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Research Article

Island Characteristics Within Wetlands Influence Waterbird Nest Success and Abundance

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ABSTRACT Coastal waterbird populations are threatened by habitat loss and degradation from urban and agricultural development and forecasted sea level rise associated with climate change. Remaining wetlands often must be managed to ensure that waterbird habitat needs, and other ecosystem functions, are met. For many waterbirds, the availability of island nesting habitat is important for conserving breeding populations. We used linear mixed models to investigate the influence of pond and island landscape characteristics on nest abundance and nest success of American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and Forster's terns (*Sterna forsteri*) in San Francisco Bay, California, USA, based on a 9-year dataset that included >9,000 nests. Nest abundance and nest success were greatest within ponds and on individual islands located either <1 km or >4 km from San Francisco Bay. Further, nest abundance was greater within ponds with relatively few islands, and on linear-shaped, highly elongated islands compared to more rounded islands. Nest success was greater on islands located away from the nearest surrounding pond levee. Compared to more rounded islands, linear islands contained more near-water habitat preferred by many nesting waterbirds. Islands located away from pond levees may provide greater protection from terrestrial egg and chick predators. Our results indicate that creating and maintaining a few, relatively small, highly elongated and narrow islands away from mainland levees, in as many wetland ponds as possible would be effective at providing waterbirds with preferred nesting habitat. © 2016 The Wildlife Society.

KEY WORDS American avocet, black-necked stilt, California, Forster's tern, *Himantopus mexicanus*, island shape, island size, *Recurvirostra americana*, *Sterna forsteri*, waterbirds, wetland management.

More than half of all wetlands worldwide have been lost over the past century, and many of those remaining have been degraded by human activities (Millennium Ecosystem Assessment 2005, Davidson 2014). Coastal wetlands are particularly vulnerable because increasing human populations have resulted in loss and degradation of wetlands for urban and agricultural development (Dahl and Stedman 2013). Sea level rise and other consequences of climate change threaten inundation, displacement, and further loss (Millennium Ecosystem Assessment 2005, Dahl and Stedman 2013, Clausen and Clausen 2014). Consequently, waterbird populations that depend on coastal wetlands for breeding, wintering, or migration often are threatened or in decline (Parnell et al. 1988, Page and Gill 1994, Millennium Ecosystem Assessment 2005). Management actions often focus on ensuring that adequate habitat features of coastal wetlands remain to support waterbirds, and to stem, or even reverse such declines.

For breeding waterbirds, islands can be extremely important nesting habitat because they may isolate nesting birds from terrestrial predators and limit human disturbances. Previous studies have reported waterbird nest abundance, nest density, and nest success can be greater on island habitats relative to mainland habitats (Lokemoen and Woodward 1992, Clark and Shutler 1999, Hötker 2000, Anteau et al. 2014, Eason et al. 2012). As a result, wetland management for breeding waterbirds often includes the construction or maintenance of island nesting habitat (Parnell et al. 1988, Quinn and Sirdevan 1998, Erwin et al. 2003). Yet, how to construct or manage islands for nesting waterbirds can be difficult to determine. A number of landscape characteristics may affect island use by nesting waterbirds including size, shape, topography, location, and

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land cover (Giroux 1981, Erwin et al. 1995, Dahl et al. 2003, Shaffer et al. 2006, Eason et al. 2012), and preferred island characteristics can vary dramatically among waterbird species. Thus, identifying island characteristics that promote greater use and nest success on islands could benefit waterbird habitat management efforts.

We investigated the influence of island characteristics on nest abundance and nest success of 3 waterbird species: American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and Forster's terns (*Sterna forsteri*). American avocets (hereafter avocets) are semi-colonial nesters that breed within ephemeral and managed wetlands throughout much of western North America, including coastal locations in California and the Gulf of Mexico (Ackerman et al. 2013). Avocets typically nest on island or mainland shoreline areas characterized by bare ground, or areas with short, sparse vegetation (Hamilton 1975, Sordahl 1996, Ackerman et al. 2013). Black-necked stilts (hereafter stilts) have a similar breeding distribution, nest in similar wetland habitats, and often breed sympatrically with avocets (Robinson et al. 1999). Compared to avocets, stilts nest closer to water, in more vegetated areas, and less colonially, with nests more evenly distributed and farther apart from one another (Hamilton 1975, Sordahl 1996, Robinson et al. 1999, Ackerman et al. 2014*b*). Forster's terns (hereafter terns) are highly colonial nesters, and nest on islands and mainland habitats within freshwater and brackish marshes scattered throughout much of North America, including coastal locations in California, the Gulf of Mexico, and the eastern United States (McNicholl et al. 2001). Because avocets, stilts, and terns all regularly use natural and artificial islands as nesting habitat, the construction and maintenance of nesting islands can be an important component in managing breeding populations of these waterbird species.

We evaluated how island characteristics influence nest abundance and nest success of avocets, stilts, and terns in San Francisco Bay, California, USA at 2 spatial scales using >9,000 individual nest records collected from 2005 to 2013. We focused on several characteristics likely to be important in planning of island habitat construction or restoration. First, we examined how the number of islands and total island area across a wetland pond, and the location of the pond affected nest abundance and nest success (i.e., pond scale). We predicted that nest abundance and nest success within ponds would be positively correlated with the number of islands and total island area within a pond because ponds with relatively few islands, or little total island habitat, would have fewer potential nesting sites. Further, we predicted that islands within ponds closer to San Francisco Bay would have greater nest abundance and nest success because such ponds are closer to attractive foraging habitat along the bay margins, and farther from sources of disturbance in this highly urbanized area. Next, we examined how island size, shape, and location within a pond affected nest abundance and nest success on individual islands (i.e., island scale). Because larger islands contain more potential nesting habitat than smaller islands, we predicted that nest abundance and nest success would be positively correlated with island size. We also predicted that linear-shaped, elongated islands would have greater nest abundance than rounded islands. Previously, we demonstrated that avocets and terns select nest sites close to the water's edge (Hartman et al. 2016). Thus for a given island area, a linear shape would contain more potential nesting sites close to the water's edge than a more rounded island. Lastly, we predicted that nest abundance and nest success would be positively correlated with island distance to the surrounding pond levee. Reduced anthropogenic disturbance may attract more birds to, and limited access by terrestrial predators may improve nest success on, islands farther from pond levees.

