in reservoirs and ditches. The two large species, grey herons and great egrets, selected deeper sites than little egrets, but no difference is shown between the two larger species. Grey herons and great egrets foraged in deeper sites in reservoirs than in ditches ( $\chi^2$ test, grey herons: $\chi^2$=26.6, *df*=3, $p<0.001$; great egrets: $\chi^2$=17.5, *df*=3, $p<0.001$). Little egrets foraged at shallow sites in both habitats, but foraged at deeper sites in ditches than in reservoirs ( $\chi^2$=23.5, *df*=3, $p<0.001$).

### Changes of Feeding Location in Rice Fields

In the early part of the field season, most feeding herons or egrets were located in the interior areas of rice fields, but they used the edges more in the later stages of the season (Fig. 6). For the two freshwater habitat foragers, grey herons and great egrets, only a small number of individuals foraged in the edges of rice fields in the later part of the season. The other three small species (intermediate, little, and cattle egrets) shifted their feeding locations from the interior areas of rice fields in the early part of the study season to the edges of rice fields in the late season.

## DISCUSSION

The availability of feeding habitat is an important factor affecting bird populations. Many natural wetlands worldwide have been damaged by human activities during the last two centuries, and accordingly, many waterbirds have suffered population declines and range contractions (Dugan 1990). Agricultural wetlands, particularly rice fields, have provided year-round feeding and nesting habitats for several species waterbirds (Fasola and Ruiz 1996, Czech and Parsons 2002). In this study, rice fields were the most abundant habitat type and many herons and egrets foraged in rice fields. Moreover, more feeding herons were located in the north-east area of the nesting colony, which has the largest area of rice fields, than in any other part of the study area. Rice-field landscapes, including irrigation channels, ditches and reservoirs for providing water to fields, provide adequate populations of various aquatic prey (e.g., amphibians, crustaceans, fishes and insects) to support a large number of waterbirds (Fasola et al. 1996, Lane and Fujioka 1998, Richardson et al. 2001).

In our study area, all heron and egret species foraged in multiple habitat types but frequencies of use of each habitat differed among species. Correspondence analysis showed that feeding habitat selection divided the species into group with similar niches (freshwater or field habitat foragers). Generally, the two largest species, grey herons and great egrets, preferred freshwater habitats over rice fields. On the other hand, intermediate egrets and cattle egrets entirely depended on rice fields and grasslands. These results suggest that different species display differences in foraging habitat preferences (Ramo and Busto 1993, Dimalexis et al. 1997, Smith 1997, Wong et al. 1999). Moreover, species employing the same habitat type tend to overlap little in their time of feeding, prey size or microhabitat characteristics such as water depth and vegetation type (Fasola 1986, Dimalexis et al. 1997). In reservoirs, most feeding grey herons and great egrets were located in open-water areas and in submerged or emergent vegetation, while little egrets were generally found on the shoreline, or in shallow water not exceeding half

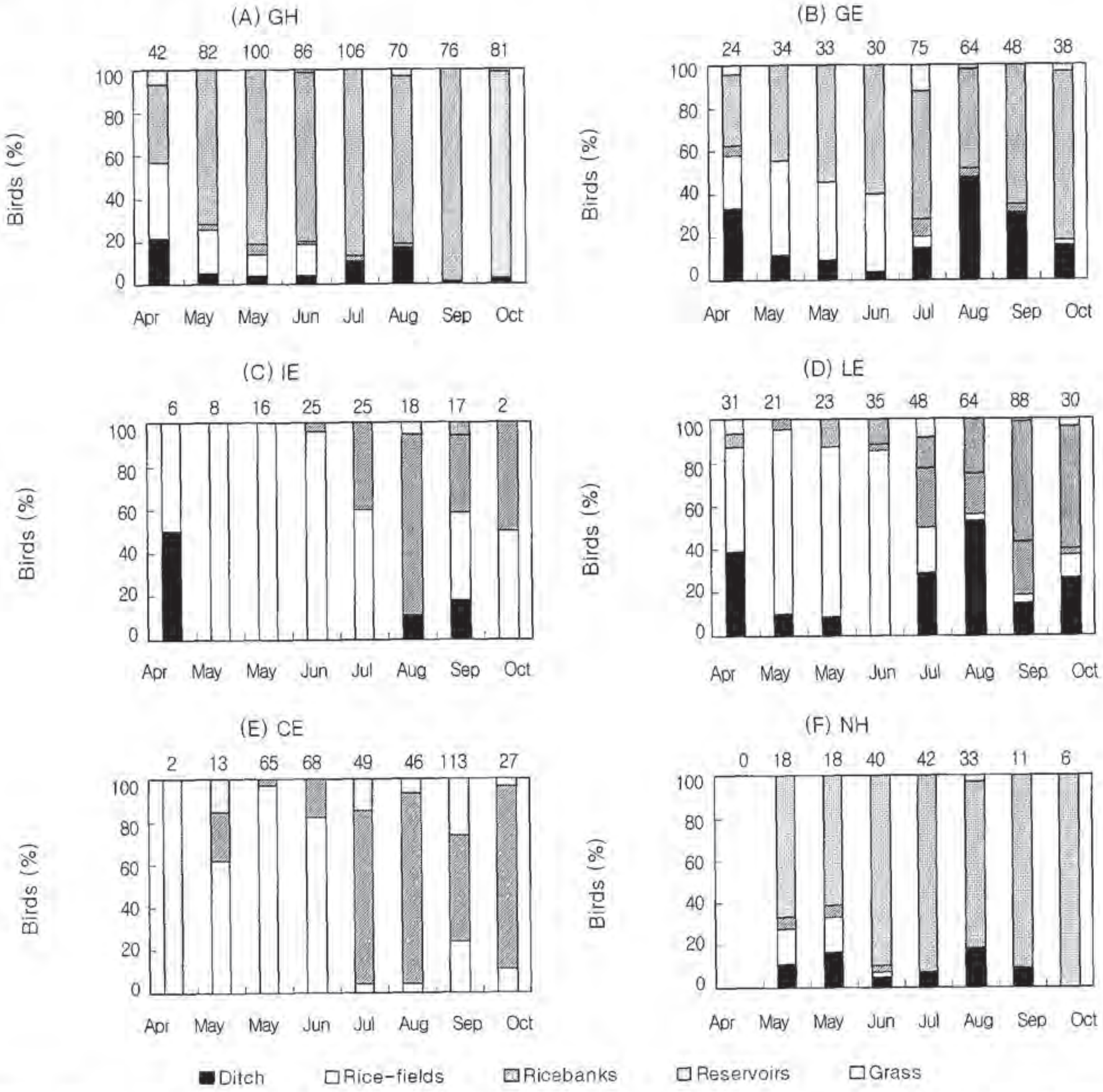

Fig. 4. Monthly changes in feeding habitat selection of grey herons (A), great egrets (B), intermediate egrets (C), little egrets (D), cattle egrets (E), and black-crowned night herons (F). Figures above bars indicate the numbers of feeding birds.

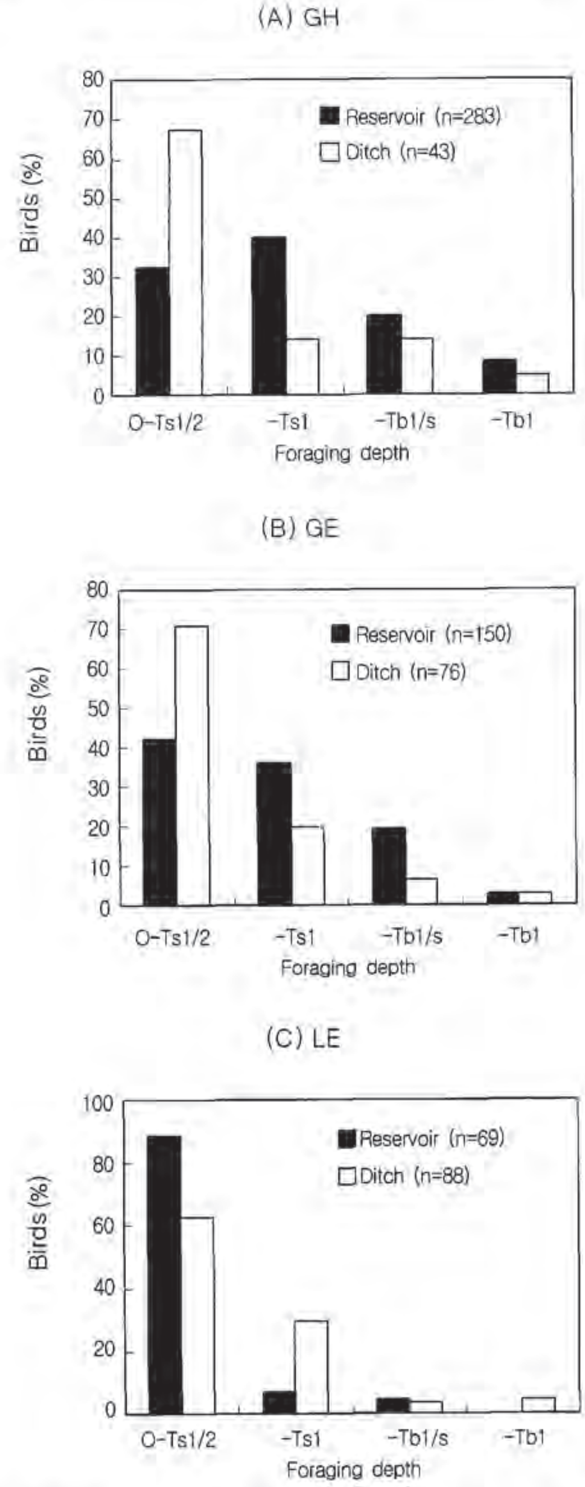

Fig. 5. Foraging water depths of grey herons (A), great egrets (B), and little egrets (C) in reservoirs and ditches.

the length of the tarsus. In addition, grey herons primarily hunted large fishes in reservoirs, whereas the great egret preyed upon somewhat smaller prey in ditches as well as reservoirs (Choi YS and Kwon IK, personal communications). Two rice-field-dependent species, intermediate and cattle egrets, also differed in their choices of prey and feeding methods (Choi YS, unpublished data). The little egret is a habitat generalist that can forage in various habitats (Hafner et al. 1986, Tojo 1996, Dimalexis et al. 1997, Wong et al. 1999). Black-crowned night herons were more often observed in reservoirs than in rice fields. However, their nocturnal and cryptic feeding habits made it difficult to determine their primary feeding habitat (Voskamp and Zoetebier 1999) and our study methods were also somewhat inadequate for this species (Lane and Fujioka 1998).

In the present study, all species displayed seasonal changes in feeding habitat use, which is related to changes in the availability of feeding habitats. Feeding in rice fields was observed more frequently in May~June for most species than from July~September. Moreover, most feeding individuals preferred rice banks (or levees) or edge areas and avoided the inner parts of rice fields from July~September. Rice fields systems showed seasonal changes in field conditions; the rice crop developed gradually, and fields transitioned from open water in April~May to densely vegetated habitat after July. It is difficult to spot prey in densely vegetated rice fields, which may encourage herons to change their feeding sites or methods (Maeda 2001, Richardson et al. 2001). In the periods when rice fields were covered with dense vegetation, rice banks provided vegetation gaps suitable for birds foraging on aquatic prey (Sato and Maruyama 1996, Maeda 2001). Also, when water levels are high, reservoirs are unavailable to some birds and foraging habitat is generally restricted to a narrow band of edge (Powell 1987, David 1994). In our study area, during the early part of the breeding season (April~early May) the water level was normally high in reservoirs and thereafter declined gradually as water was provided to rice fields. In our study, the little egret was present in the rice fields during the early part of the season, but they shifted to various other habitats, particularly reservoirs, during the later part of the season.

In conclusion, it appears likely that each heron species has avoided competition for limiting resources by selecting different habitats or microhabitats and also that they make seasonal adjustments to their habitat preferences in response to changes in the availability of feeding habitats. The present study suggested that rice fields provide valuable feeding habitats for herons and egrets. However, rice fields may not be equally suitable in all regions, as crop development and local water conditions may affect ardeid feeding efficiencies in rice fields.

## ACKNOWLEDGEMENTS

We wish to express our gratitude to Seung-Hwa Yoo and Sun-Sook Kim for field assistance. We also thank the anonymous re-

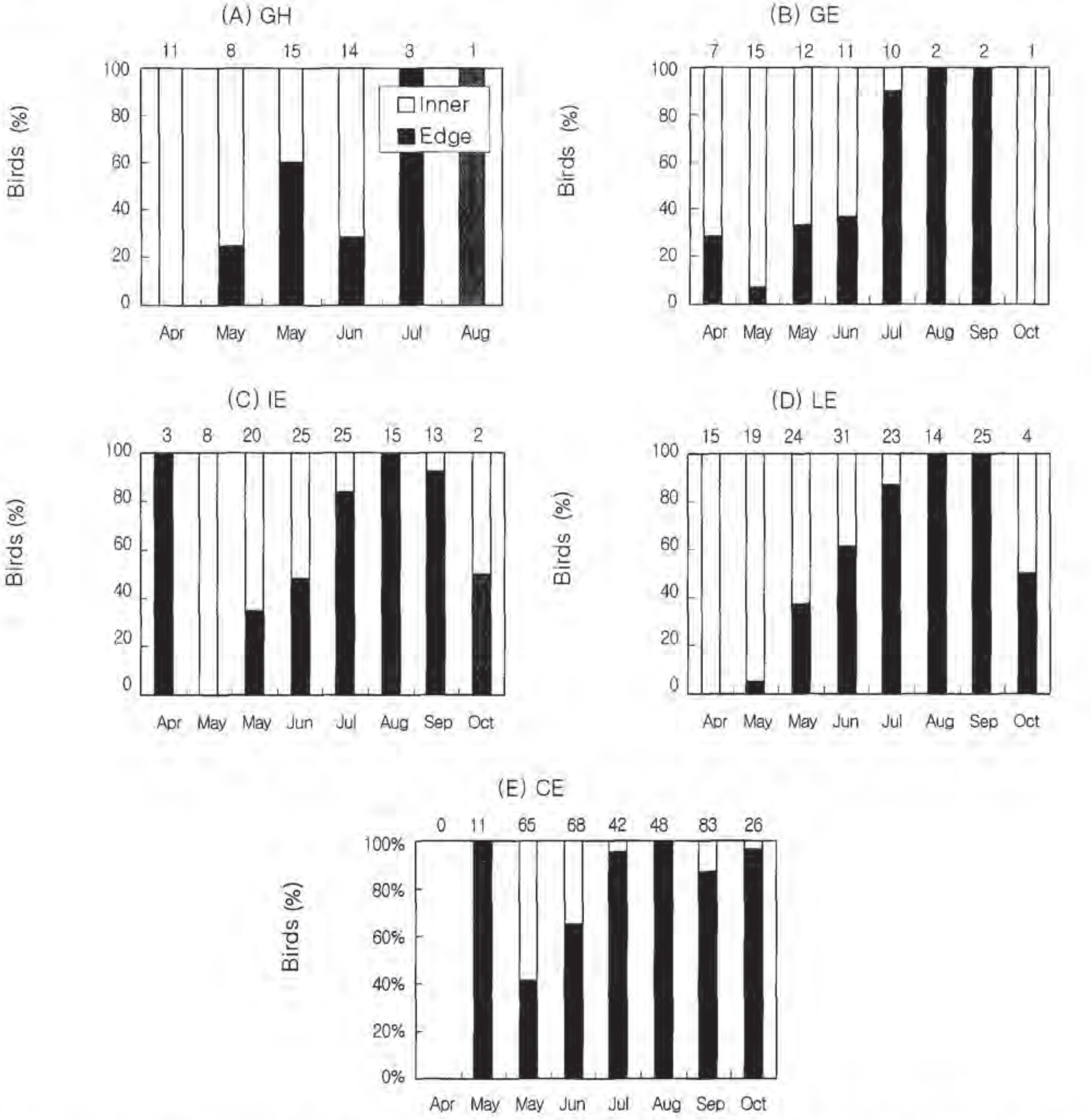

Fig. 6. Feeding site selection of herons and egrets in rice fields (interior areas vs. edges, including rice banks). GH: grey herons, GE: great egrets, IE: intermediate egrets, LE: little egrets, CE: cattle egrets. Figures above bars indicate the numbers of feeding birds.

viewers for constructive comments and also thank to Dr. Susan Lappan for English revision on the manuscript.