STUDY AREA

We studied avocet, stilt, and tern nests among 100 islands within 22 managed ponds at the Don Edwards San Francisco Bay National Wildlife Refuge (37.4° N, 122.0° W) and the Eden Landing Ecological Reserve (37.6° N, 122.1° W), in San Francisco Bay, California from 2005 to 2013 (Fig. 1). The climate in San Francisco Bay is characterized by warm, dry summers and mild, wet winters. More than 1 million waterbirds use various habitats in San Francisco Bay annually (Stenzel et al. 2002; Takekawa et al. 2011, 2012), including tidal marsh, seasonal wetlands, and managed ponds. These ponds were formerly commercial salt evaporation ponds that have recently been transferred to government ownership and are managed to provide fish and wildlife habitat. Pond boundaries were delineated by surrounding earthen levees and ponds ranged in size from 22 to 277 ha, were 0 to 5 km from the bay, and contained 1 to 30 islands each. With one exception, all islands in this study were constructed from dredge material prior to 2005. The exception was that prior to the 2011 breeding season, 30 islands were constructed within 1 pond as part of an effort to replace island nesting habitat forecasted to be lost with the conversion of managed ponds to tidal marsh habitat in association with the South Bay Salt Pond Restoration Project (Goals Project 1999). Islands within ponds varied in shape from rounded to more linear and elongated, ranged in size from 0.00015 ha to 2.5 ha, and were located 0.1 km to 6.5 km from the bay and 10 m to 300 m from the nearest pond levee. Island vegetation varied from sparse to dense, and was comprised mostly of pickleweed (*Sarcocornia pacifica*) and alkali heath (*Frankenia salina*).

Avocets and stilts are the 2 most abundant breeding shorebirds in San Francisco Bay (Stenzel et al. 2002, Rintoul et al. 2003). San Francisco Bay is the largest breeding area for avocets and stilts along the Pacific coast (Stenzel et al. 2002, Rintoul et al. 2003), and approximately 75% of avocet nests occur on islands within managed ponds (Ackerman et al. 2013). Similarly, approximately 30% of the Pacific coast breeding population of terns nest in San Francisco Bay and as many as 80% of these terns nest on islands within managed ponds (McNicholl et al. 2001, Strong et al. 2004). Stilts also nest on islands within managed ponds but more often nest within marsh habitat not associated with islands (Ackerman et al. 2014*b*).

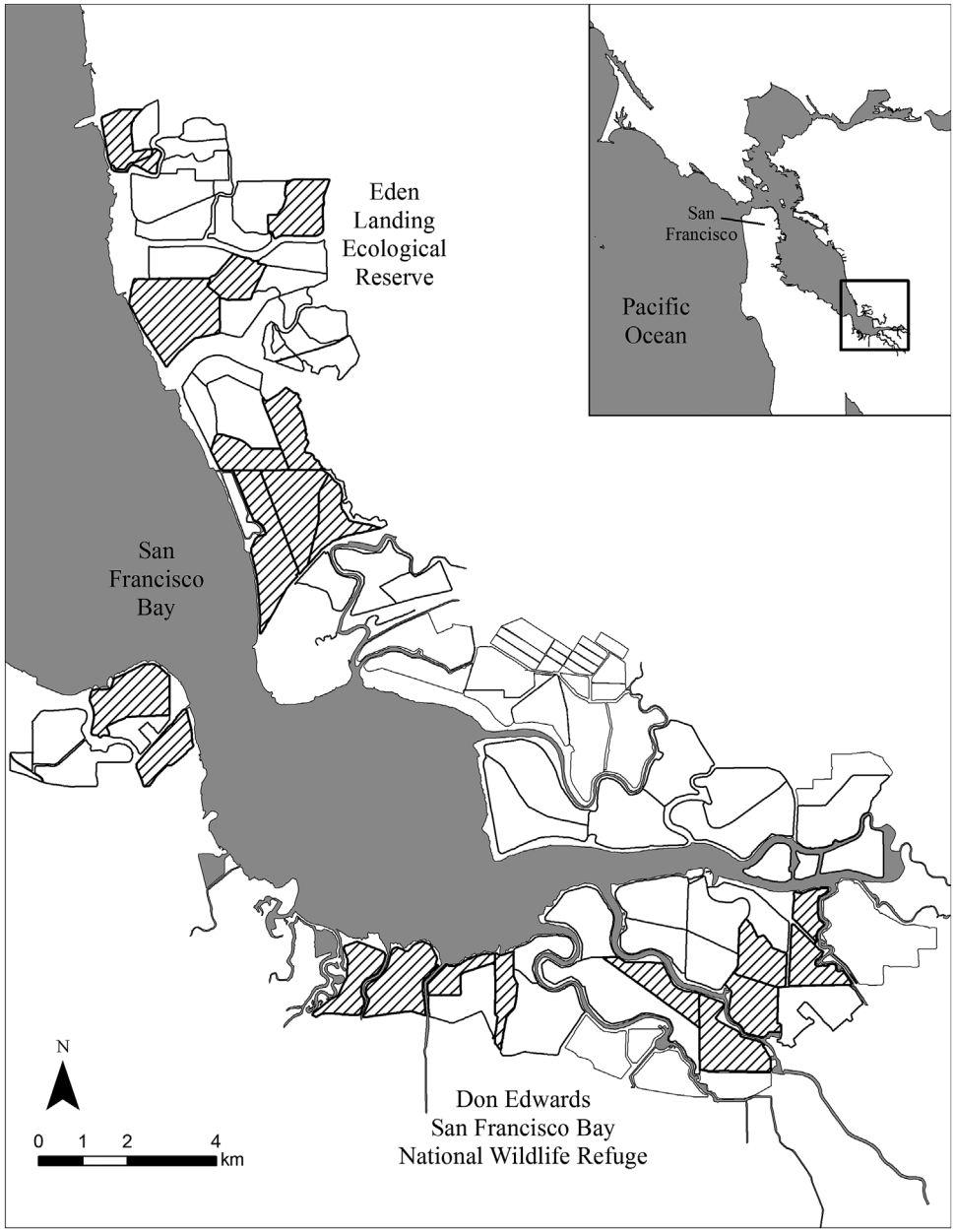

Figure 1. Managed ponds at the Don Edwards San Francisco Bay National Wildlife Refuge and Eden Landing Ecological Reserve in South San Francisco Bay, California, USA. Hatched areas denote ponds where we studied waterbird nesting in 2005–2013.

METHODS

Nest Abundance and Nest Success

We monitored nests under the guidelines of the United States Geological Survey (USGS), Western Ecological Research Center's Animal Care and Use Committee. Throughout the nesting season (Apr–Aug), we visited islands weekly to monitor nesting activity. We marked each newly initiated nest with a uniquely numbered metal tag held in place just south of the nest bowl with a garden staple, and recorded Universal Transverse Mercator (UTM) coordinates of each nest (Garmin GPSMAP 76, Garmin International Inc., Olathe, KS, USA). At each weekly nest visit, we floated eggs to estimate embryo age (Ackerman and Eagles-Smith 2010), recorded clutch size, and determined overall nest fate (i.e., hatched, failed, abandoned, depredated). We calculated annual nest abundance within each pond by summing the number of nests observed among all islands within each pond, and we calculated annual nest abundance on each individual island by summing the number of nests observed on each island.

We calculated nest daily survival rates based on weekly nest visits using logistic exposure models (Shaffer 2004). We considered a nest to have survived an interval if the clutch was still completely or partially intact, embryo development had progressed, and there were no signs of nest abandonment (such as cold eggs). We considered a nest successful if $\geq$1 eggs successfully hatched, as evidenced by observing

≥1 chicks, or tiny eggshell fragments indicative of hatch, in the nest. We considered a nest unsuccessful if it was destroyed or abandoned. We calculated exposure days as the number of days between nest visits, except when a final nest fate occurred between visits (i.e., hatched, depredated, abandoned). For hatched nests, we calculated exposure days for the final interval based on the expected hatch date (Ackerman and Eagles-Smith 2010). For depredated nests, we calculated exposure days for the final interval as the mid-point between nest visits. For abandoned nests, we calculated exposure days for the final interval as the difference between the developmental age of the eggs when the nest was abandoned (estimated by egg flotation) and the developmental age of the eggs when the nest was last visited. For the pond-scale analysis, we used a model with the class variables species, pond, and year, and nest age as an individual covariate to calculate nest daily survival rates for each species, within each pond, in each year. For the island-scale analysis, we used a model with the class variables species, individual island, and year, and nest age as an individual covariate to calculate nest daily survival rates for each species, on each island, in each year. We calculated nest success as the product of daily nest survival over the approximate 27-day egg-laying and incubation period (Robinson et al. 1999, McNicholl et al. 2001, Ackerman et al. 2013).

Pond and Island Attributes

At the pond scale of analysis, we investigated whether the amount and distribution of island habitat within a pond influenced waterbird nest abundance and nest success. We evaluated the effects of the number of islands within a pond, total island area (ha), and the ratio of island area to pond area. We also evaluated the effects of total pond area (ha) and pond distance to bay (km) because these variables could be linked to food availability, predator numbers, and disturbance levels. We calculated pond areas in ArcMap 10.2 (Environmental Research Systems Institute [ESRI], Redlands, CA, USA) using 2005 digitized imagery from the National Agricultural Imagery Program (NAIP) for South San Francisco Bay. We calculated island areas from island perimeters derived using 1 of 2 methods. For 29 islands, we used a real-time kinematic global positioning system (GPS; Leica® Smart Rover GPS1200, Leica Geosystems, Atlanta, GA, USA) to trace the island perimeter at the water's edge in April and May 2011. For the remaining 125 islands in the study ponds, we digitized island perimeters from USGS high-resolution orthoimagery of the San Francisco Bay area (resolution: 0.3 m) using ArcMap 10.2. Orthoimagery data were collected in April 2011, thereby matching the period of data collection of island perimeters using the real-time kinematic GPS. Moreover, among islands where we derived perimeters using both methods, estimates of island area were similar. We calculated total island area in each pond by summing the area of all islands within a given pond. We calculated pond distance to the bay as the minimum distance from the pond's edge to San Francisco Bay using the Near Geoprocessing Tool in ArcMap10.2.

Next, for the island-scale analysis, we evaluated the effects of island size (ha), shape, distance to bay (km), and distance to nearest surrounding pond levee (m) on waterbird nest abundance and nest success among individual islands. We included the distance to nearest surrounding pond levee because this may influence island accessibility by terrestrial egg and chick predators and the potential for human disturbance from people walking along trails on pond levees (Trulio and Sokale 2008). We calculated island size from island perimeters as previously described. We quantified island shape by calculating an island shape index using the following equation:

$$\text{Island Shape Index} = \frac{0.25 \times \text{Island perimeter (m)}}{\sqrt{\text{Island Area (m}^2)}}$$

where a larger island shape index indicates an island with more shoreline relative to the island's size (McGarigal 2014). Because study islands varied from rounded (little shoreline relative to size) to highly elongated (abundant shoreline relative to size), the island shape index provided a metric of island linearity that was independent of island size. For reference, a perfectly round island would have an island shape index of 0.9, whereas a rectangular island that was roughly 10 times longer than it was wide would have an island shape index of approximately 1.7. Islands in this study had shape indices ranging from 0.92 to 4.77. Lastly, we calculated the distance from the edge of each island to the nearest pond levee and to the bay using the Near Geoprocessing Tool in ArcMap10.2.

Statistical Analyses

For the pond-scale analysis, we used linear mixed models (PROC MIXED, SAS/STAT® software, release 9.4, SAS Institute, Cary, NC, USA) to evaluate the effects of species, total pond area, the number of nesting islands within a pond, the total island area within the pond, the proportion of total island area to pond area, and distance to San Francisco Bay on nest abundance and nest success within ponds. We used apparent nest abundance, defined as the number of nests observed within a pond in a given year. Often nest abundance studies use adjusted nest abundance estimates that account for nests that failed before they could be found (Miller and Johnson 1978). However, because we visited colonies weekly, and islands represented a finite area where nests on each island were easily found, we determined that adjustments to apparent nest abundance were unnecessary. Additionally, because sample sizes of nests per species, per pond, per year were sometimes <10, adjusting nest density by nest survival, especially low nest survival, led to grossly inflated estimates of adjusted nest density. We included only data from ponds for which we monitored all islands in the pond, thereby providing us with an accurate nest abundance estimate among all islands within a given pond. Additionally, in analyzing nest success, we included only data from ponds for which we monitored ≥10 nests of a given species in a given year, so as to provide a reasonably accurate estimate of nest success. Because the variables island area and proportion of island area to pond area were highly correlated ($r = 0.96$), we

did not allow these variables to appear in the same model. None of the other variables examined were highly correlated ($r \leq 0.54$). We limited models to only 3 predictor variables because despite multiple years of data from each pond, our sample of ponds was 22 for nest abundance and 20 for nest success analyses. Allowing for these restrictions, we built a relatively balanced set of candidate models for the nest abundance and nest success analyses based on all combinations of $\leq$3 variables including the class variable species, and linear and quadratic terms for the variables pond area, number of islands, island area, proportion of island area to pond area, and distance to bay, plus a null model (65 total models). In all models, we included year as a random effect. Pond nest abundance values were not normally distributed so we used a natural log data transformation to meet the assumption of normality. We arcsine transformed pond nest success values prior to analysis.