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*(Received May 29, 2007; Accepted July 25, 2007)*

1990

# Habitat utilization by great blue herons (Ardea herodias) in Elkhorn Slough, California

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Recommended Citation
Buchanan, Scott Charles, "Habitat utilization by great blue herons (Ardea herodias) in Elkhorn Slough, California" (1990). *Master's Theses*. 3247.
DOI: https://doi.org/10.31979/etd.7p8e-zhqq
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San Jose State University, 1990

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# HABITAT UTILIZATION BY GREAT BLUE HERONS (ARDEA HERODIAS) IN ELKHORN SLOUGH, CALIFORNIA

A Thesis
Presented to
The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment of the
Requirements for the Degree
Master of Science

by
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May, 1990

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# ABSTRACT

# HABITAT UTILIZATION BY GREAT BLUE HERONS (ARDEA HERODIAS) IN ELKHORN SLOUGH, CALIFORNIA

Scott Charles Buchanan

Observations of individual herons within Elkhorn Slough, California indicated differences in social interactions and foraging strategies within six sub-habitats. There are four primary foraging habitats. Two habitats are mainly used for loafing, preening and social interactions. I hypothesize that these social interactions may involve a hierarchy which is carried into the foraging habitats and occur primarily to increase individual foraging success. Significant differences in foraging behavior within and between habitats existed for both 1986 and 1987. Differences in foraging success and prey size were also significant. The observed foraging success reflects the primary use of each habitat. These results were consistent with the behavioral trends found in the habitats. The effects of weather and tide on foraging success were also assessed. Cloud cover significantly reduced foraging success, while wind and tidal conditions did not affect foraging success. Observations of a newly colonized rookery were made to determine numbers of nesting pairs and nesting success.

# ACKNOWLEDGEMENTS

I would like to thank Bernd Würsig, John S. Oliver, and Dan Anderson for serving on my committee. Special thanks to Marc Silberstein for his understanding and encouragement during my time in the field. Further support was provided by the David and Lucile Packard Foundation and the Monterey Chapter of the Audubon Society. I also wish to express my gratitude to my wife and family for their efforts and support. Most especially I thank Bernd Würsig for being my educator and friend.

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# INTRODUCTION

The Great Blue Heron represents an ideal subject for a habitat utilization study. Large size, standing over one meter, and relatively slow movement of this bird make it easily observable from great distances.

In this study, I examined the foraging behaviors of Great Blue Herons Ardea herodias within several distinct estuarine sub-habitats to determine if different foraging strategies and success exist within those habitats. Behavioral patterns of each sub-habitat reflects the adaptability of herons to utilize available habitats. Variations in prey, weather, and tidal conditions affect heron behavior and foraging success (Krebs 1974). These patterns and conditions give insight into the overall utilization of Elkhorn Slough by Great Blue Herons.

The question of how and why animals budget their time and utilize their space has been a central theme in behavioral ecology (Schoener 1971, Charnov 1976, Krebs 1978, Krebs et al 1981).

Although the list of references on foraging optimization is becoming extensive, a discrepancy exists between what animals ought to do in theoretical models and what animals actually do in the field (Erwin 1983, 1985). An increasing number of field studies have begun to address foraging behavior and ecology (Gill and Wolf 1975, 1978, Pyke 1978, Howell and Hartl 1980, Rudolph 1982).

Herons in estuarine habitats are faced with complex feeding situations (Richner 1986). Prey density and habitats are in constant change with the tide. These differences in density, type, distribution and quality of prey all influence what a predator eats. This becomes most interesting, and most difficult to resolve, in mobile, wide ranging animals such as large birds whose selection of prey may be expected to vary from habitat to habitat within a region (Kushlan 1979).

Several studies of feeding behavior (Jenni 1969, Recher and Recher 1969, 1972, Multon 1972, Kushlan 1972, 1976) provide an initial understanding of heron ecology. The role of habitat in determining heron foraging behavior was not addressed in these studies. Differences in prey densities, water depth, plant cover and other characteristics of foraging sites may vary, and therefore foraging behaviors and efficiency are likely to vary. These variables in habitat conditions are essential in the ecological analysis of heron behavior (Kushlan 1976).

The estuarine habitat of Elkhorn Slough is a unique system that has been altered through human disturbances, creating a number of sub-habitats. Thus, herons foraging within this system must make a variety of foraging decisions based on physical conditions, prey availability and past experiences. Once a decision to forage in a particular habitat is made, a further choice in foraging strategy is essential to maximize foraging success.

# STUDY AREA AND METHODS

## Study Area

Elkhorn Slough is a large marine estuary covering about 2,500 acres. The slough lies between Santa Cruz and Monterey, California, and empties into Monterey Bay almost directly at the head of the Monterey Submarine Canyon at Moss Landing (Figure 1). The main channel extends almost 7 km. inland and has an axial length of nearly 11 km. (Browning 1972). It averages between 100 m. wide and 5 m. deep at the mouth to roughly 15 m. wide and 1.5 m. deep near Hudson's Landing (Smith 1973).

The slough has been altered many times through human intervention since the 1880's. In 1947, Moss Landing Harbor jetties were constructed, opening the slough to direct tidal action. Recent action in 1983 and 1985 has attempted to restore marsh lands to a semi-natural state (Ken Moore and Marc Silberstein, pers. comm.). The resulting influences have created a unique and diverse environment comprised of several distinct sub-habitats determined by physical and biological parameters. Based on these

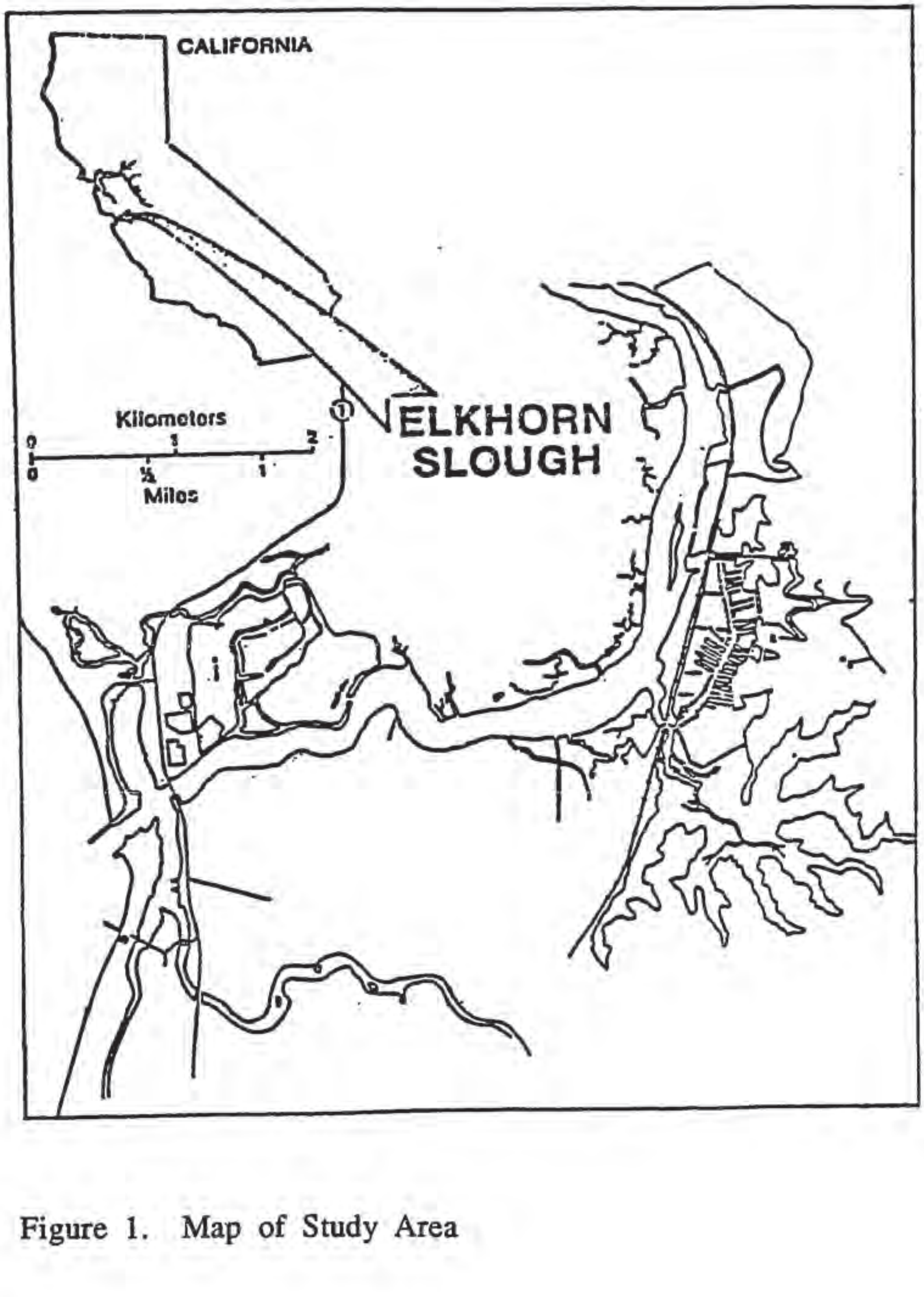


Figure 1. Map of Study Area

parameters, six sub-habitats were identified:

1) The Salicornia flats habitat is comprised of low lying pickleweed Salicornia pacifica which is entirely exposed at low tides and submerged to varying degrees at high tides. This habitat is transected by an extensive network of tidal channels. The Salicornia flats occur on both banks of the main channel and range in width between 50 - 200 m. from channel bank to upland slopes.

2) The islands habitat has been altered the most by recent human efforts to restore a wetland habitat. It is an area comprised of many man-made earthen islands and benches with varying heights and therefore varying tidal influences. Low tides expose all of the islands and benches. Extremely low tides expose mud flats in several areas, while high tides totally submerge several of the islands and benches. Sparse coverage of Salicornia and several other salt-tolerant plant species exists on the exposed areas of the islands and benches. The topography of this habitat is the most varied and has the greatest range of physical and biological factors in the six described habitats.

3) The inland shallows habitat is the shallow banked transition zone between the fluctuating water levels and the muddy shore line of the inner slough. This habitat is comprised of three distinct zones: a vegetated bank above high tide, a gradual mud sloped bank advancing at low tide and retreating at high tide, and the shallow waters of the inner most slough. This habitat is the smallest in area, yet it is found in several locations throughout the study area.

4) The restored marsh is a habitat altered through human intervention. A tide gate was built in 1984 to re-establish a low lying marsh area. A channel was cut through the low lands permitting slough waters to flood the area via the tide gate. The vegetation is dominated by patches of Salicornia which are inundated by a relatively constant depth of water only slightly influenced by tides. This habitat is expansive and is homogeneous in nature.

5) The main channel habitat is strongly influenced by tides. At high tide it is restricted to the steep mud banks typically found at the transition with the Salicornia flats. At low tides the habitat

extends from these steep eroding banks into the mud shoals and the water of the main channel. Erosion is a strong factor determining the bank condition. Fast flowing tidal waters undercut the banks and accumulate debris forming shallow mud shoals.

6) The mud flat is an expansive habitat characterized by smooth tidal channels and pools exposed at low tides. High tide inundates the area via two main channels and connecting tributaries. There is very little standing vegetation in this habitat, but algal blooms of Entromorpha sp. cover large areas sporadically through the summer and fall months.

## Methods

These habitats can be observed from several vantage points within the ESNES. From these vantage points individual birds were observed from distances of 50m to 500m, with a 20x spotting scope. Precautions were taken at close range to ensure that my presence did not alarm the observed bird. Observations closer than 100m were rare and resulted from careful stalking or, more often, a heron approaching my position. Herons were observed by the same observer between 0800 hours and 1800 hours from 16 January to 29 July, 1986 and 1 February to 1 June, 1987 for a total of 5,500 minutes. Since the entire slough is extensive and some areas are inaccessible by foot, observations were concentrated within areas observable from the ESNES. Although all observations occurred from the ESNES, several censuses indicated that at least 25-30 individual herons frequent the observed area. It was possible through variations in plumages to identify adult, immature, and fledgling birds (Bent 1926). Since foraging efficiency of juvenile herons is lower than adults (Recher and Recher 1969), only adult birds were observed for the comparison of forage and habitat use. The closely related Grey Herons of Europe were found to be territorial foragers (Cook 1978). Efforts were made to obtain data from as many different individuals as possible. This was accomplished by noting locations and movements of all visible herons. Efforts were made to observe as many of the visible herons in as many different habitats as possible.

A Great Blue Heron can capture and swallow a small fish within seconds; therefore individuals were kept under constant surveillance during 30 minute observation periods. The habitat type and depth of water (gauged by the water level on the heron's leg) were noted. Also, when foraging, estimated lengths of captured prey (using the bird's beak as a reference) and, when possible, prey species were recorded. Time of day, tidal height, cloud cover, and wind strength were noted as well as each successful and unsuccessful prey strike. Activity was noted at one minute intervals, in an attempt to determine the frequency with which different behaviors and foraging strategies were utilized. These activities were categorized into seven different foraging and non-foraging behaviors based on a list of heron behaviors published by Kushlan (1976).

Hunched Stand - Primarily a non-foraging stance commonly associated with loafing behaviors. A heron holds its head and neck in an "S" curve tight against its upright body.

Upright Stand and Wait - A position epitomized by the Great Blue Heron (Kushlan 1976). This behavior indicates an alert bird foraging or watching for other herons or possible threats. The posture is upright with head and neck fully extended away from the body. When foraging, the heron remains motionless except for quick eye and head movements.

Crouched Stand and Wait - A motionless posture characterized by the body being held roughly horizontal to the water surface or ground. The legs are bent while the neck and head are partially retracted. This stance typically occurs prior to a strike.

Walk Slowly Upright - This is a position identical to the Upright Stand and Wait except that the heron moves slowly, stalking prey. Typically less than a step a second occurs during Walk Slowly.

Walk Slowly Crouched - This position is described by Recher and Recher (1972) as a slow stalk. A heron moves slowly, normally less than a step a second, with body held low and nearly horizontal to the substrate with neck partially retracted.

Walk Quickly - A behavior characterized by a heron walking through water or ground cover catching disturbed prey or simply chasing mobile prey. This behavior is different from Walk Slowly, since the heron flushes prey rather than stalking, and the posture is less rigid. Also, a heron typically takes several steps per second.

Other behaviors noted include mainly non-foraging activities. Preening was a prevalent non-foraging behavior, as well as flights of varying distances of 10 to 200 meters. Inter-specific interactions included being chased and chasing, often covering great distances by air. Confrontation occurring on the ground often included a threatening head up and wing out posture. Intra-specific interactions occurred between herons and both Snowy Egrets Egretta thula and Great Egrets Casmerodius albus. These interactions were characterized mainly by displacement of a foraging egret or egrets by a heron. Several foraging related behaviors include hopping, described as a short jump and flight resulting in a simultaneous landing and strike at potential prey. Wing flicking is described as a quick opening flex of a single wing or both wings in an attempt to startle prey into motion and make it visible to the foraging heron (Meyerriecks 1960a:89).

# RESULTS

## ANALYSIS OF HABITATS

The percent time of observed behaviors for each habitat for 1986 and 1987 indicate general trends within and between habitats (Figures 2 and 3). The Salicornia flats and islands habitats are similar: the highest percent time of observed behaviors is the hunched stand and wait. These habitats are markedly different in the percent time in both the upright stand and wait behavior and the other behavior category. The Salicornia flats has higher time observed in the other behaviors while the islands habitat has a higher time observed in the upright stand and wait. Unlike the Salicornia flats and islands habitats, the inland shallows, main channel and Mud Flat habitats have low times in the hunched stand behavior. Similarly these three habitats have high times utilizing the upright stand and wait behavior. Also, these habitats have higher times in the crouched stand and wait and walk slowly crouched behaviors.

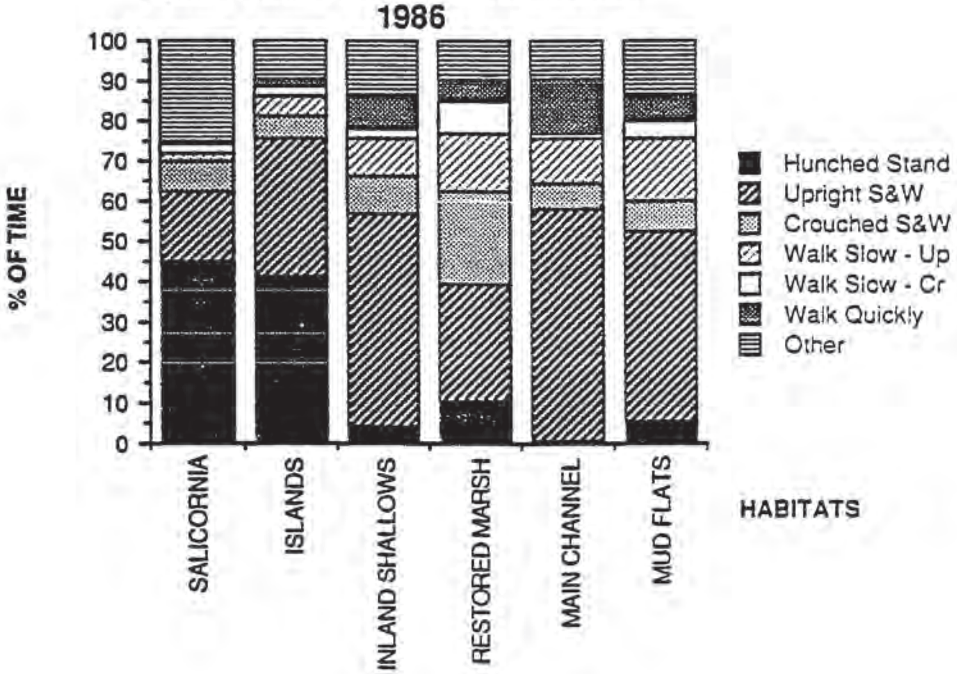
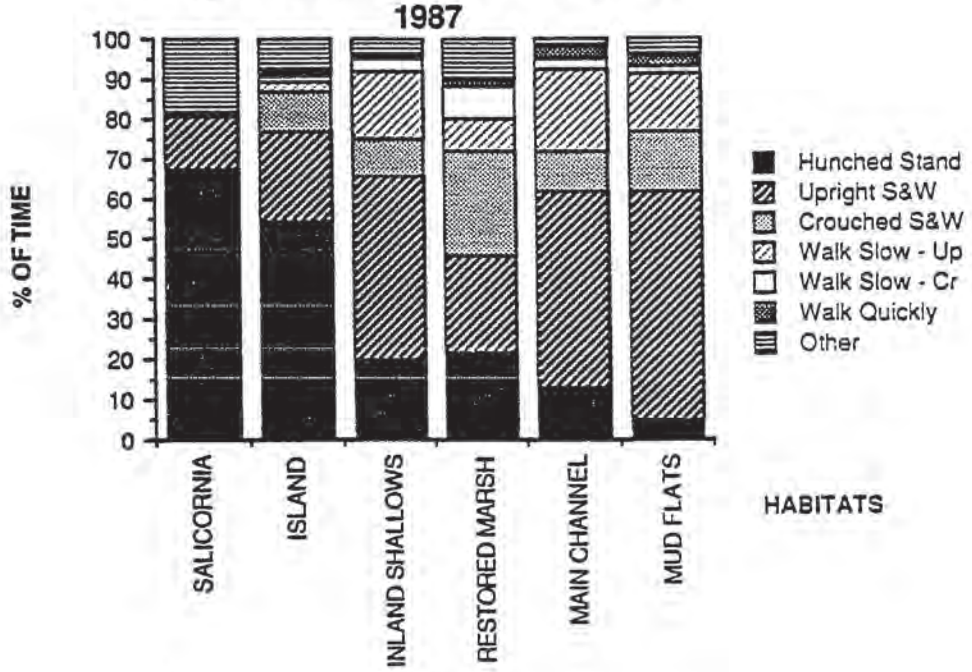


Figure 2 Percent Time of Observed Behaviors

Figure 3 Percent Time of Observed Behaviors



The most noticeably different habitat, as far as percent time of observed behaviors, is the restored marsh. The restored marsh has a high percent time in both upright stand and wait and crouched stand and wait. Also, this habitat has the highest percent time in the walk slowly crouched behavior of any habitat.

Combined data for both 1986 and 1987 were used in Anova testing to reveal significant patterns between habitats and behaviors. Four habitats -- the Salicornia flats, the islands, the restored marsh, and mud flats -- had distinct behavioral patterns within each habitat (Figure 4.). These patterns within also reveal different behavioral patterns between habitats. In general the inland shallows and main channel closely parallel the behavioral patterns of the mud flats habitat.

Behavioral patterns exist between habitats. Four behaviors -- hunched stand, upright stand and wait, crouched -- stand and wait, and walk slowly crouched reveal these differences between habitats (Figure 5). The walk quickly behavior did not have any significant patterns between habitats. The behavior "other" showed a significant difference in time observed in the Salicornia flats. All other habitats, except the islands habitat, were significantly lower in observed time of the "other" behavior.

Significant differences ($P< .05$) in foraging success and prey size exist between habitats for both 1986 and 1987 (Tables 1 - 2).

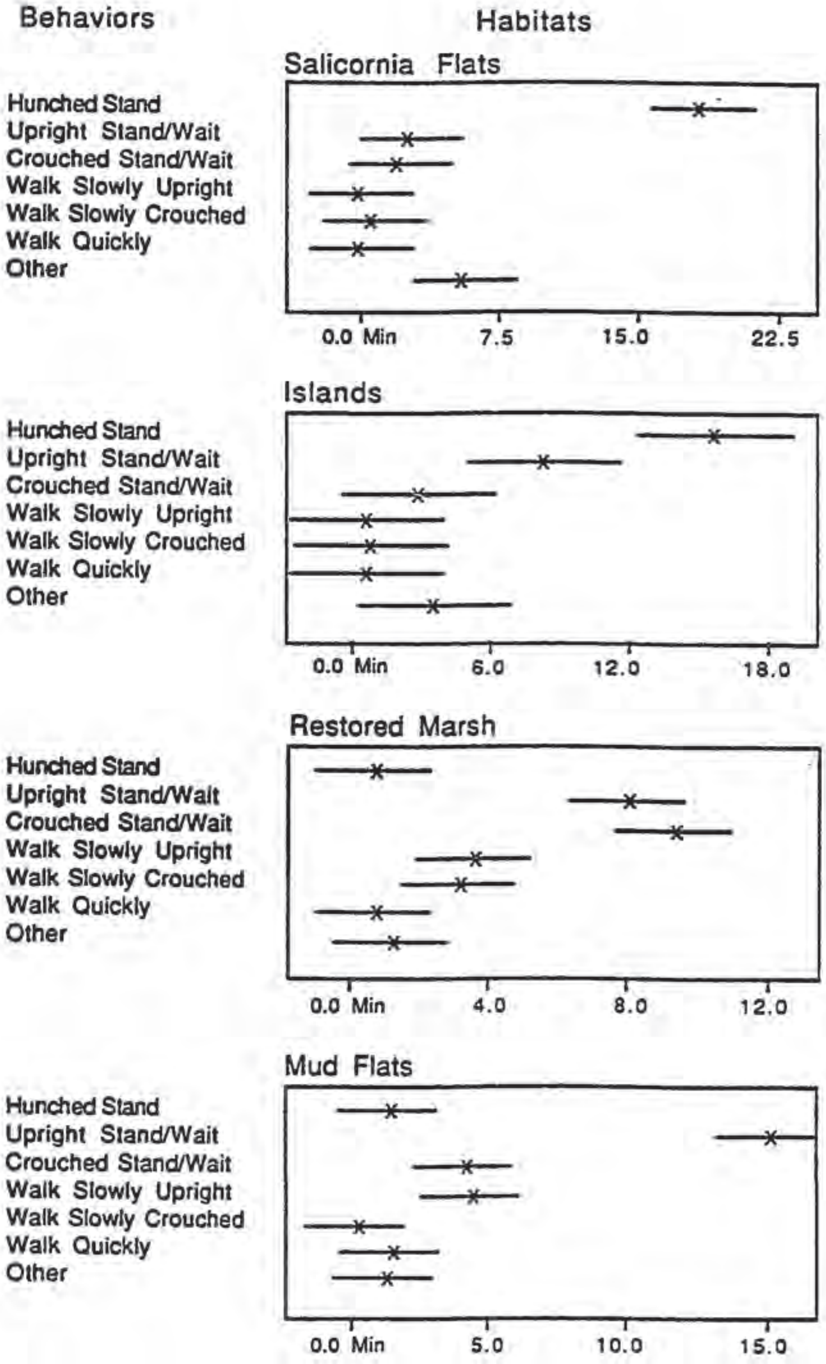


Figure 4. Comparisons of Observed Behaviors Within Each Habitat ($P < .05$ Based on pooled standard deviations).

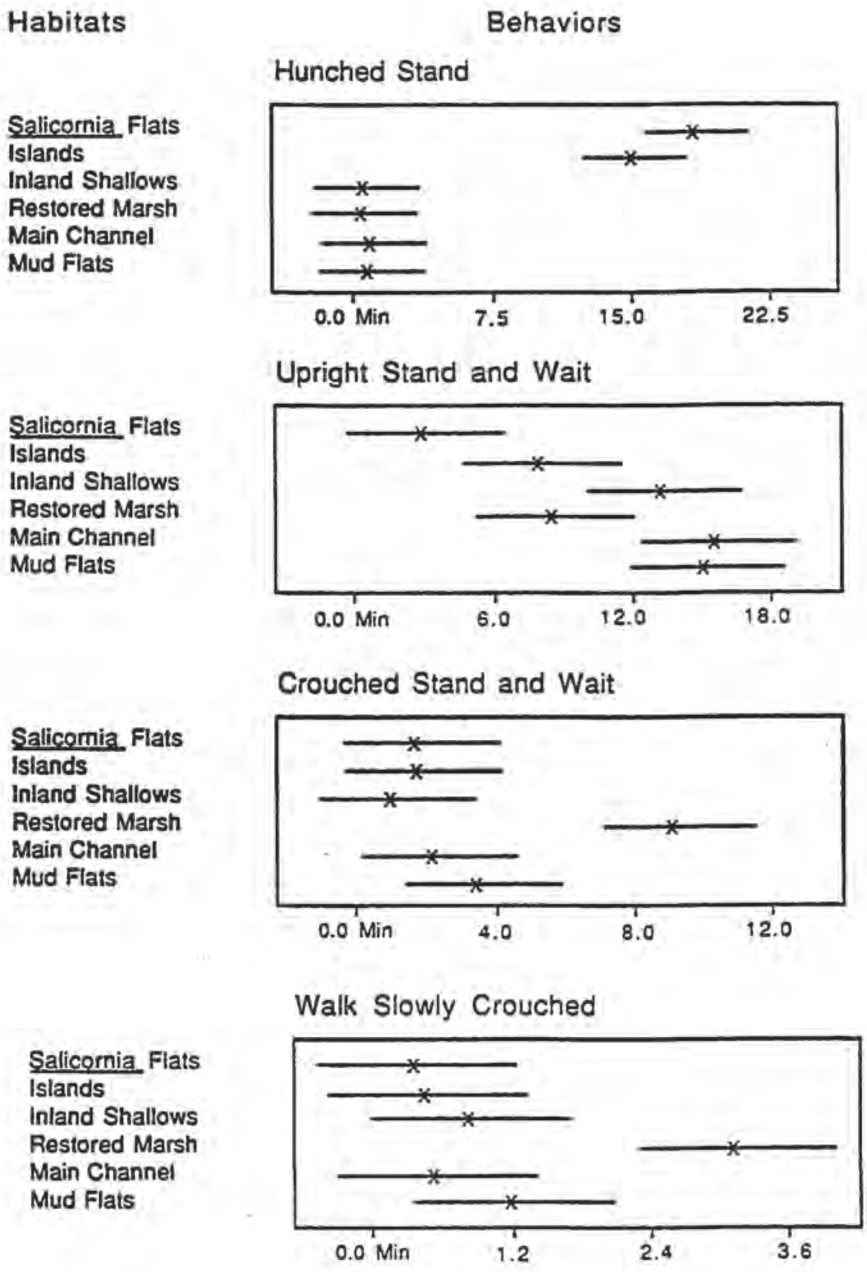


Figure 5. Comparisons of Observed Behaviors Between Habitats ($P < .05$ Based on pooled standard deviations).

Table 1 Foraging Success

| 1986 | Salicornia Flats | Islands | Inland Shallows | Restored Marsh | Main Channel | Mud Flats |
|---|---|---|---|---|---|---|
| Strikes/Minute | .02 | .08 | .11 | .30 | .13 | .17 |
| Successful Strikes/Minute | .01 | .04 | .06 | .19 | .04 | .04 |
| Percent Successful Strikes | 27 | 48 | 56 | 62 | 33 | 25 |
| Minutes Observed | 661 | 628 | 171 | 171 | 190 | 470 |
| **1987** | | | | | | |
| Strikes/Minute | | .03 | .13 | .09 | .11 | .17 |
| Successful Strikes/Minute | | .02 | .07 | .08 | .03 | .07 |
| Percent Successful Strikes | | 53 | 52 | 49 | 25 | 41 |
| Minutes Observed | 510 | 580 | 364 | 690 | 435 | 626 |

Table 2 Average Prey Length (a)

|  | HABITAT |  |  |  |  |  |
|---|---|---|---|---|---|---|
| **1986** | Salicornia Flats | Islands | Inland Shallows | Restored Marsh | Main Channel | Mud Flats |
| Total # of Prey | 3 | 23 | 18 | 32 | 8 | 20 |
| Mean Prey Length $\bar{x}$ | .33 | .68 | 0.8 | .30 | .34 | .40 |
| Standard Deviation (S) | .12 | .23 | .15 | .09 | .10 | .21 |
| **1987** |  |  |  |  |  |  |
| Total # of Prey |  | 10 | 25 | 30 | 15 | 44 |
| Mean Prey Length $\bar{x}$ |  | .48 | .41 | .36 | .38 | .39 |
| Standard Deviation (S) |  | .20 | .19 | .14 | .14 | .19 |

(a) Prey length was determined relative to Heron's bill length.