For the island-scale analysis, we again used linear mixed models (PROC MIXED, SAS/STAT) to evaluate the effects of species, island size, shape index, distance to San Francisco Bay, and distance to nearest surrounding pond levee on waterbird nest abundance and waterbird nest success on individual islands. We used apparent nest abundance, defined as the number of nests observed on an island in a given year. We only included data from an island when we monitored all nests on that island, thereby providing us with an accurate estimate of nest abundance on each island. Further, in analyzing nest success, we included only data from islands for which we monitored $\geq$10 nests of a given species in a given year. None of the examined variables at the island scale were highly correlated ($r \leq 0.51$) so we did not restrict variable inclusion in models. We limited models to only 6 predictor variables because despite multiple years of data from each island, our sample of islands was 100 for nest abundance and only 44 for nest success analyses. Allowing for this restrictions, we built a balanced set of candidate models, for the nest abundance and nest success analyses, based on all combinations of $\leq$6 variables including the class variable species, and linear and quadratic terms for island size, shape index, distance to bay, and distance to levee, plus a null model (143 models). In all models, we included year and the pond where the island was located as random effects. Island nest abundance values were not normally distributed so we used a natural log data transformation to meet the assumption of normality. We arcsine transformed island nest success values prior to analysis.

For the pond and island scales of analysis, we ranked models using an information-theoretic approach and second-order Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). We considered the model with the lowest AIC_c score to be the most parsimonious, and we used the difference in AIC_c values (ΔAIC_c) between the top-ranked model and each other model in the candidate set to assign model rank. We considered models with a ΔAIC_c score ≤ 2.0 to be competitive and calculated parameter estimates by model averaging all models in the candidate set. We determined the weight of evidence for each model using Akaike model weights (w_i), defined as the relative likelihood of a model given all models in the candidate set, and we estimated the relative importance of predictor variables using the cumulative weights of all models with those variables. Furthermore, we used evidence ratios, or the ratio of the Akaike model weight of one model to the Akaike model weight of another model, to determine the importance of

Table 1. Akaike's Information Criterion (AIC) scores for linear mixed models of the effects of pond characteristics on waterbird nest abundance within 22 ponds and nest success within 20 ponds in South San Francisco Bay, California, USA, 2005–2013. All models include year as a random effect. For each analysis, all models with a cumulative model weight of 75% plus the null model are shown.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Evidence ratio[f]
Nest abundance – pond scale					
Species + distance to bay + distance to bay^2	7	658.1	0.00	0.27	1.00
Species + islands + islands^2	7	659.0	0.92	0.17	1.59
Species + islands	6	659.8	1.69	0.11	2.33
Species + islands + proportion of island area	7	660.4	2.32	0.08	3.19
Species + islands + island area	7	660.7	2.64	0.07	3.74
Species + distance to bay + islands	7	661.2	3.13	0.06	4.77
Null	3	727.1	69.00	0.00	0.00
Nest success – pond scale					
Distance to bay + distance to bay^2 + species	7	67.6	0.00	0.29	1.00
Distance to bay + distance to bay^2 + island area	6	69.3	1.77	0.12	2.43
Distance to bay + distance to bay^2	5	69.4	1.79	0.12	2.45
Distance to bay + distance to bay^2 + islands	6	69.7	2.09	0.10	2.85
Distance to bay + distance to bay^2 + proportion of island area	6	70.0	2.42	0.09	3.35
Distance to bay + distance to bay^2 + pond area	6	71.5	3.90	0.04	7.02
Null	3	79.1	11.58	0.00	326.30

[a] Distance to bay: distance to San Francisco Bay; islands: number of islands within the pond; proportion of island area: the ratio of island area to pond area; island area: island area of all the islands within a pond.
[b] The number of parameters in the model including the intercept and variance.
[c] Akaike's Information Criterion corrected for small sample size.
[d] The difference in the AIC_c values of the current model and the model with the lowest AIC_c.
[e] Akaike model weight. The likelihood of the model given the data, relative to other models in the candidate set.
[f] The weight of evidence that the model with the lowest AIC_c value is better than the current model.

each variable in the top-ranked model, by comparing the likelihood of the top-ranked model to the same model structure but with one of the variables omitted. We used the delta method (Seber 1982) to estimate standard errors of the back-transformed values for nest abundance and nest success.

RESULTS

Between 2005 and 2013, 73% of avocet, 21% of stilt, and 96% of tern nests we monitored in South San Francisco Bay were on islands within managed ponds. Terns were the second-most numerous island-nesting species (following California gulls [*Larus californicus*]), and accounted for 65% (6,134) of the 9,404 nests on 100 islands monitored within the 22 study ponds. Avocets were the third-most numerous island-nesting species, and accounted for 32% (3,022) of nests monitored on islands. Stilts, in contrast, accounted for the remaining 3% (248) of nests monitored on islands.

Pond Scale

The most parsimonious model describing nest abundance within ponds included the effects of species and a quadratic term for distance to bay, had an Akaike weight of 0.27, and was 1.59 times more likely than the second-ranked model (Table 1). Two other models were competitive (i.e., $\Delta AIC_c < 2.0$), and included the effects of species and linear or quadratic terms for the number of islands. To further evaluate the importance of the variables in the top-ranked models, we compared evidence ratios between the top-ranked models and identical models but with one of the variables removed. Using evidence ratios, we found that the top-ranked model was 1.67×10^{15} times more likely than a similar model but without species, and 8.27 times more likely than a similar model but without distance to bay. Similarly, the second-ranked model was 3.01×10^{14} times more likely than a similar model but without species, and 5.21 times more likely than a similar model but without number of islands. Model-averaged parameter estimates indicated large species differences in nest abundance within ponds, with terns being most numerous, followed by avocets and then stilts (Table 2, Fig. 2). Further, distance to bay and the number of nesting islands were important predictors of nest abundance (Table 2). Conversely, the effects of proportion of island area to pond area and total island area did not improve model fit, and were considered to be uninformative parameters (Table 2). Model predictions of the effect of distance to bay on nest abundance within ponds exhibited a U-shaped pattern, most notably for terns, and to a lesser extent avocets and stilts, in which nest abundance decreased as a pond's distance to the bay increased to approximately 2 km, and thereafter nest abundance increased as distance to the bay increased, with ponds 4–5 km from the bay exhibiting the highest nest abundance (Fig. 2a). Model predictions also showed that for terns and avocets, and to a lesser extent stilts, nest abundance within ponds decreased as

Table 2. Model-averaged parameter estimates, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits, and relative variable importance (VI) for variables examined for their effects on American avocet, black-necked stilt, and Forster's tern nest abundance and nest success among managed ponds in South San Francisco Bay, California, USA, 2005–2013.

Effect[a]	Estimate	SE	LCL	UCL	VI
Nest abundance – pond scale					
Intercept	3.98832	0.28581	3.42813	4.54851	1.00
Island area	0.06541	0.38050	−0.68037	0.81119	0.12
Island area^2	0.17910	0.11230	−0.04101	0.39921	0.01
Islands	−0.06100	0.04471	−0.14863	0.02663	0.37
Islands^2	0.00296	0.00172	−0.00041	0.00632	0.17
Pond area	0.00243	0.00322	−0.00387	0.00874	0.09
Pond area^2	−0.00003	0.00003	−0.00009	0.00003	0.01
Proportion of island area	−0.09615	0.56376	−1.20112	1.00881	0.12
Proportion of island area^2	0.22980	0.11340	0.00754	0.45206	0.03
Distance to bay	−0.33943	0.30865	−0.94438	0.26553	0.11
Distance to bay^2	0.11240	0.04154	0.03098	0.19382	0.27
American avocet	−0.99165	0.20461	−1.39270	−0.59061	1.00
Black-necked stilt	−2.66760	0.25759	−3.17249	−2.16272	1.00
Nest success – pond scale					
Intercept	0.771229	0.070646	0.632762	0.909695	1.00
Island area	−0.103463	0.085160	−0.270376	0.063451	0.16
Island area^2	0.052462	0.038039	−0.022095	0.127020	0.01
Islands	−0.009041	0.007330	−0.023408	0.005327	0.17
Islands^2	0.000874	0.000662	−0.000424	0.002172	0.01
Pond area	0.000380	0.001483	−0.002527	0.003287	0.07
Pond area^2	−0.000019	0.000010	−0.000039	0.000001	0.01
Proportion of island area	−0.076011	0.088480	−0.249432	0.097410	0.12
Proportion of island area^2	0.049546	0.041269	−0.031342	0.130434	0.01
Distance to bay	−0.207860	0.101900	−0.407585	−0.008136	0.22
Distance to bay^2	0.038208	0.014602	0.009588	0.066827	0.77
American avocet	−0.110416	0.044382	−0.197404	−0.023428	0.40
Black-necked stilt	−0.088495	0.077371	−0.240142	0.063151	0.40

[a] Distance to bay: distance to San Francisco Bay; islands: number of islands within the pond; proportion of island area: the ratio of island area to pond area; island area: island area of all the islands within a pond.

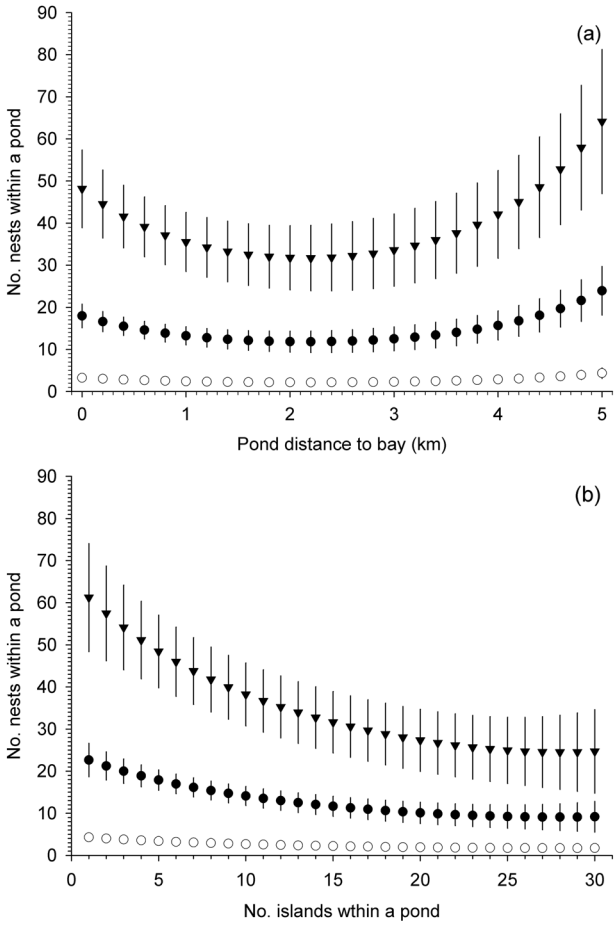

Figure 2. Nest abundance for American avocets (filled circles), black-necked stilts (unfilled circles), and Forster's terns (triangles) according to (a) pond distance to San Francisco Bay, California, USA and (b) the number of islands within a pond, 2005–2013. We derived pond nest abundance estimates (±SE) from back-transformed model-averaged predictions from all candidate linear mixed models, where all other variables were set to their mean value.

the number of islands within a pond increased, and was greatest within ponds with ≤5 islands (Fig. 2b).

We examined nest success among 2,865 avocet, 163 stilt, and 6,091 tern nests within 20 ponds from 2005 to 2013. The most parsimonious model describing nest success within ponds included the effects of species and a quadratic term for distance to bay, had an Akaike weight of 0.29, and was 2.43 times more likely than the second-ranked model (Table 1). Two other models were competitive, and also included a quadratic term for distance to bay with either a linear term for total island area or no additional effects. Using evidence ratios, we found that the top-ranked model was 197 times more likely than a similar model but without distance to bay and 2.45 times more likely than a similar model but without species. Model-averaged parameter estimates indicated small species differences in nest success, with nest success slightly greater among terns than avocets or stilts (Table 2, Fig. 3). Distance to bay was an important predictor of nest success within ponds. Total island area, the number of islands within a pond, the proportion of island area to pond area, and total pond area did not improve model fit, and were considered to

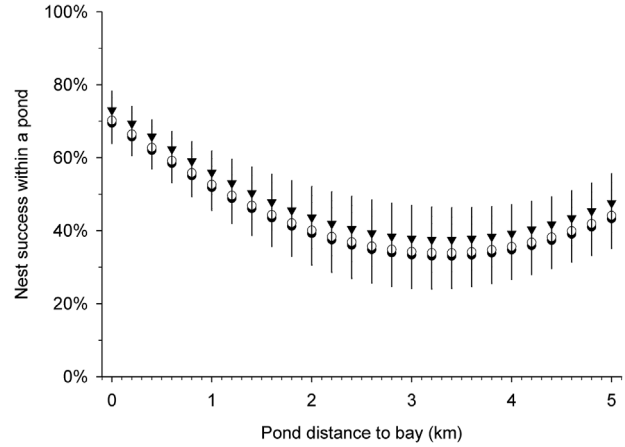

Figure 3. Nest success for American avocets (filled circles), black-necked stilts (unfilled circles), and Forster's terns (triangles) according to pond distance to San Francisco Bay, California, USA, 2005–2013. We derived pond nest success estimates (±SE) from back-transformed model-averaged predictions from all candidate linear mixed models, where all other variables were set to their mean value.

be uninformative parameters (Table 2). As with nest abundance, model predictions of the effect of distance to bay on nest success within ponds exhibited a U-shaped pattern, in which nest success decreased as a pond's distance to the bay increased to approximately 3 km, and then thereafter nest success increased slightly (Fig. 3).