Total strikes per minute of observation in each habitat during 1986 were significantly different. The Salicornia flats habitat had the lowest strikes per minute value of any habitat. The islands habitat had a greater strikes per minute value than the Salicornia flats, yet both were lower than those of all other habitats. The restored marsh habitat had the highest strikes per minute of any habitat. The main channel habitat and mud flats had significantly lower strikes per minute than the restored marsh, yet both had greater values than the remaining habitats.

The successful strikes per minute in two habitats were different from the other habitats. The Salicornia flats had the lowest successful strikes per minute; the restored marsh had the highest successful strikes per minute. The percentage successful strikes values also indicate a significant difference between habitats. The inland shore, island levee and restored marsh habitats, although not significantly different between themselves, were significantly greater in percent successful strikes than the Salicornia flats, main channel and mud flats habitats.

Prey size for 1986 was significantly different between the habitats. The islands and inland shallows habitats had greater mean prey size compared to the remaining habitats. The inland shallows had the highest mean prey size and was significantly greater than the islands habitat (Table 2).

Significant differences (P< .05) of total strikes per minute exist between several of habitats during 1987. The major differences occur between the mud flats with the greatest strikes per minute and the Salicornia flats with the lowest strikes per minute. The mud flats are significantly greater than all habitats except for the inland shallows habitat. However, the inland shallows habitat is not significantly different from the islands, restored marsh and main channel habitats. The Salicornia flats, as in the 1986 data, are markedly lower in strikes per minute than all other habitats in 1987.

Successful strikes per minute were different between several of the habitats. The main channel had greater successful strikes per minute than all other habitats while the Salicornia flats had the lowest value. The remaining habitats have similar values. The percent successful strikes for 1987 are the same as 1986. The inland shallows, islands and restored marsh have significantly greater values than the remaining habitats. Prey size for 1987 unlike 1986 showed no significant differences between habitats.

## EFFECTS OF WEATHER ON FORAGING

Foraging success was not significantly affected by wind (Table 3). Total strikes were no more frequent when winds were calm than when winds were high (Table 3; $t = 1.65$, $t = .385$, $P < .05$). Prey size was not significantly affected by wind during 1986 (Table 4; $Z = .538$, $P < .05$), but during 1987, was significantly affected by wind ($Z = 2.30$, $P < .05$). Larger prey was more frequently caught during calm winds in 1987.

Foraging success was significantly affected by cloud cover (Table 5). Total strikes were more frequent on clear days ($t = 6.82$, $t = 4.77$, $P < .001$). Successful strikes were also more frequent during clear days ($t = 5.34$, $t = 4.03$, $P < .001$). Prey size was not significantly affected by cloud cover in either year (Table 6).

Table 3 Effects of wind on foraging success

| | Calm | Windy |
|---|---|---|
| **1986** | | |
| Strikes/Minute | .09 | .11 |
| Successful Strikes/Minute | .04 | .05 |
| Percent Successful Strikes | 43 | 43 |
| Minutes Observed | 1680 | 780 |
| **1987** | | |
| Strikes/Minute | .08 | .08 |
| Successful Strikes/Minute | .04 | .03 |
| Percent Successful Strikes | 48 | 35 |
| Minutes Observed | 1710 | 1170 |

Table 4 Effects of wind on relative prey size(a)

| | Calm | Windy |
|---|---|---|
| **1986** | | |
| Total # of prey | 58 | 27 |
| Mean prey length | .40 | .46 |
| Standard deviation | .38 | .22 |
| **1987** | | |
| Total # of prey | 74 | 46 |
| Mean prey length | .42 | .35 |
| Standard deviation | .18 | .15 |

(a) Prey length was determined relative to heron's bill length.

Table 5 The effects of cloud cover on foraging success (a)

| | Calm | Windy |
|---|---|---|
| **1986** | | |
| Strikes/Minute | .14 | .05 |
| Successful Strikes/Minute | .06 | .02 |
| Percent Successful Strikes | 43 | 33 |
| Minutes Observed | 990 | 1110 |
| **1987** | | |
| Strikes/Minute | .10 | .05 |
| Successful Strikes/Minute | .05 | .02 |
| Percent Successful Strikes | 45 | 35 |
| Minutes Observed | 1560 | 1170 |

(a) Cloud cover was determined by percentage of cloud cover over visable sky, Clear ≤ 25%, Cloudy ≥ 50%.

Table 6 Effects of cloud cover on relative prey size

**1986**

| | | Clear | Cloudy |
|---|---|---|---|
| Total # of prey | | 66 | 15 |
| Mean prey size | $\bar{x}$ | .47166 | .566 |
| Standard Deviation (S) | | .25600 | .24445 |

**1987**

| | | | |
|---|---|---|---|
| Total # of prey | | 86 | 35 |
| Mean prey size | $\bar{x}$ | .40116 | .36714 |
| Standard Deviation (S) | | .17429 | .18412 |

## EFFECTS OF TIDE ON FORAGING

Overall foraging success was not significantly affected by tidal height. Although total strikes were significantly more frequent during low tide than high tide only during 1986 (Table 7 $t = 8.12$, $P < .001$). Neither successful strikes nor prey size were significantly affected by tide during 1986 and 1987 (Table 8).

Table 7 The effects of tidal height on foraging success

| | Calm | Windy |
|---|---|---|
| **1986** | | |
| Strikes/Minute | .12 | .06 |
| Successful Strikes/Minute | .04 | .03 |
| Percent Successful Strikes | 34 | 44 |
| Minutes Observed | 977 | 562 |
| **1987** | | |
| Strikes/Minute | .10 | .09 |
| Successful Strikes/Minute | .04 | .04 |
| Percent Successful Strikes | 43 | 43 |
| Minutes Observed | 1548 | 844 |

Table 8 Effect of tidal height on relative prey size

**1986**

| | | Low | High |
|---|---|---|---|
| Total # of prey | | 50 | 11 |
| Mean prey size | $\bar{x}$ | .44 | .34 |
| Standard Deviation (S) | | .258 | .220 |

**1987**

| | | Low | High |
|---|---|---|---|
| Total # of prey | | 79 | 13 |
| Mean prey size | $\bar{x}$ | .39 | .43 |
| Standard Deviation (S) | | .180 | .167 |

# DISCUSSION

The complexity of the estuarine habitats of Elkhorn Slough provides the foraging herons with a variety of choices. As expected, the herons temporal and spatial use patterns are highly variable (Richner 1986). The main patterns drawn from the results reveal major differences between two of the six habitats. The Salicornia flats and the islands habitat both are used primarily for non foraging activities. Of the remaining four habitats all are primary foraging habitats. One of these, the restored marsh, herons utilize with the greatest range of behaviors.

The foraging success also varies from habitat to habitat. The foraging success supports and reflects the behavioral patterns of each habitat. The non foraging habitats have low values while the remaining foraging habitats have higher success rates. The foraging success of these primary foraging habitats vary and reflect the nature of the habitat as well as the availability of prey, and prey type. The prey size of each habitat does not reflect the behavioral patterns of the habitats nor does it necessarily reflect the foraging success of each habitat.

The weather patterns and tidal actions of the slough are variable yet had little influence upon foraging behavior or success. Winds presumably reduce the visibility of fish beneath a rippled surface (Bovino and Burtt 1979), yet foraging success was not reduced during 1986 and 1987. The effects of clear skies opposed to overcast skies on foraging success are contrary to expected and those observed by (Bovino and Burtt 1979). Foraging success was greater during clear skies. Tides influence all slough habitats to some extent and in turn influence the foraging behaviors of herons. Yet foraging success was not noticeably affected by tidal height.

The Salicornia flats is not a primary foraging habitat, yet is important for loafing behavior and social interactions. The dominant behavior is the hunched stand which is closely associated with loafing. Much of a loafing heron's time on the Salicornia flats is spent preening. Social behavior occurred in the form of displacement flights by one heron directed at another. Since this habitat is not a foraging area, these social interactions are only indirectly associated with territoriality at foraging habitats as described by Cook (1978) and Richner (1986). These aggressive acts occur at foraging habitats and suggest that some territoriality is present. One social interaction, the wing out behavior, was only observed in the Salicornia flats. This behavior is a direct confrontation between two herons within close proximity. This behavior frequently resulted in one bird moving away in an alert upright walk, or flying a short distance before assuming an alert upright posture. This social interaction may determine a social hierarchy among loafing herons that influences territories and dominance in foraging habitats.

An important function of the Salicornia flats may provide a staging area for early courtship and nesting. The large social gatherings of up to 12 individuals in early February of both 1986 and 1987 may have been important in restoring the nesting colony in the slough. These gatherings may provide the herons with a gauge of nesting readiness. These groups may help recruit other herons to the area and into the breeding population. It has been shown by Hafner ( ? ), Krebs (1974) and Kushlan (1977) indicate that live decoys as well as model herons attract free flying herons. In this context, the Salicornia flats, although not a primary foraging habitat, is likely important to the stability and growth of the heron population in Elkhorn Slough.

Within the islands habitat the hunched stand behavior was the most frequently observed, followed by the upright stand and wait behavior. Like the Salicornia flats, the islands habitat is not a primary foraging area. Unlike the Salicornia flats the island habitat is used as a secondary foraging area. The upright stand and wait occurred in or at water's edge along with the crouched stand and wait. These long term motionless behaviors would facilitate foraging of mobile prey. Active foraging behaviors would only serve to startle mobile prey beyond the striking range of a heron. Standing and waiting for mobile prey to move within a strike zone is the most efficient means of foraging in the islands habitat. Actual foraging time within this habitat was low, indicated by few strikes per minute, yet the herons were successful when foraging.

Herons use the variety of conditions provided by the islands habitat for loafing and foraging. The exposed islands provide a refuge for resting herons while the channels between islands provide a continuous foraging habitat, determined by the ebb and flow of tide and prey. A heron must invest a great deal of time waiting for mobile prey to move within the habitat. This would encourage herons to maintain a small territory while discouraging other herons from displacing the residing heron since little is gained in the short term. This may explain the low interactions between herons in the islands habitat reflected in the low time spent in other behaviors.

The inland shallows is the least utilized habitat. This is a result of the difficulties encountered by a foraging heron. Although the habitat is influenced by tide, a low tide does not create a more suitable foraging habitat. The shallow sloped banks and relatively deep water make foraging on either schooling or sedentary prey difficult. Herons utilized the stand and wait behavior the most, either on the mud banks or in water normally less than half a meter in depth. This behavior, as in all habitats, is a primary foraging strategy for locating moving prey. When used from shore a heron can search for moving prey in shallow water. The difficulty for the heron occurs when a prey item is identified outside the heron's immediate strike range. The walk upright is the most frequently observed active foraging behavior in the inland shallows. Yet active pursuit on shore or upon entering the water encourages escape of sedentary prey to deeper water inaccessible to the heron. The depth and turbidity of the open water in the inland shallows makes foraging on bottom dwelling sedentary prey difficult. The upright walk in open water does not provide a foraging heron with the ability to capture fleeing prey as in the shallow water habitats. This is unlike the foraging conditions in the mud flats where the upright walk is used to pursue fish in confined shallow pools. Standing and waiting in the open water of the inland shallows provides the opportunity to forage on mobile prey. This is similar to the foraging behavior in the islands habitat where herons are also foraging for mobile prey in deep water. Motionless foraging allows a heron to strike at prey within the immediate area. This is a benefit and is reflected in the high successful strikes per minute and high percentage of successful strikes. The low strikes per minute in the inland reflects the investment of time required to forage on unpredictable mobile prey. The inland shallows is not the most productive foraging as indicated by low overall foraging success and relatively low usage by herons.

The restored marsh is an important foraging habitat for the herons of Elkhorn Slough. The restored marsh provides a rich foraging habitat as revealed by the highest strikes per minute and highest successful strikes per minute of any habitat. This foraging success suggests that the herons are effectively utilizing this habitat to meet the demands of nesting.

The foraging methods used by herons in the restored marsh are markedly different than in other habitats. The upright stand and wait is the most often observed behavior, as in the other foraging habitats, yet it is often replaced by the crouched stand and wait behavior in the restored marsh habitat. The increase in the crouched stand and wait is related to this unique habitat.

Unlike the other foraging habitats, the restored marsh has submerged vegetation, namely Salicornia, that provides ample cover for fish. Along with an increase in the crouched stand and wait there is an increase in the walk slowly crouched behavior. These crouched behaviors would allow herons to seek out prey in the submerged vegetation and strike quickly at prey as it escapes into cover. The crouched behaviors allow rapid strikes since little time is lost crouching down from an upright stance into the striking stance. The total strikes per minute indicate high foraging activity while the high rate of successful strikes per minute reveal the advantages of foraging in the crouched position in this habitat. The observed walk slowly upright behavior often followed periods of active foraging and seems primarily used in locating new undisturbed patches of prey.

The time spent in the "other" behavior category indicates that interactions between foraging herons in the restored marsh did occur. Although the habitat is large and seemingly can support a number of herons, intraspecific competition limits the number of herons that can successfully forage. Of the observed interactions, most involved direct encounters and aerial chases. The relative stability of this habitat and its foraging advantages encourage herons to defend a foraging area. The duration a heron maintains a foraging area is determined by the amount of habitat switching that occurs. Although the foraging success is high in the restored marsh, the relative prey size was the smallest of any habitat; thus it may be most efficient to switch and forage in other habitats during advantageous tides or seasonal changes in prey populations. Richner (1986) found that herons switching between two different foraging habitats achieved a significantly higher food intake than birds that used only one habitat.

The restored marsh habitat is the most unique foraging habitat. Although the shallow channels and standing water would support similar prey as the mud flats the foraging strategies is markedly different. The lack of open waters may restrict large fish from utilizing this habitat. This is reflected in the small prey size captured by the herons.

The mud flats and main channel are utilized in similar ways by foraging herons. At first glance these two habitats appear nothing alike: the main channel with water flowing from bank to bank, the mudflats with a large expanse of shallow standing water. The link between these two habitats is the effect of tide that alters and provides similar foraging habitats for herons. The main channel is an ideal habitat for schooling prey, yet the herons are forced by the tide to forage along the steep mud banks, shallow shoals and small channels suited for sedentary prey. The mud flats are inaccessible at high tides, yet provide shallow pools, channels and flats during low tide. The habitat is ideal for sedentary prey and like the main channel has a long renewal time, restricting herons to forage only during falling and low tides.

The mud flats habitat is continually flooded and drained by the tides. This changing habitat is dominated by Goby species and Sculpin species. Therefore, herons utilize this shallow water habitat to forage on burrowing and sedentary prey.

While the herons' foraging behaviors differ between sub-habitats many of the similarities of the sub habitats can be explained by different prey compositions throughout the slough habitat. Fish composition varies between the main slough and tidal creeks, as well as intertidal areas that are occasionally completely drained (Barry 1983). Therefore, it is likely that both behavior specialties displayed by foraging herons and type of habitat lead to differences in prey taken (Willard 1977). The islands, and inland shallows habitats are similar habitats for prey species. Both have deep water channels and are connected distantly to the main channel. These habitats seem more suitable for schooling prey, such as Topsmelt Atherinops affinis, Northern Anchovy Engraulis mordax and Pacific Herring Clupea pallasii.