Island Scale

We monitored 3,050 avocet, 250 stilt, and 5,805 tern nests on 100 islands within 22 ponds during 2005–2013. The average annual number of nests per island was 12 (range = 1–145) for avocets, 4 (range = 1–14) for stilts, and 45 (range = 1–305) for terns. The most parsimonious model describing nest abundance on islands included the effects of species, a linear term for island shape index, and a quadratic term for distance to bay, had an Akaike weight of 0.17, and was 1.25 times more likely than the second-ranked model (Table 3). Five other models were competitive, and each was similar to the top-ranked model but also included a linear term for distance to pond levee (2 models), a linear term for island size (1 model), a quadratic term for distance to pond levee (1 model), and a quadratic term for island shape index (2 models). However, the variables distance to pond levee and island size did not improve model fit and were considered uninformative parameters. Using evidence ratios, we found that the top-ranked model was 3.08×10^{36} times more likely than a similar model but without species, 2,443 times more likely than a similar model but without island shape index, and 55.3 times more likely than a similar model but without distance to bay. Model-averaged parameter estimates indicated large species differences in nest abundance on islands, with terns being most numerous, followed by avocets and then stilts (Table 4, Fig. 4). Further, distance to bay and island shape index were important predictors of nest abundance on islands (Table 4). As with the pond-scale analysis, model predictions of the effect of distance to bay on nest abundance on islands exhibited a U-

Table 3. Akaike's Information Criterion (AIC) scores for linear mixed models of the effects of island characteristics on waterbird nest abundance on 100 islands and nest success on 44 islands in managed ponds of South San Francisco Bay California, USA, 2005–2013. All models include year and pond as a random effect. Nest abundance models with a cumulative model weight of 75% plus the null model and nest success models with a cumulative model weight of 60% plus the null model are shown.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Evidence ratio[f]
Nest abundance – island scale					
Species + shape index + distance to bay + distance to bay^2	9	1,442.9	0.00	0.17	1.00
Species + shape index + distance to bay + distance to bay^2 + distance to levee	10	1,443.3	0.45	0.14	1.25
Species + shape index + shape index^2 + distance to bay + distance to bay^2 + distance to levee	11	1,443.6	0.73	0.12	1.44
Species + shape index + distance to bay + distance to bay^2 + distance to levee + distance to levee^2	11	1,443.9	1.05	0.10	1.69
Species + shape index + shape index^2 + distance to bay + distance to bay^2	10	1,444.4	1.52	0.08	2.14
Species + shape index + distance to bay + distance to bay^2 + island size	10	1,444.8	1.92	0.07	2.61
Species + shape index + distance to bay + distance to bay^2 + island size + distance to levee	11	1,445.3	2.47	0.05	3.44
Species + shape index + shape index^2 + distance to bay + distance to bay^2 + island size	11	1,446.4	3.53	0.03	5.85
Null	4	1,623.6	180.76	0.00	0.00
Nest success – island scale					
Distance to bay + distance to bay^2 + distance to levee	7	156.1	0.00	0.14	1.00
Distance to bay + distance to bay^2 + distance to levee + island size	8	157.1	1.01	0.08	1.66
Distance to bay + distance to bay^2 + distance to levee + distance to levee^2	8	157.3	1.21	0.08	1.83
Distance to bay + distance to bay^2 + distance to levee + species	9	158.1	1.99	0.05	2.71
Distance to bay + distance to bay^2 + distance to levee + shape index	8	158.2	2.18	0.05	2.97
Distance to bay + distance to bay^2 + distance to levee + distance to levee^2 + island size	9	158.7	2.63	0.04	3.72
Distance to bay + distance to bay^2 + distance to levee + island size + island size^2	9	159.2	3.16	0.03	4.87
Distance to bay + distance to bay^2 + distance to levee + island size + shape index	9	159.3	3.22	0.03	5.01
Distance to bay + distance to bay^2 + distance to levee + shape index + shape index^2	9	159.4	3.36	0.03	5.36
Distance to bay + distance to bay^2 + distance to levee + distance to levee^2 + shape index	9	159.5	3.42	0.03	5.54
Distance to bay + distance to bay^2 + distance to levee + distance to levee^2 + species	10	159.6	3.50	0.02	5.74
Distance to bay + distance to bay^2 + distance to levee + island size + species	10	159.6	3.57	0.02	5.96
Distance to bay + distance to bay^2 + shape index + shape index^2	8	160.0	3.97	0.02	7.30
Null	4	160.2	4.18	0.02	8.08

[a] Distance to bay: distance to San Francisco Bay; distance to levee: distance to the nearest surrounding pond levee; island size: area of the island; shape index: measure of island perimeter to island area.
[b] The number of parameters in the model including the intercept and variance.
[c] Akaike's Information Criterion corrected for small sample size.
[d] The difference in the AIC_c values of the current model and the model with the lowest AIC_c.
[e] Akaike model weight. The likelihood of the model given the data, relative to other models in the candidate set.
[f] The weight of evidence that the model with the lowest AIC_c value is better than the current model.

shaped pattern, most notably for terns, and to a lesser extent avocets and stilts, in which nest abundance decreased as a island's distance to the bay increased to approximately 4 km, and thereafter nest abundance increased slightly as distance to the bay increased (Fig. 4a). Model predictions also showed that nest abundance on islands increased as island shape index increased (i.e., became more linear), such that nest abundance was approximately 3 times greater on highly linear islands (shape index = 3.0) than on rounded islands (shape index = 0.9; Fig. 4b).

We examined nest success among 2,430 avocet, 51 stilt, and 5,675 tern nests on 44 islands within 20 ponds during 2005–2013. The most parsimonious model describing nest success on islands included a quadratic term for distance to bay and a linear term for distance to nearest pond levee, had an Akaike weight of 0.14, and was 1.66 times more likely than the second-ranked model (Table 3). Three other models were competitive, and each was similar to the top-ranked model but also included species (1 model), a linear term for island size (1 model), or a quadratic term for distance to pond levee (1 model). However, these variables did not improve model fit and were considered uninformative parameters. Using evidence ratios, we found that the top-ranked model was 11.4 times more likely than a similar model but without distance to bay, and 11.4 times more likely than a similar model without distance to pond levee. Model-averaged parameter estimates indicated that distance to bay and distance to pond levee were important predictors of nest success on islands (Table 4). Model predictions indicated that nest success decreased with island distance to bay to approximately 4 km, and thereafter nest success increased as distance to the bay increased (Fig. 5a), and nest success increased as island distance to pond levee increased, such that islands 300 m from the pond levee exhibited nest success rates approximately 1.8 times higher than islands 10 m from the pond levee (Fig. 5b).