The main channel, although similar to the deep water inland habitats, has greater prey diversity due to its larger expanse, and thus greater spatial heterogeneity. These factors, coupled with the stable ocean characteristics, host a less restricted fish fauna than inland channels (Barry 1983). These three habitats may support similar prey species which is reflected in the similar foraging behavior and success of herons. Unlike the islands and inland shallows, the main channel is also similar to the mud flats as falling tides expose mud shoals. Therefore, foraging strategies similar to the mud flats are also present.

Winds presumably reduce the visibility of fish beneath a rippled surface (Bovino and Burtt 1979), yet foraging success was not reduced during 1986 and 1987. Presumably, visibility of prey when wind rippled water surfaces and water turbidity exist would greatly reduce the foraging success of herons in certain habitats. These results are contrary to the Bovino and Burtt (1979) study in which foraging success was markedly affected by wind. Why? Are fish more active near the surface on windy days, allowing herons to capture prey near the surface rather than below the surface? On windless days fish may be less active. If so, this may partially explain why larger fish were caught on windless days during 1987. Larger fish would be more likely seen under the surface, compared to smaller fish. An observed behavior that directly reduces the effects of wind was the use of natural wind breaks by foraging herons. By foraging on the lee side of levees and islands, herons were able to forage in relatively calm water, thus increasing their chance of visually locating prey beneath the surface. Perhaps the most likely reason wind did not have an effect on foraging success is the inability to isolate and observe a single element from the ever changing habitat of a foraging heron.

The effects of clear skies opposed to overcast skies on foraging success are contrary to expected and those observed by (Bovino and Burtt 1979). Sunny days can reduce the herons' ability to see prey below on near the water surface. Occasionally herons attempt to reduce glare off the water by tilting their head and neck to varying angles (Krebs and Patridge 1973). This behavior was noticed most frequently when herons were in the crouched stand and wait, and walk slowly crouched behaviors. Furthermore, the dark coloring of a Great Blue Heron is more conspicuous against a clear sky than that of a light colored bird. Yet, the observed herons had a greater foraging success during clear skies. Possibilities of heightened fish activity or attractiveness towards shadows by fish as described by Meyerriecks (1962) may explain the foraging success of the herons on clear days. The adaptive nature, varied habitats, and physical factors affecting heron foraging make it difficult to isolate a single element to determine its effect on foraging.

On rainy days foraging was rarely observed in any habitats. Herons were observed loafing in the Salicornia flats or in the hunched stance in the other habitats. Rain directly affects herons' ability to forage in the disturbed water surface. On four different occasions, herons were observed stalking on the grassy fields during rain showers. Several of these herons were observed pursuing vocalizing frogs. Although successful strikes were not observed, this foraging behavior is an example of the adaptability of herons to maximize their foraging in adverse conditions.

Tides influence all slough habitats to some extent and in turn influence the foraging behavior of herons. The tidal influences were documented during 1986 in which total strikes were more frequent during low tide. Tidal heights are not consistent throughout the slough; lag times between the main channel, and the mud flats and inland shallows are variable in time and duration. Thus, herons move out of habitats inundated by incoming tides to habitats not yet affected by the changing tide. Herons also utilized the restored marsh habitat that is not greatly affected by tides.

# SUMMARY

The herons of Elkhorn Slough are utilizing different foraging strategies within the sub-habitats to maximize foraging success. Therefore, the choice to forage in a particular habitat in this complex system affects both foraging success and size of prey captured. Weather played a small role in affecting foraging strategy and success. Tidal influences affect foraging directly by altering several sub-habitats to the point of being inaccessible at high tide. Herons are well adapted to make decisions about a variety of habitats, physical factors and appropriate behaviors to successfully utilize the available prey.

# LIFE HISTORY

## INTRODUCTION

I examined the renewed nesting of Great Blue Herons within the Elkhorn Slough National Estuarine Sanctuary (ESNES) to determine the success of nesting and possible factors contributing to recurrence of nesting. Nesting has occurred sporadically in several areas within the slough in recent times; it has been roughly 30 years since the currents site was an active rookery.

## METHODS

Regular counts were made of Great Blue Herons on the newly established colony before and during the breeding season which occurs from mid February to July. The proportions of adult to second year birds at the colony were observed during the breeding season to determine the number of breeding individuals. The height and inaccessibility of nesting trees made nest counts from the ground difficult and breeding states hard to determine. Although all the active nests were not visible, observation of nesting herons did provide information about nest building, incubation and first hatching, estimates of chick age, clutch size and approximate numbers of fledglings.

## RESULTS

### Pre-breeding Behavior

Relatively few Great Blue Herons occupied the sanctuary through the winter. Foraging occurred over the entire Elkhorn Slough habitat during this season. During January of 1986 and 1987 the numbers of birds remained low and no intraspecific behavior was observed. On February 2, 1986 and February 2, 1987, groups of herons were first observed loafing and interacting in the Southern Salicornia flats. Numbers of herons increased during February and as many as 12 individuals were observed loafing in loose groups. Along with the increasing number of herons, an increase of threat displays and inflight chases occurred. These aggressive behaviors were most frequently observed among the groups of herons loafing in the Salicornia flats. Aggressive behavior also occurred in other habitats among individuals.

## Nesting Behavior

Prior to 1986, only one pair of herons were reported nesting in Elkhorn Slough in 1985. As this study began there was no evidence to indicate nesting would occur in 1986. Likely nesting sites were frequently observed in the beginning of this study. A small grove of Monterey Pines (Pinus radiata) toward the North end of the sanctuary received attention since it was the location of the 1985 sighting. Also, this location was discovered to have been the site of a previous nesting colony of herons in the 1950's.

On February 27, 1986 and February 9, 1987 a group of herons were first observed roosting in the Monterey Pine grove. During the rest of February and early March, courtship behavior was observed. Pair formation and associated behaviors and vocalizations, as described by Cottrille and Cottrille (1958) occurred. Sudden flights, described by Cottrille and Cottrille

(1958) and Pratt (1970), by as many as 27 individuals occurred several times during the early stages of pair formation courtship.

Stick carrying is a behavior associated with pair bonding, copulation and nest construction (Ives 1972). Herons carried sticks from the canopy of an adjacent Eucalyptus grove to the nest sites through late February and March. Short circle flights associated with establishing nest territory and pre-copulatory behavior (Mock 1976) occurred during March of 1986 and 1987. On March 11, 1986, the first nests were located within the canopy of the pines. A total of 10 nests were counted on July 13, 1986. The following year on March 16 a total of 12 nests were counted. The nests were 30-40 meters above the ground and roughly a half meter in diameter of loosely stacked branches. During the early stages of pair formation and nest construction activity increased at the rookery, and among the groups of herons on the Salicornia flats.

## Incubation and Brooding of Young

The first indication of incubation during 1986 was on March

13. Incubation duties are performed by both sexes for 28 days. Further indications of incubating herons occurred on March 18 as 8 birds were startled from nest sites at the sound of a gun shot. These birds circled the nest sites and quickly returned. Egg laying and incubation took place from late March through the middle of April. Few short circling flights and little stick carrying behavior occurred in early April.

On April 16 fragments from four recently hatched eggs were found below the nest sites, and chick vocalizations from two were heard on this day. Also, at least five other herons continued incubating or brooding.

Depending on weather conditions, brooding of hatchlings is nearly continuous until they reach 2 weeks of age. At this age the attending adult was often at nests edge, preening and waiting for its mate to return from foraging. On June 4, one nest contained four 7-8 week olds, a second contained two 4 week olds while a third contained three 4 week old chicks. During this time both adults were frequently away from the nests for extended periods of time. On June 6, two nestlings perched in branches above a nest site while two fledglings loafed in the island levee habitat. From early June through early August fledglings left the nest site to forage in the nearby mud flats and island levee habitats. Begging vocalization was heard at the nest site as late as July 23. During the fledgling period, increased interaction among herons at all habitats occurred. Many of the interactions by adults were aggressive flights and threats directed at the fledged individuals.

The first indication of incubation during 1987 occurred on March 9 when eight herons were observed on nests. On March 15, a total of thirty-two herons roosted in the rookery, again eight herons were seen incubating. The following day 15 herons were roosting in the rookery. On March 19, 12 nests were counted from directly below the rookery. The number of birds at the nesting site remained high through the middle of April. During this time many birds flew in to relieve their mates from incubation duties. Often these exchanges caused a great deal of disturbance of the rookery as mates vocalized and neighboring herons defended their nest site. On April 23, two 2 week old chicks were heard and seen at a nest while seven herons continued to incubate.

Exchanges of mates at the nest site increased during the end of April. On April 30, chicks were heard vocalizing from several nests. On May 7, three 2-3 week old chicks crouched low in a nest while the attending heron shaded them with extended wings. A single one week old chick vocalized from a nest. Observations of eight nests during May revealed 2-3 chicks of varying ages in six nests. Two nests were occupied by an attending heron. During the end of May the first fledged birds began perching away from the nests, trying their wings. On May 28 three nests contained nine 6-7 week old herons. June through August fledged birds foraged in the mud flats, island levee and inland shores while many returned to the rookery to roost.

## DISCUSSION

The return of a nesting colony in 1986 is partially due to the creation of the restored marsh. Studies on the factors affecting the distribution of heronries (Gibbs 1987, Fasola and Barbieri 1978) and the development or creation of breeding populations (Hafner, Walmsley 1975) conclude: location depends on the availability and size of suitable natural wet habitats, while the spacing between heronries is determined by the reduction of intraspecific competition on foraging grounds. Since the closest heronry is along the Watsonville River, there appears to be little competition with the colony at the slough. Therefore, it is likely that the newly developed rookery is due to the increased availability of a good, stable foraging habitat.

The nesting behavior during 1986 and 1987 was consistent with behaviors described by Cotrille and Cotrille (1985), Ives (1972) and others. Of the 10 nests observable in 1986, five nests revealed clutches of varying size. Two nests contained 3 nestlings while the remaining nests had 2 and 4 nestlings each. Obstruction by the tree canopy, concealment by attending adults, and varying states of activity of chicks at the observable nests are the major problems with obtaining accurate counts from the ground. Since all the nests were not observed, only estimates of clutch sizes can be made for the colony. To obtain a rough figure on number of eggs laid and fledgling success data was used from a well studied colony at Audubon Canyon Ranch, Bolinas, California. During a 13 year study by Pratt and Winkler (1985) the mean clutch size at this northern California colony ranged between 2.72 and 3.35 eggs, with an overall mean of 2.87. Using these figures, an estimated 30 eggs were laid at the Elkhorn Slough colony during 1986. The overall mean number of fledglings produced at the Bolinas colony was 1.45, with annual means ranging from .89 to 2.38 fledglings (Pratt and Winkler 1985). Total counts of fledglings range between 6-10 based on direct observations at the nest sites and at foraging area. Although relatively few fledglings were observed, the numbers of fledglings observed at the Elkhorn Slough Colony fall within the low end of the annual means found at the Bolinas Colony by Pratt and Winkler (1985). Thus, a low fledgling success and the dispersal of young from the nest site to area outside the study area would explain the low fledgling numbers.

During 1987, a total of 12 nests were observed from directly below the nest sites. Eight nests observed from vantage points nearby revealed clutchs of 2 to 3 chicks per nest. Estimates of clutch size from the remaining nests were estimated by vocalizations, especially pronounced on the return of adults to the individual nests. Using the Pratt and Winkler (1985) figures of mean clutch size, the estimated number of eggs laid in 1987 was 36. The estimated number of fledglings using the Pratt and Winkler (1985) figures range between 11 and 29. Observations of fledgling numbers at the nest site and foraging ground indicated the number of birds fledged per nest fall near the low end of the range.

There are no clear reasons to explain the low nesting productivity during 1986 and 1987. There was no evidence of predation at the nest site by either aerial or climbing predators. Crows, a common threat, were not seen at the nesting colony. A nearby pair of nesting Red-tailed Hawks Buteo jamaicensis, were observed harassing herons flying into the colony on several occasions. There was no indication of predation by the hawks on adults or chicks at the colony. Nocturnal predators were present. Both Great Horned Owls, Bubo verginianus, and raccoons Procyon lator, are notorious predators of chicks and eggs, yet no indications of predation were present in the observed nests nor underneath the rookery. Although the effects of continued predation can devastate colonies (Pratt 1985, Hjertaas 1982) the effects vary from year to year. Herons are more likely to lose chicks to starvation rather than predation. The only evidence of predation was an adult heron found 500 meters from the nest sites on February 20, 1986 with puncture wounds to the head and bill.

Direct losses to nestling occurred during a wind storm on June 6, 1986 where three 4 week old chicks were displaced from their nest. Of these chicks, one survived and was rehabilitated at the Monterey County Society for the Prevention of Cruelty to Animals.

Estimates of nesting mortality are in excess of 40 per cent (Millers 1943). Pratt (1970) found that 45 per cent of nestlings known to have hatched died, with most deaths occurring before 4 weeks of age. Competition for food both by foraging herons and by chicks at the nest has the highest impact on mortality. Although competition at foraging sites did occur, displaced birds returned to forage within a short distance and time. Little travel time is required to reach extensive foraging areas from the colony.

Therefore, nestling mortality occurred due to normal competition among nestlings rather than excessive competition by adults or poor foraging conditions.

The rapid growth of the colony, from a nesting pair in 1985 to 17 active nests in 1987 was unexpected. Similar growth of breeding populations have been found in the Grey Heron populations in Camargue, France. Between 1968 and 1971 a colony grew from 3 breeding pairs to 25 pairs (Walmsley 1975). Although there is additional space available for nesting pairs, as evidence by three unused nests in 1987, further growth of the heronry is limited to expansion to several pine trees adjoining the main rookery.

Aerial photographs of the rookery during May of 1987 reveal 17 active nests and 3 apparently inactive nests (Figures 5 - 6). Of the 17 active nests, 13 were occupied by adult herons. The three inactive nests appear unused, lacking the characteristic white wash of guano unique to the occupied nests.

These nests are of the previous year or previously abandoned nests from the current nesting year. Ground observations from directly below the colony gave an estimate of 12 nests during 1987 while only 7 nests were clearly observed from ground points around the colony.