DISCUSSION

Islands within managed wetland ponds once used as salt evaporation ponds provide critical nesting habitat to waterbirds in South San Francisco Bay. However, the results of our study indicate that nest abundance and nest success of avocets, stilts, and terns on islands varied markedly according to key island and pond landscape characteristics. Distance to San Francisco Bay greatly affected nest abundance and nest success at the pond and island scales of analysis. Specifically, nest abundance and nest success were high within ponds and on individual islands <1 km from the bay. Because breeding

Table 4. Model-averaged parameter estimates, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits, and relative variable importance (VI) for their effects on American avocet, black-necked stilt, and Forster's tern nest abundance and nest success on individual islands in South San Francisco Bay, California, USA, 2005–2013.

Effect[a]	Estimate	SE	LCL	UCL	VI
Nest abundance – island scale					
Intercept	2.04148	0.54252	0.97815	3.10482	1.00
Island size	0.15675	0.23125	−0.29650	0.61001	0.23
Island size^2	−0.12212	0.18429	−0.48332	0.23909	0.07
Distance to bay	−0.51160	0.23420	−0.97063	−0.05258	0.14
Distance to bay^2	0.07780	0.03124	0.01657	0.13904	0.80
Distance to levee	0.00051	0.00314	−0.00563	0.00666	0.39
Distance to levee^2	0.00002	0.00002	−0.00001	0.00005	0.15
Shape index	0.62530	0.29587	0.04540	1.20520	0.70
Shape index^2	−0.09118	0.09465	−0.27669	0.09434	0.30
American avocet	−1.15536	0.12144	−1.39339	−0.91733	1.00
Black-necked stilt	−2.44638	0.16311	−2.76607	−2.12669	1.00
Nest success – island scale					
Intercept	0.887594	0.170831	0.552765	1.222423	1.00
Island size	−0.061157	0.095761	−0.248848	0.126534	0.30
Island size^2	0.019733	0.084045	−0.144995	0.184462	0.09
Distance to bay	−0.253022	0.101854	−0.452657	−0.053388	0.06
Distance to bay^2	0.038268	0.013400	0.012004	0.064531	0.83
Distance to levee	0.001921	0.001389	−0.000801	0.004644	0.54
Distance to levee^2	−0.000006	0.000007	−0.000021	0.000008	0.24
Shape index	−0.098965	0.153658	−0.400134	0.202205	0.23
Shape index^2	0.043182	0.036571	−0.028498	0.114861	0.13
American avocet	−0.065769	0.049193	−0.162188	0.030650	0.24
Black-necked stilt	−0.160499	0.157462	−0.469125	0.148127	0.24

[a] Distance to bay: distance to San Francisco Bay; distance to levee: distance to the nearest surrounding pond levee; island size: area of the island; shape index: measure of island perimeter to island area.

terns, avocets, and stilts primarily forage in ponds, tidal marshes, and managed marshes (Ackerman et al. 2007, Demers et al. 2010, Bluso-Demers et al. 2016), nesting close to these preferred foraging habitats may be more attractive, prompting greater nest abundance on near-bay islands and ponds. Moreover, near-bay nesting locations are farther from urban centers and therefore may have lower disturbance and numbers of nest predators, which could correspond to greater nest success. Nest abundance, and to a lesser extent nest success also was higher within ponds >4 km from the bay relative to ponds 2–4 km from the bay. This result is due mostly to the influence of 2 ponds, both of which were more than 3.5 km from San Francisco Bay and historically have had large numbers of nesting waterbirds. Greater nest success within ponds and on islands close to and far from the bay also may be the result of the greater nest abundance observed in such ponds and islands. Larger nesting colonies may exhibit lower nest predation rates and greater nest success because of more effective predator detection and deterrence and greater predator swamping (Brunton 1999). Terns, avocets, and stilts aggressively mob potential egg and chick predators (Robinson et al. 1999, McNicholl et al. 2001, Ackerman et al. 2013). If large colonies are more effective at driving away potential nest predators than small colonies, the effect of proximity to the bay on nest success may instead have more to do with greater nest abundance, communal colony defense, and predator swamping than other ecological factors.

Nest abundance also was greater within ponds with relatively few islands (i.e., <5) compared to ponds with many islands (i.e., >5), and total island area within a pond had no effect on nest abundance. Thus, a pond with a few, relatively small (i.e., <1 ha) islands exhibited similar or greater numbers of waterbird nests as a pond with many (i.e., >5), relatively large (i.e., >1 ha) islands. This result may seem counterintuitive because ponds and islands with more potential nesting area may be expected to support more nesting waterbirds. Yet, the availability of food resources within a pond may limit the total number of nesting birds it may support. If island nesting area within a pond can support more nesting waterbirds than can be supported by the food resources within the pond, large portions of the nesting area will go unoccupied. Further, terns, avocets, and to a lesser extent stilts, are colonial nesters (Robinson et al. 1999, McNicholl et al. 2001, Ackerman et al. 2013) and have high affinity for nesting near conspecifics and heterospecifics (Hartman et al. 2016). Individual islands, once settled upon by a few individuals, are likely more attractive to other prospecting birds than unoccupied islands, resulting in the formation of nesting colonies on only a few islands within a pond even though many islands are available. In such instances, additional islands within a pond contribute little to maintaining waterbird nesting populations.

At the island scale, island size had no influence on nest abundance on individual islands. Thus, small islands averaged similar nest numbers compared to large islands. Previous studies have reported that some waterbirds nest in greater numbers on small- to intermediate-sized islands compared to large islands, perhaps to avoid predators large islands may harbor (Erwin et al. 1995, Eason et al. 2012). We