Figure 6. Map of Nesting Colony From Aerial Photograph

Side View

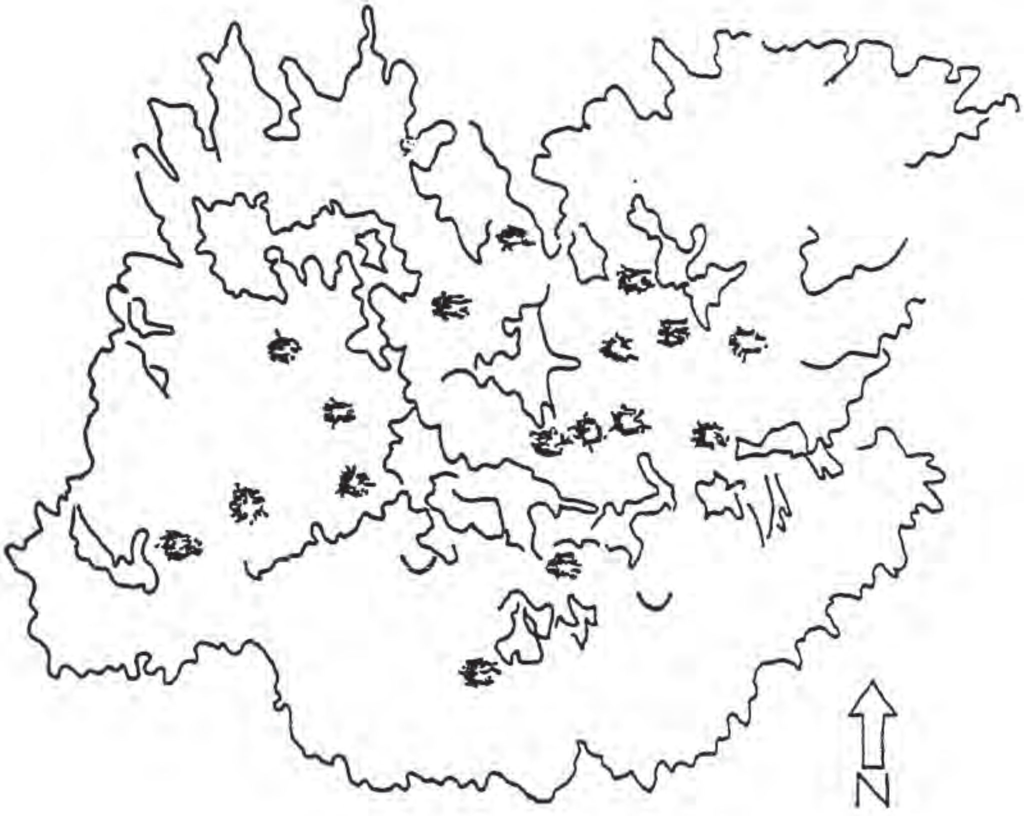


Figure 7. Map of Nesting Colony From Aerial Photograph

Top View

There are discrepancies between what can be observed from ground and what is actually present in a colony nesting in a dense tree canopy. Nests located on the top of the canopy and among heavy branches can easily be concealed from view. Therefore, aerial photographs become an indispensable tool in determining numbers of colonial nesters. Another benefit of aerial photography, as a means of determining nesting numbers, is the relatively low disturbance to the nesting colony. A low flying aircraft alarms nesting herons less than noises originating from ground level (personal observation). Disturbance of a nesting colony must be considered, especially in the early stages of nesting where herons are more apt to abandon nest sites (Henny 1978). Although aerial photography may reveal a great deal about a nesting colony, it may not be feasible and cannot replace careful day to day observations from ground.

## SUMMARY

Foraging decisions become crucial during the nesting season when food is in demand and time limited. The renewed nesting is a promising sign that man-made attempts to restore habitats can be successful. The variety of habitats along with newly expanded foraging habitats have played an important role in the re-establishment of the nesting colony. Although ground observations of the colony limit data on nesting success, all indications from the colony are favorable for its future success.

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# APPENDIX I

A summary of Great Blue Heron behavior that is not covered in the main body of this paper provides a basis for an understanding and additional references on this species. There are several studies that detail breeding biology, and the factors affecting breeding success such as predation and human disturbances. Also, the colonial nesting of Great Blue Herons have inspired studies that reveal social aspects and benefits of this behavior such as increased foraging success.

The breeding biology of colonial nesting Great Blue Herons has been studied extensively by a number of researchers at many different locations (Pratt and Winkler 1985, Werschkul 1977, Henny and Bethers 1971, Vermeer 1969). Behavior was documented in an early study of a colony in Michigan (Cottrile and Cottrile 1958). Courtship typically involves pair bonding, presentation of nest material, erection of plumes and crest, clapping bills and mutual preening. The nest is described as a flat and flimsy platform constructed during the first year or a previous year's nest added to and repaired. Herons prefer nest sites well off the ground, in trees, although man made structures have been utilized. When trees are not available for nesting, herons will often nest in low bushes. Copulation occurs within two weeks of pair bonding and nest building.

Breeding season is progressively delayed as herons breed further north (Pratt 1970, Vermeer 1969). The season is variable for a specific area as well, with weather the determining factor (Pratt 1970). A study of a colony at Audubon Canyon Ranch, Marin County, California (Pratt and Winkler 1985) gives an estimate of the breeding season in Central California. The breeding season begins in mid February when nest sites become occupied. Copulation occurs in late February to early March. Egg laying proceeds throughout March and late clutches may occur as late as July. The incubation period between the last egg laid and the hatching of all eggs is approximately 28 days. After 7 to 8 weeks of age the young are fledged and begin taking short flights. Parental care continues for another few weeks, but by September the majority of fledglings have dispersed.

Breeding success is well documented by Pratt (1974). The overall mean clutch size at Audubon Canyon Ranch is roughly 3 eggs. The most productive size, meaning the clutch size leading to the highest fledgling success is 4 eggs, while the most frequent clutch size is 3 eggs. At higher latitudes there is an increase in the mean clutch size. This is an adaptive strategy of birds to insure breeding success in less favorable environmental conditions.

Vermeer (1969) estimated a mean clutch size of ~5 eggs (N = 11) in Alberta, Canada, while Mc Aloney (1973) estimated a mean clutch of ~4 eggs (N = 36) in Nova Scotia, Canada. The overall mean number of fledglings produced per nest also follows this latitudinal trend.

Further studies have involved the ecological factors affecting breeding success. Predation, human disturbances and the presence of organochloride residues are the major factors. Predation, by raccoons for example, can have devastating effects on colonial nesters (Pratt 1985). Other predators include Ravens, Great Horned Owls, Bald Eagles and Golden Eagles. Simon and

Kelshall (1978) witnessed raids on nests by Ravens taking both eggs and young. They also found that Golden Eagles attack young, and at times even kill adults.

Grubb (1978) investigated the effects of increased noise levels on nesting birds and found a level of desensitivity by the herons. The sensitivity of nesting herons and wild flights by the entire colony are reported to cause reduced reproductive success (Bent 1926, Palmer 1976). Simpson and Kelshall (1978) compared the breeding behavior of an undisturbed versus a disturbed colony near a residential construction site. A greater number of active nests were abandoned (11) in disturbed than undisturbed colonies (1). Relocated nests and chick mortality also occurred more often at the disturbed colony. Interestingly, those adults that persevered in the presence of the disturbance were equally successful at raising young as those adults undisturbed.

Pollutants adversely affect breeding success, especially organochlorides which accumulate in fish eating birds. Lower reproductive rates are directly associated with increased contamination. Both egg shell thickness and levels of DDE, dieldrin and PCB's within eggs have been analyzed in several locations in the United States and Canada (Vermeer and Reynolds 1970, Laporte 1982). Cooke et al (1976) provide additional information on pollution impact on Grey Herons, Ardea cinerea, in Great Britain.

A number of studies have addressed the reasons for colonial nesting. Nesting facilitation and anti predator mechanisms were suggested (Krebs 1973), as well as a strategy for exploiting food resources through "information centers" (Fisher 1954). The timing of departures from colonies by individuals and feeding behavior were recorded by Krebs (1973) and Pratt (1974). Krebs (1974) observed a "parasitic" association between herons leaving colonies and neighboring birds following them. Pratt (1974) observed that herons leaving the colony behaved independently. Tidal height and number of herons departing from a colony has also been correlated (Krebs 1974), however, and it is possible that apparent independence of behavior is often influenced by common external factors.

Further studies focus on feeding behaviors such as prey species taken, handling time of prey and ecological overlap among herons. Myerriecks (1961) reported the existence of specialized foraging techniques as the major factor allowing the variety of herons species to coexist. Hom (1983) concluded that the large size of the Great Blue Heron and its particular foraging technique are adaptive for capturing large fish. Co-occurring species such as Snowy Egret, *Egretta thula*, and the Great Egret, *Casmerodius albus*, are restricted to capturing smaller prey items; thus little overlap occurs between Great Blue Herons and Egret species. In general though, few long term studies on competitive relationships and feeding ecology have been completed.

Local

# Hard To Swallow: Great Blue Herons Eating Gophers In Golden Gate Park

**Walter Thompson, Hoodline**

Updated: June 24, 2016 12:53 p.m.

Great Blue Herons are eating gophers in Golden Gate Park.
Walter Thompson/ Hoodline

*Hoodline is an online news publication that covers the issues, people, community organizations and local businesses that make up San Francisco neighborhoods. The following article is by Walter Thompson and was first published on June 23, 2016.*

The gophers of Golden Gate Park spend most of their lives below ground, but as soon as they emerge, they're a potential meal for coyotes, great horned owls and other raptors. However, many park visitors have been astonished to learn that these furry critters have another mortal enemy: the great blue heron.

According to Victoria Heyse, a waterbird biologist at The San Francisco Bay Bird

Observatory (SFBBO), there's a heron colony in Golden Gate Park that hosts five nests. Given the chance, every resident could make a meal of a pocket gopher, which can weigh up to 8.5 ounces.

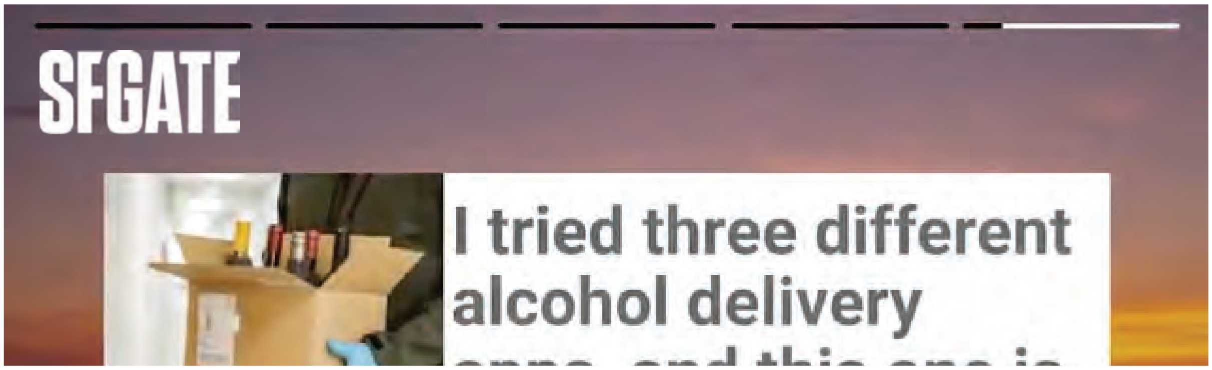
**Elliot**
@Loh

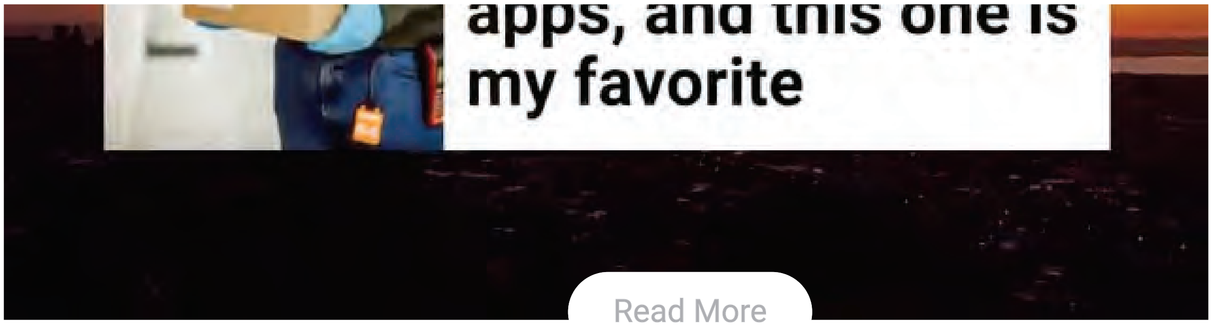
@coolbiRdpics yesterday in Golden Gate Park, San Francisco

6:41 PM · May 6, 2016

16 2 Share this Tweet

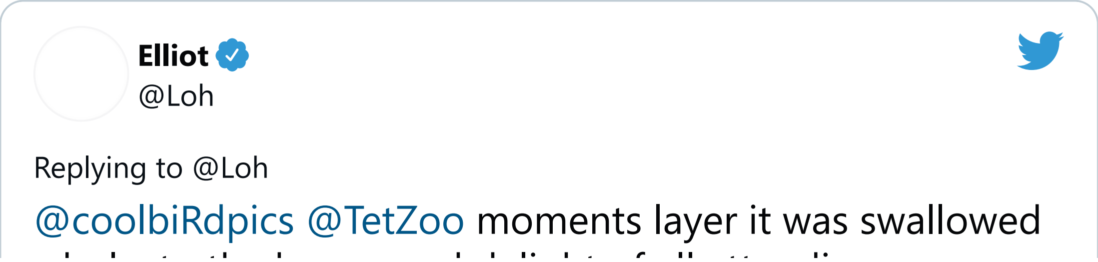
Great blue herons are wading birds, but "they eat a variety of things," said Heyse. "They like to stalk their prey, so they'll wander around and really go for anything." Fish, amphibians and smaller birds are all on the menu, "as are small mammals, if they can manage to get them."





Mature great blue herons top out at just under five feet tall, and have a wingspan of about 80 inches. Using its tapered bill as a spear, a heron on a hunt will hover over a hole until it detects movement. Once an unsuspecting gopher disturbs the loosely packed dirt that serves as its front door, the heron drives its spear-like beak into the hole.

Voila: one gopher kebab, to go.



**Elliot**
@Loh

Replying to @Loh

@coolbiRdpics @TetZoo moments layer it was swallowed whole, to the horror and delight of all attending

7:30 PM · May 6, 2016

8 1 Share this Tweet

Since they lack teeth, great blue herons "can swallow a lot of things," said Heyse, who added that they manipulate their prey to get the easiest angle. Unlike birds of prey, which regurgitate small bones and fur, great blue herons digest everything. According to Heyse, that the birds usually live for five to seven years, although they've been known to live into their 20s in captivity.

The heronry in Golden Gate Park is watched over by volunteers from SFBBO's Colonial Bird Monitoring Program. Since 1982, trackers have visited the park to take population counts and map nest sites. Other heron colonies in San Francisco are located near Lake Merced, the Palace of Fine Arts and Stow Lake.

Heron captures gopher at San Francisco Golden Gate

SFBBO accepts applications to the waterbird monitor program year-round, but volunteers won't be assigned until January/February. Applicants must have prior experience identifying relevant species and be able to drive on dirt roads. They're also required to attend an orientation before joining the monthly surveys, which take place between March and August.

To apply, contact Kristin Butler at kbutler [AT] sfbbo DOT org.

Written By
**Walter Thompson**

Written By

# HUNTING HERONS AT POINT REYES NATIONAL SEASHORE

NOVEMBER 11, 2019 / SHEILA NEWENHAM

Gophers are everywhere in this part of Northern California. The landscape is literally pockmarked with their holes. Their vision is poor, living mostly underground, finding food by smell and navigating with their exquisitely sensitive whiskers. They eat primarily grasses, shoots and roots sometimes pulling a whole plant through the ground into their tunnel like some sort of magic disappearing act. When these Botta's Pocket Gophers show up at their burrow openings, they will retreat disappearing in one-tenth of a second. And reasonably so since *everybody* here eats gophers – raptors, ravens, bobcats, coyotes, foxes and even great blue herons.

Walking the fields looking and listening

This is a seldom-seen hunting behavior in great blue herons and great egrets. These feathered hunters are classified as wading birds and commonly eat fish, crabs, frc and insects. But here at Point Reyes National Seashore, they've adapted to what is most readily available: gophers. The herons slowly stalk the open fields, stopping to tilt their head one way and then another listening and waiting. They can hear the gophers moving underground. And the gopher can “hear” them walking, too, by the vibrations picked up by its whiskers.

When I first saw a great blue heron standing in a field here, I didn’t know he was hunting standing quietly by a burrow hole, listening and waiting. I would have driven right by. Patience is rewarded here. The heron freezes. He tenses and slowly, smoothly and deliberately coils his head and neck backward, carefully starts to unfurl his wings and in an instant is off the ground. The full force of his body is thrown behind the piercing, razor-sharp beak aimed at a five-inch long gopher at the opening of its burrow.

The Leap

The Strike

When the heron’s feet hit the ground again, a struggling gopher hangs from its bill.

The heron's aim for a fatal strike was off the mark and the gopher is desperately trying to free himself from this grasp. Meanwhile, the heron is trying to readjust his grip for a better hold and ease of swallowing without losing his catch.


Sheila Newenham

It’s fascinating and a little gruesome at the same time.  I feel compassion for the ill-fated, little gopher so violently torn from his home and at the same time, I know this is the web of life, necessary for all of us in one way or another.


Sheila Newenham


Sheila Newenham


Sheila Newenham


Sheila Newenham


Sheila Newenham

Daniel Dietrich, of Point Reyes Wildlife Safaris, tells me that the Great Blue Herons here usually strike at a gopher every 5-10 minutes while hunting the fields.  They certainly aren't always successful.  However, he once watched a single heron swallow five or six gophers in the span of 45minutes.  Where would this five-pound bird put that much much food??

The Swallow

Look at how fat that neck is now!

After several tense minutes, the meal was complete and the heron hunted on.

This was amazing to see; the adaptations, techniques and skill of these birds, and even more spectacular to be able to photograph it.

**Related**

*WETLANDS,* Vol. 28, No. 2, June 2008, pp. 257–275

# 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-*

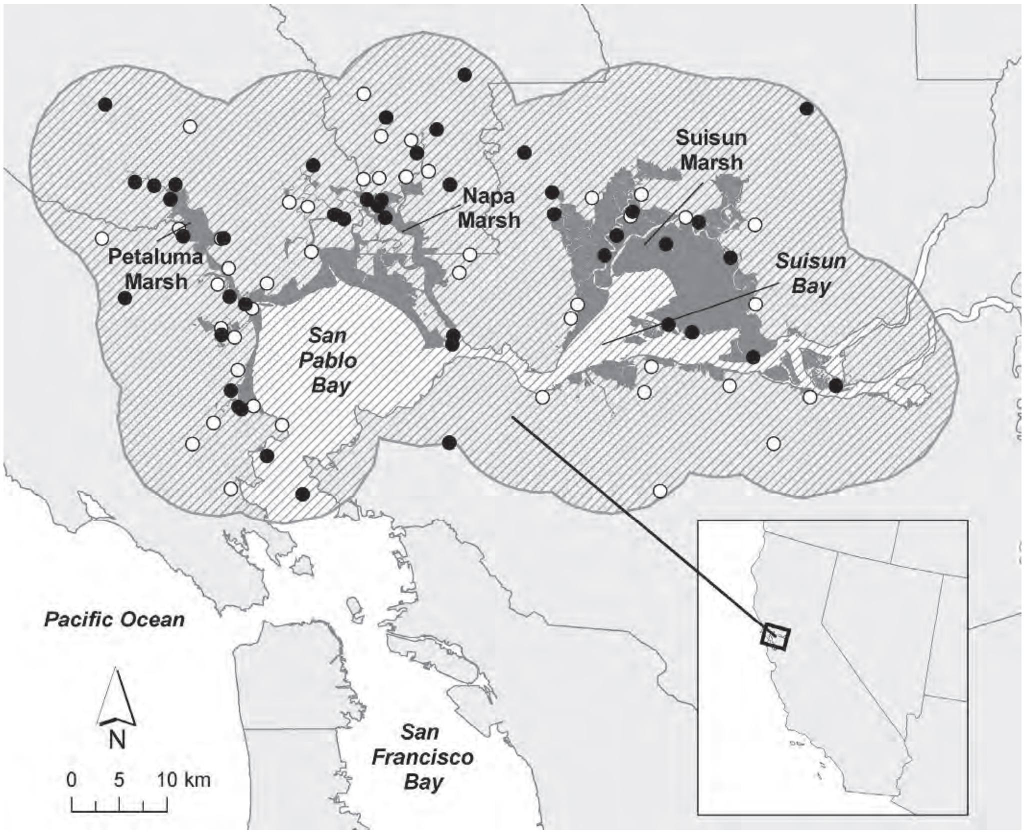

Figure 1. Heron and egret nesting colonies (solid circles) and randomly selected, unoccupied sites (open circles) within 10 km of historic tidal marsh in northern San Francisco Bay, 1991–2005. The study area is indicated by diagonal hatching.

*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 $\text{yr}^{-1}$). 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

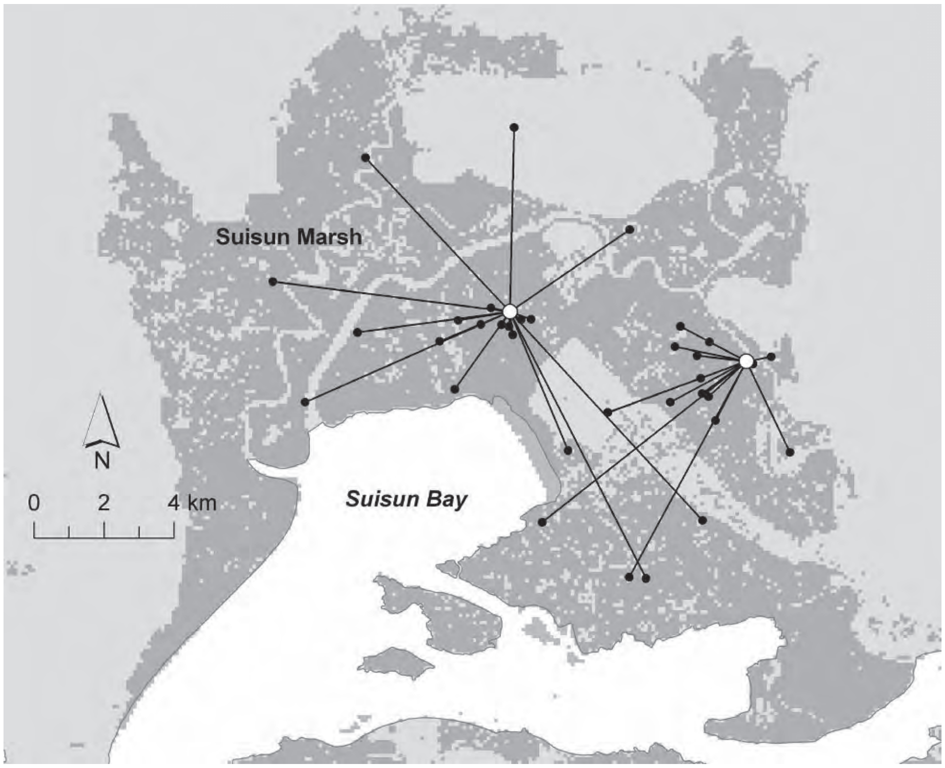

Figure 2. Foraging flight vectors and landing sites of great egrets from two nesting colonies in Suisun Marsh, California.

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 ($\Delta AIC_c$) 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 habitat 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 AIC*c* ($\Delta AIC_c$), 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 | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | 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

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

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

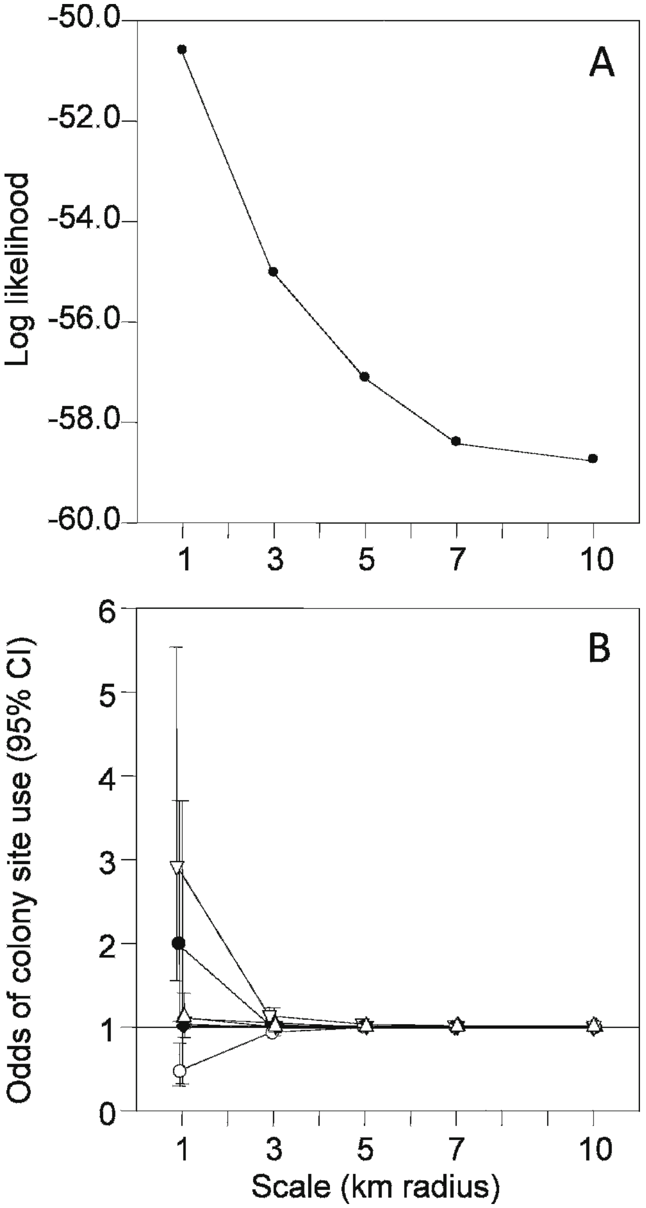

Figure 3. Logistic regression results from *a priori* models of landscape effects on heron and egret colony site selection in northern San Francisco Bay, 1991–2005, showing A) model-averaged log likelihood and B) odds of colony site use (95% confidence interval, CI) associated with landscape variables. 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).

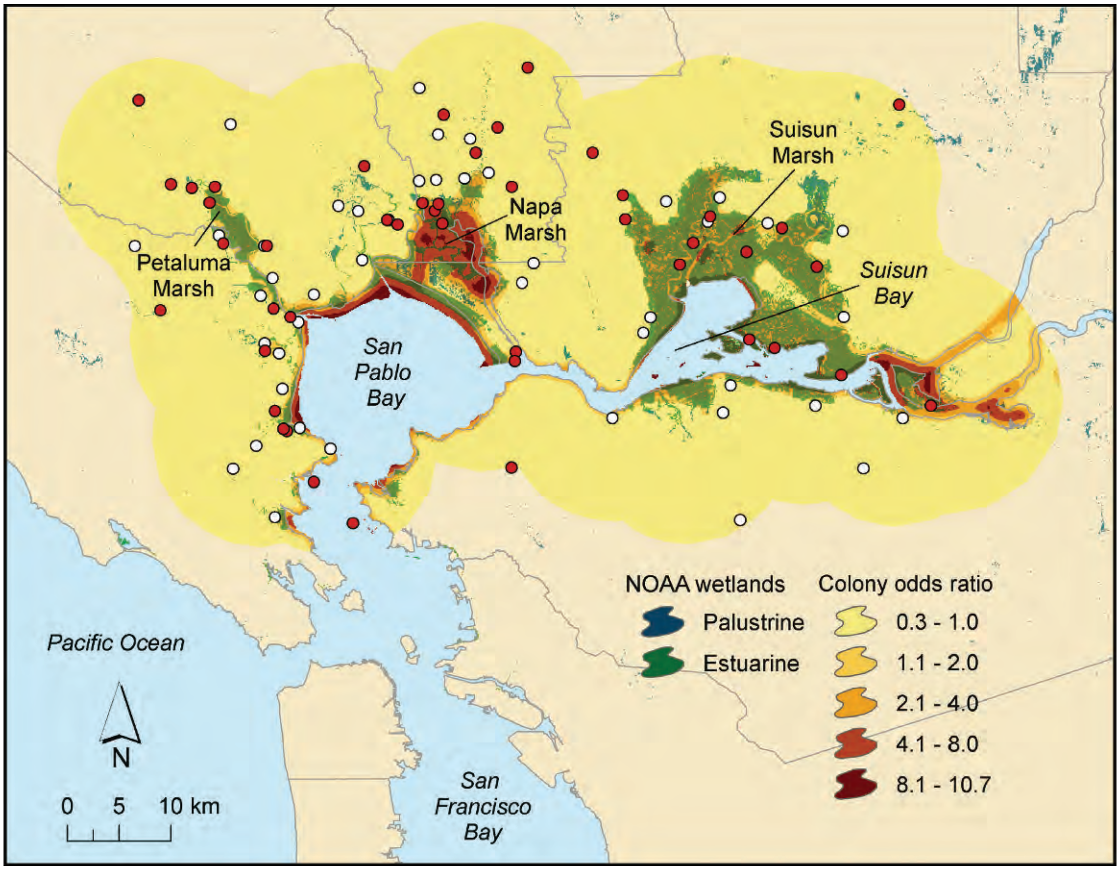

Figure 4. Odds of colony site use by herons and egrets relative to landscape conditions in northern San Francisco Bay, based on logistic regression (Table 2) of actual colony sites (solid circles), 1991–2005, vs. randomly selected, unoccupied sites (open circles).

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 $AIC_c$ ($\Delta AIC_c$), 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 | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ |
|---|---|---|---|---|---|---|
| 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(ESTUAR1) + 0.0038(ESTUAR3) + 0.0005(ESTUAR5) + 0.0002(ESTUAR7) + 0.0005(ESTUAR10) + 0.0165(OPENW1) + 0.0048( OPENW3) + 0.0008( OPENW5) + 0.0003( OPENW7) + 0.0005(OPENW10) + 0.0186(LOWINT1) + 0.0132(LOWINT3) + 0.0014(LOWINT5) + 0.0005(LOWINT7) + 0.0009(LOWINT10) − 0.0006(GRASSL3) − 0.0001(GRASSL7) − 0.0001(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(ESTUAR10) − 0.0043( OPENW10) − 0.0077(PALUSTR10) + 0.0156(LOWINT10) + 0.0002(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

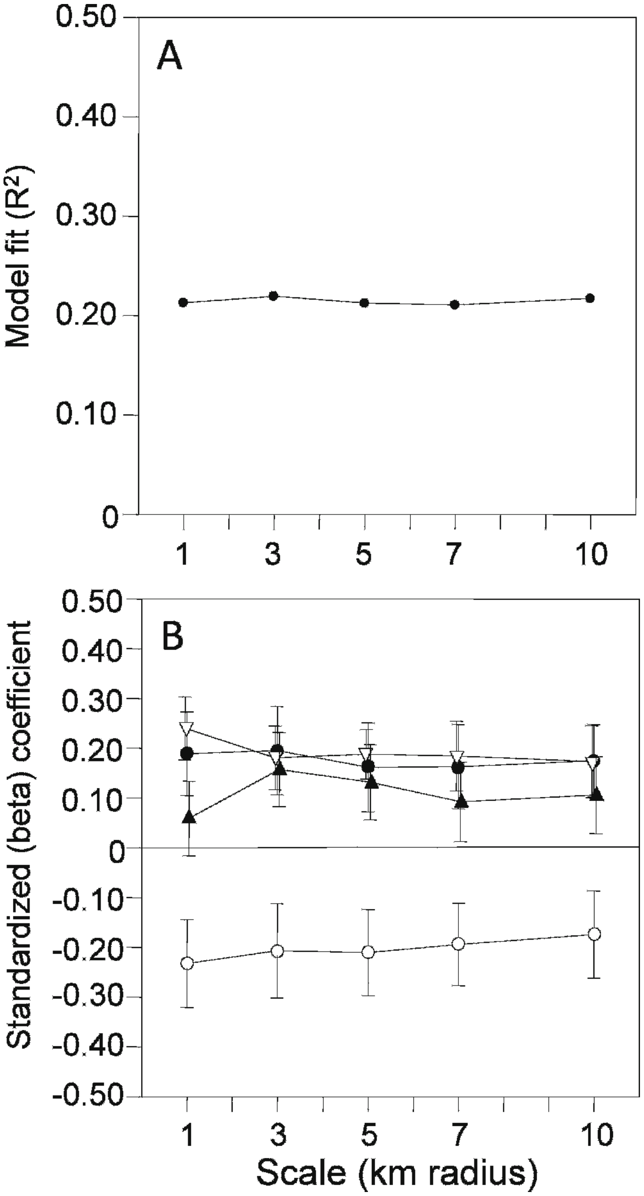

Figure 5. Multiple regression results from *a priori* models of landscape effects on mean prefledging brood size in great blue heron colonies in northern San Francisco Bay, 1991–2005, showing A) model-averaged fit ($R^2$) and B) standardized (beta) coefficients of landscape variables (± standard error). 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).