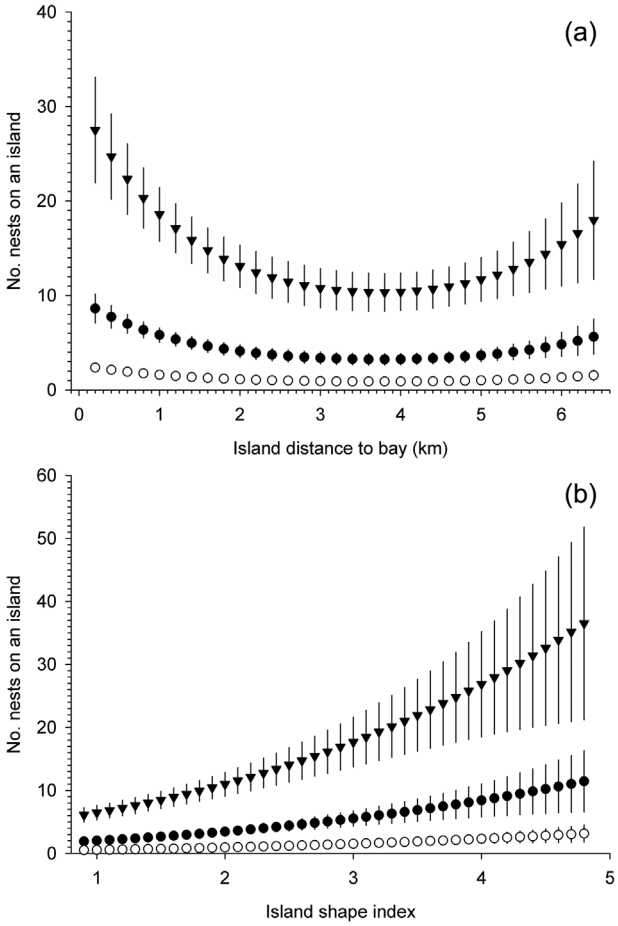

Figure 4. Nest abundance for American avocets (filled circles), black-necked stilts (unfilled circles), and Forster's terns (triangles) according to (a) island distance to San Francisco Bay, California, USA and (b) island shape index, 2005–2013. Higher shape indices denote more linear-shaped islands. We derived island nest abundance estimates (±SE) from back-transformed predictions from all candidate linear mixed models, where all other variables were set to their mean value.

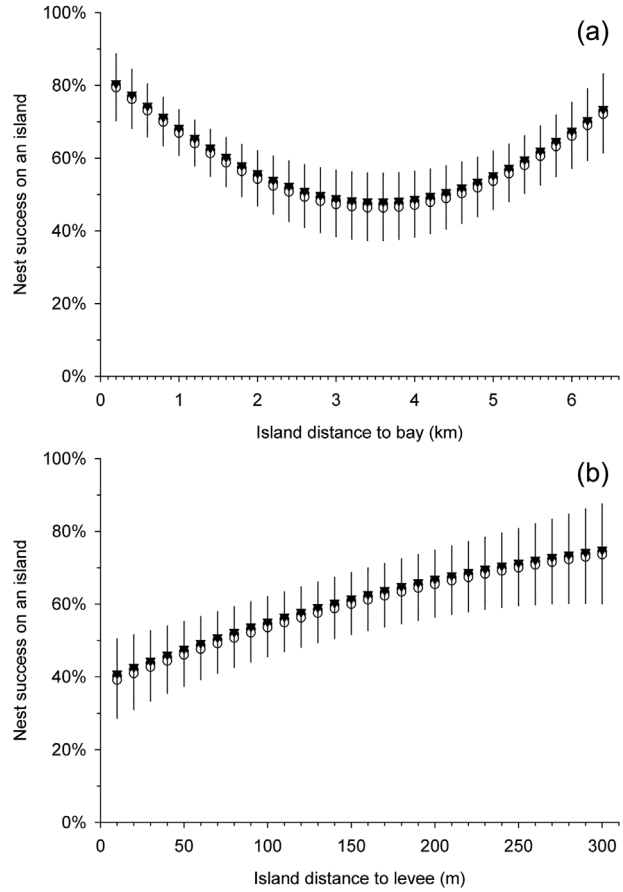

Figure 5. Nest success for American avocets (filled circles), black-necked stilts (unfilled circles), and Forster's terns (triangles) according to (a) island distance to San Francisco Bay, California, USA and (b) island distance to the nearest surrounding pond levee, 2005–2013. We derived island nest success estimates (±SE) from back-transformed model-averaged predictions from all candidate linear mixed models, where all other variables were set to their mean value.

suspect that preference for nesting near water exhibited by avocets, stilts, and terns contributed to similar numbers of nests between large and small islands. On small islands, virtually all of the available nesting area is within a few meters of the water's edge. In contrast, on large islands, much of the available nesting area is in interior areas of the island farther from the water's edge. Thus, large and small islands may actually have similar amounts of preferred nesting area than would be predicted by island size alone. However, one potential limitation of small, elongated islands is that they are more vulnerable to erosion (Erwin et al. 1995). Creating islands that are protected from erosion, or ones that are slightly larger and rounder than what may be optimal for breeding waterbirds may be one means for mitigating against erosion.

Island shape was an important predictor of nest abundance on individual islands. Linear-shaped islands had more nests than rounded islands, with the highest nest abundance observed in highly elongated islands with large perimeters relative to area. Nest abundance was predicted to be almost 3 times greater on an island with a shape index of 3.0 (i.e., island roughly 34 times longer than wide) relative to a round island (shape index of 0.9). Previous studies have reported that many waterbirds, including terns and shorebirds, often nest within a few meters of the water's edge (Cuervo 2004, Stenhouse et al. 2005, Maxson et al. 2007, Eason et al. 2012). In a companion study, we report that the probability of nesting peaked on island patches that were 2 m and 7 m from the water among terns and avocets, respectively (Hartman et al. 2016). Because highly elongated islands contain disproportionately more preferred habitat near water, they may attract a greater number of nesting waterbirds than would rounded islands, or even slightly elongated islands of the same size. Large rounded islands, on the other hand, are dominated by less attractive interior habitat far from the water's edge, and therefore are of considerably lower value for the management of waterbirds that prefer near-water nesting sites. Large rounded islands also are attractive to invasive nesting gull colonies, which compete with waterbirds for nesting habitat and can be voracious predators of tern and shorebird chicks (Jones and Kress 2012; Ackerman et al. 2014*a*, *b*).

Nest success was greater on islands farther from surrounding pond levees, such that nest success on islands 300 m from the nearest surrounding pond levee was nearly twice as high as on islands only 10 m from the nearest surrounding pond levee. In a previous study on nest predation in South San Francisco Bay, 71% of identifiable predations of avocet and stilt nests were caused by mammals, including raccoon (*Procyon lotor*), striped skunk *(Mephitis mephitis*), and gray fox (*Urocyon cinereoargenteus*; Herring et al. 2011). Islands farther from pond levees may be less accessible to mammalian predators, thereby improving nest success.

MANAGEMENT IMPLICATIONS

The results of this study demonstrate that island nesting habitat is critical for breeding waterbirds in San Francisco Bay, particularly terns and avocets, and that creating near-bay island nesting habitat would most benefit nesting populations. Within individual ponds of coastal wetlands, a few ($n \leq 5$), relatively small (<1 ha), linear-shaped islands away from surrounding levees would provide waterbirds with preferred nesting habitat that confers relatively high nest success. Perhaps due in part to the colonial nature of these species, the presence of many islands within a pond did not increase nest abundance or nest success. In fact, >5 large (>1 ha) islands within a pond may be counterproductive because predatory gulls may congregate, roost, and even nest in ponds with extensive island nesting habitat. Thus, rather than creating many islands within one pond, a more effective strategy may be to create a few islands within many ponds. Doing so would distribute potential nesting habitat over a larger area, and may insulate the overall breeding populations from local environmental fluctuations (e.g., food availability, predation pressure) that can reduce breeding success within coastal wetlands.

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