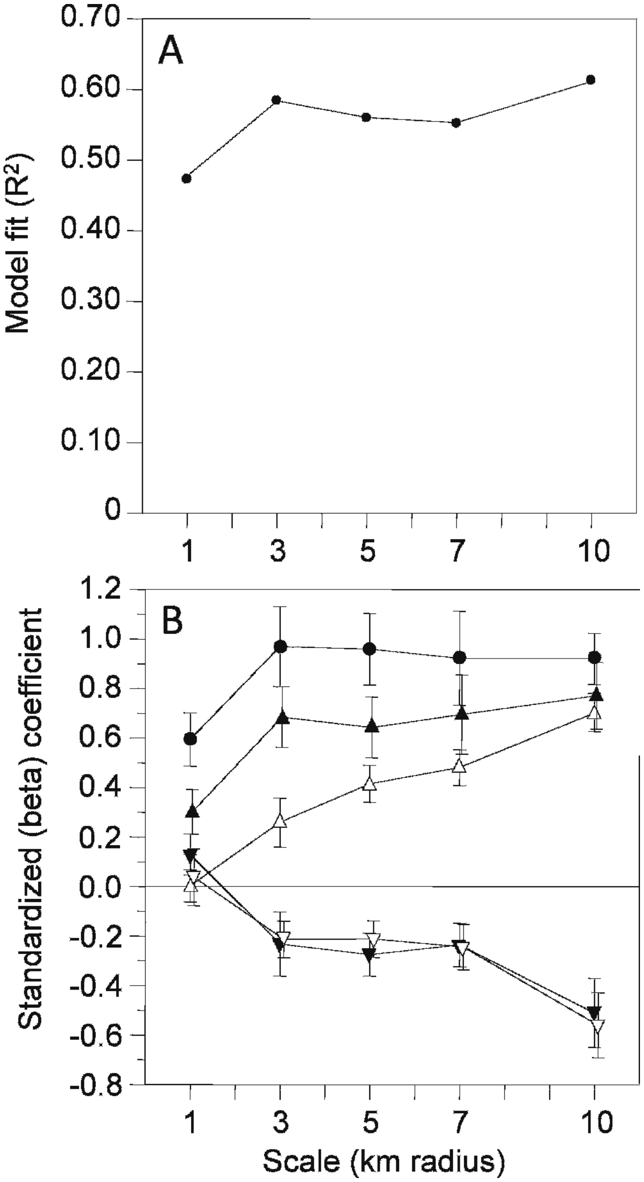

Figure 6. Multiple regression results from *a priori* models of landscape effects on mean prefledging brood size in great egret colonies in northern San Francisco Bay, 1991–2005, showing A) model-averaged fit ($R^2$) and B) standardized (beta) coefficients of landscape variables (± standard error). Only 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.

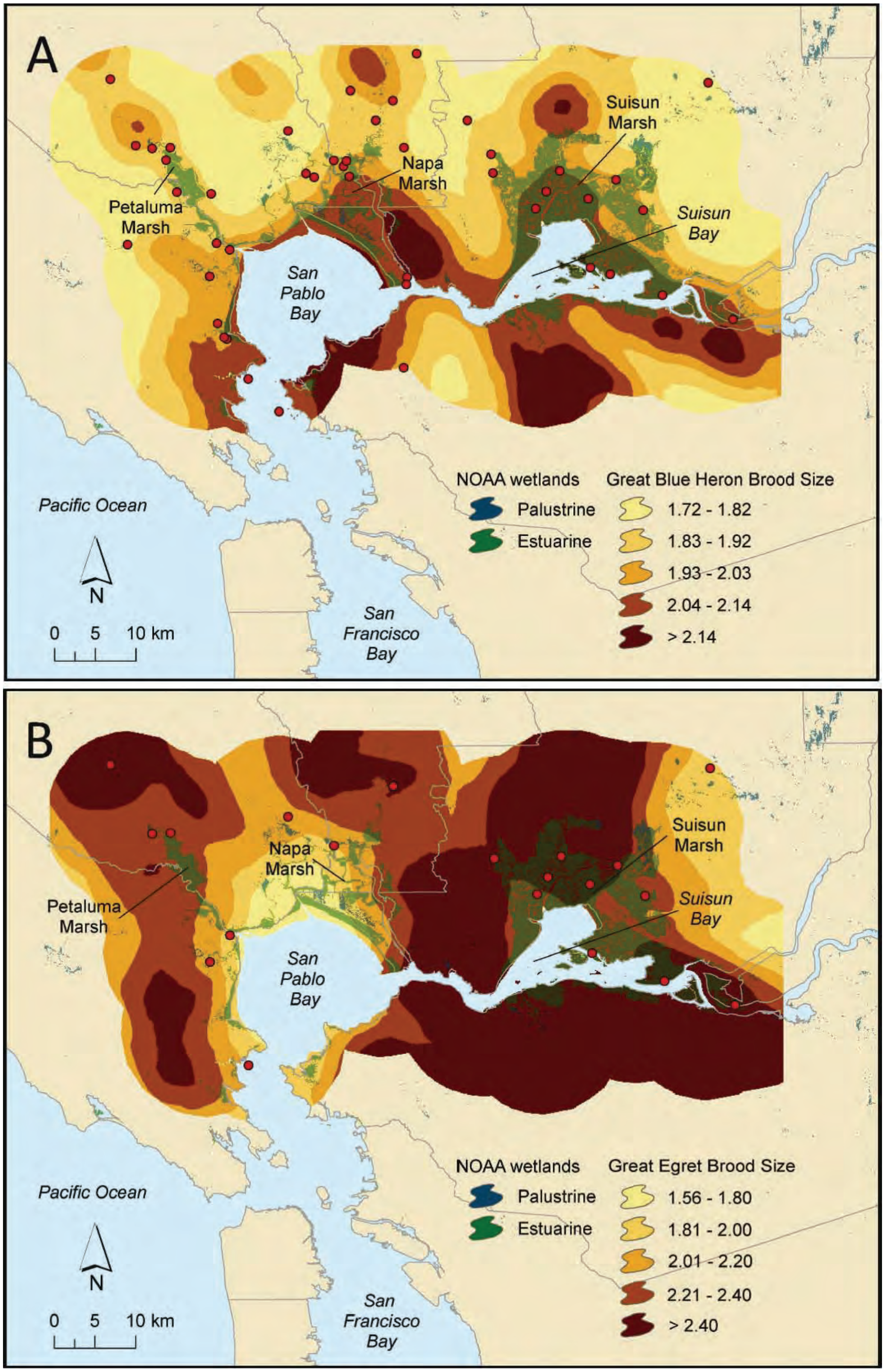

Figure 7. Prefledging brood size in successful A) great blue heron and B) great egret nests, as predicted by landscape influences in northern San Francisco Bay, based on model-averaged multiple regressions of mean colony brood sizes, 1991–2005, against land cover and wetland patch variables (Table 4).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

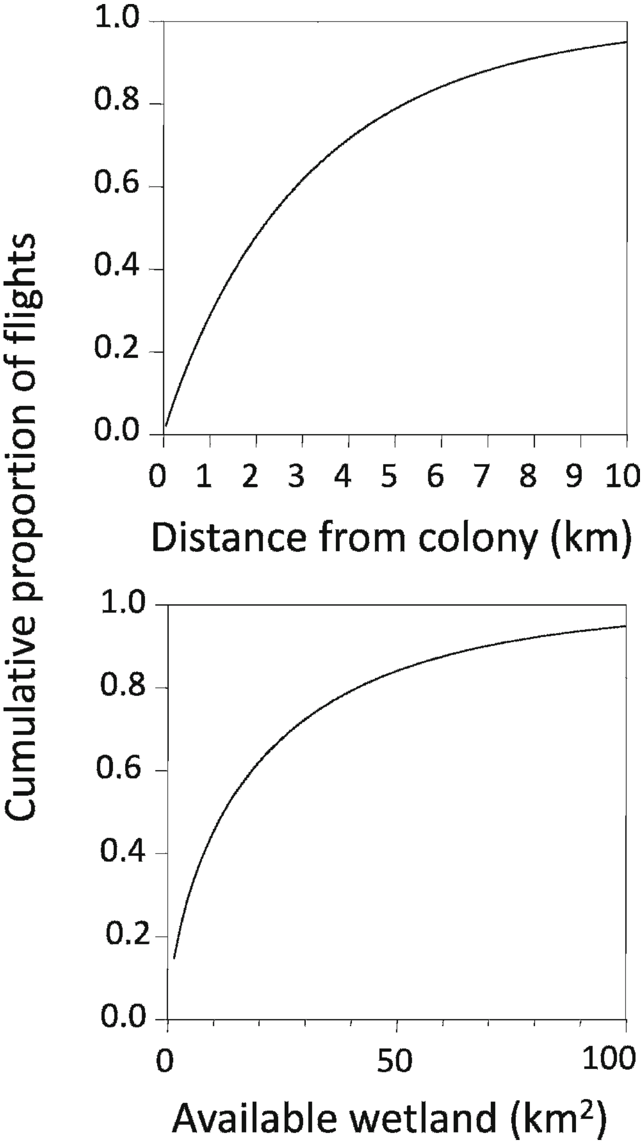

Figure 8. Estimated cumulative foraging dispersion of great egrets, based on 1,000 bootstrap samples of departure flights (n = 36) from colony sites in Suisun Marsh, modeled as a function of A) flight distance and B) areal extent of estuarine and palustrine emergent wetland accessible within flight distances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

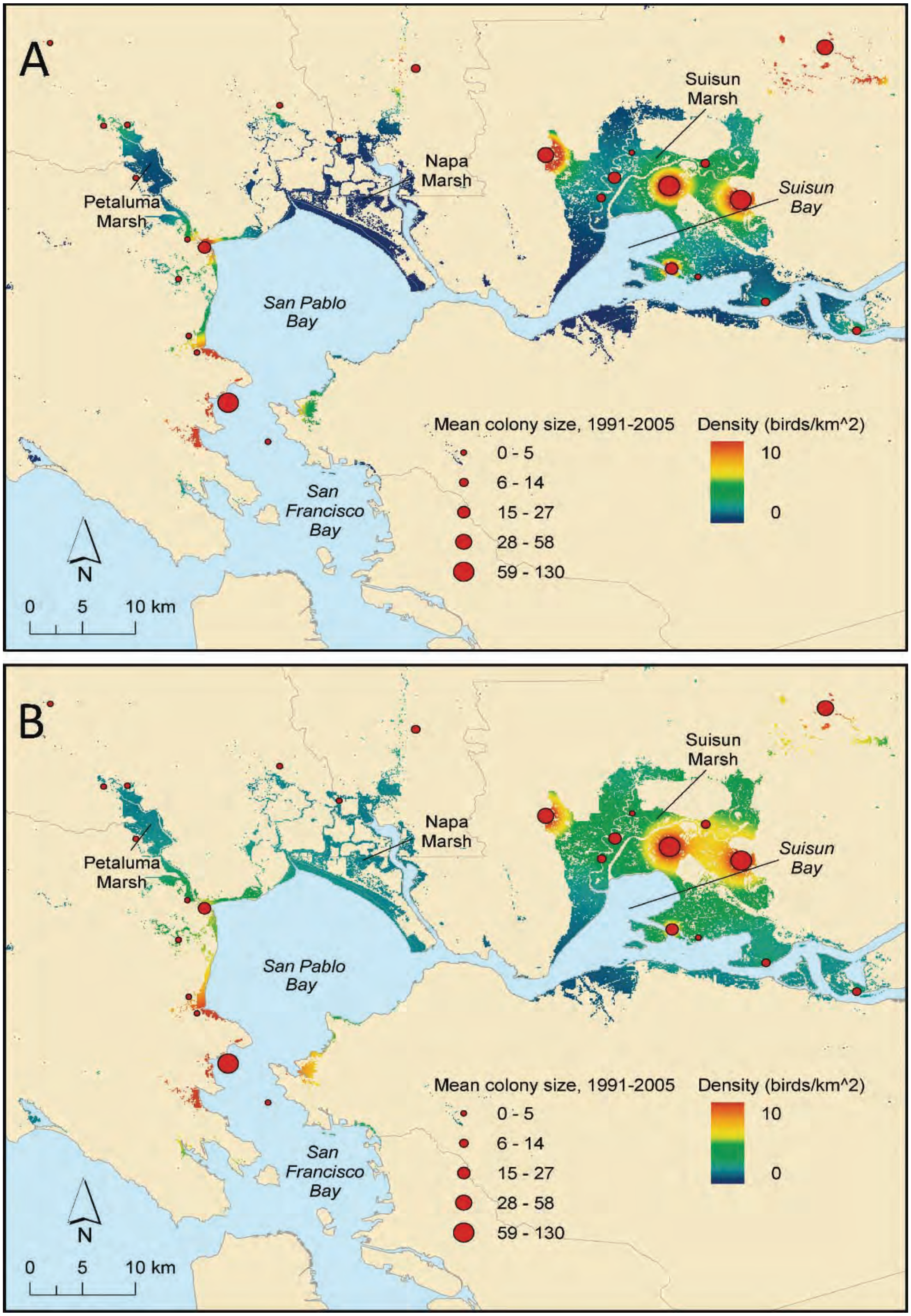

Figure 9. Predicted great egret foraging densities in estuarine and palustrine emergent wetlands in northern San Francisco Bay, based on average nesting distribution, 1991–2005, and foraging dispersion from colony sites (solid circles) relative to A) flight distance and B) the areal extent of wetland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

## ACKNOWLEDGMENTS

Financial support was provided by the CALFED Bay-Delta Science Authority Integrated Regional Wetlands Monitoring (IRWM) Pilot Project for the northern San Francisco Bay and Delta, the Dennis and Carol Ann Rockey Fund of the Marin Community Foundation, and the Robert J. & Helen H. Glaser Family Foundation. We thank the numerous field observers who assisted in monitoring heronries from 1991 to 2005. Nadav Nur, Emiko Condeso, and other IRWM team members provided helpful advice. Chris Rintoul assisted with automation of foraging density predictions. Numerous land owners and public agencies generously provided access to heronries. We thank Bob Spofford, David McConnell, and Robert Ovanin for providing and piloting planes to follow foraging egrets. This is PRBO contribution number 1571.

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Manuscript received 15 August 2007; accepted 20 February 2008.