Research Article

Waterbird Nest-Site Selection is Influenced by Neighboring Nests and Island Topography

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ABSTRACT Avian nest-site selection is influenced by factors operating across multiple spatial scales. Identifying preferred physical characteristics (e.g., topography, vegetation structure) can inform managers to improve nesting habitat suitability. However, social factors (e.g., attraction, territoriality, competition) can complicate understanding physical characteristics preferred by nesting birds. We simultaneously evaluated the physical characteristics and social factors influencing selection of island nest sites by colonial-nesting American avocets (*Recurvirostra americana*) and Forster's terns (*Sterna forsteri*) at 2 spatial scales in San Francisco Bay, 2011–2012. At the larger island plot (1 m^2) scale, we used real-time kinematics to produce detailed topographies of nesting islands and map the distribution of nests. Nesting probability was greatest in island plots between 0.5 m and 1.5 m above the water surface, at distances <10 m from the water's edge, and of moderately steep (avocets) or flat (terns) slopes. Further, avocet and tern nesting probability increased as the number of nests initiated in adjacent plots increased up to a peak of 11–12 tern nests, and then decreased thereafter. Yet, avocets were less likely to nest in plots adjacent to plots with nesting avocets, suggesting an influence of intra-specific territoriality. At the smaller microhabitat scale, or the area immediately surrounding the nest, we compared topography, vegetation, and distance to nearest nest between nest sites and paired random sites. Topography had little influence on selection of the nest microhabitat. Instead, nest sites were more likely to have vegetation present, and greater cover, than random sites. Finally, avocet, and to a lesser extent tern, nest sites were closer to other active conspecific or heterospecific nests than random sites, indicating that social attraction played a role in selection of nest microhabitat. Our results demonstrate key differences in nest-site selection between co-occurring avocets and terns, and indicate the effects of physical characteristics and social factors on selection of nesting habitat are dependent on the spatial scale examined. Moreover, these results indicate that islands with abundant area between 0.5 m and 1.5 m above the water surface, within 10 m of the water's edge, and containing a mosaic of slopes ranging from flat to moderately steep would provide preferred nesting habitat for avocets and terns. © 2016 The Wildlife Society.

KEY WORDS American avocet, Forster's tern, nest microhabitat, nest-site selection, real-time kinematics, *Recurvirostra americana*, social attraction, spatial scale, *Sterna forsteri*, topography.

Nest-site selection, whereby individuals use environmental cues to choose nest sites, often results in distinct patterns of habitat patch occupancy (Martin 1998, Clark and Shutler 1999, Kolbe and Janzen 2002). If nesting in preferred habitat provides a fitness advantage, nesting habitat preferences may be adaptive and maintained by natural selection (Martin

1998, Clark and Shutler 1999). In such instances, knowledge of the proximate cues used by birds to select nesting habitat could be used by managers to promote nesting and maximize nest success. Yet, where birds choose to place their nests can be dependent on a range of factors (Buckley and Buckley 1980, Jones 2001), including physical characteristics such as topography (Whittingham et al. 2002, Anteau et al. 2012), vegetation cover and nest predation risk (Martin 1993, Eggers et al. 2006), disturbance (Chen et al. 2011, McCarthy and Destefano 2011), and intra- and interspecific social factors (e.g., attraction, territoriality, competition; Reed and Dobson 1993, Quintana and Yorio 1998, Monkkonen and Forsman 2002). Social factors can complicate understanding

the physical characteristics preferred by nesting birds. For example, social attraction may induce individuals to nest in habitat with less preferred physical characteristics if that habitat is near conspecifics or heterospecifics nesting in preferred habitat (Stamps 1988, Giraldeau et al. 2002). Alternatively, intra- and interspecific territoriality and competition may prevent individuals from nesting in preferred sites (Buckley and Buckley 1980, Cody 1981). Thus, among highly social and colonial-nesting species, simultaneous evaluation of the effects of physical characteristics and social factors on nest-site selection may provide a more accurate assessment of preferred nesting habitat.

Nest-site selection may also occur at multiple, hierarchical spatial scales, with selection of small-scale microhabitat dependent on selection of the larger scale habitat patch (Johnson 1980, Orians and Wittenberger 1991). Moreover, birds may use different proximate cues to select a habitat patch than they do to select the nest microhabitat. An individual may select an island on which to nest using landscape features such as location, size, and shape; the patch within the island according to island topographic features; and the nest location according to microhabitat topography and vegetation cover. Management actions that neglect to incorporate multiple spatial scales of nest-site selection may not provide suitable nesting habitat for target species.

We evaluated the influence of physical characteristics and social factors on waterbird nest-site selection at 2 spatial scales in co-occurring American avocets (*Recurvirostra americana*; hereafter avocets) and Forster's terns (*Sterna forsteri*; hereafter terns). At the larger island plot scale, we examined how the physical topography of islands and the distribution and abundance of neighboring nests affected selection of 1-m^2 island plots for nesting. At the nest microhabitat scale, or the area immediately surrounding the nest, we evaluated microhabitat topography, vegetation, and proximity to the nearest active nest. At both of these spatial scales, we examined the influence of conspecific and heterospecific nests.

STUDY AREA

We studied nest-site selection of avocets and terns in San Francisco Bay, California, USA in 2011 and 2012. San Francisco Bay has a Mediterranean climate, with warm (20–22°C), dry summers and mild (15–17°C), wet winters. The avian community in San Francisco Bay is large and diverse (Takekawa et al. 2011, 2012), with >1 million waterbirds using the estuary annually (Page et al. 1999, Stenzel et al. 2002). Important habitats for waterbirds include tidal marshes, seasonal wetlands, and former salt evaporation ponds (Goals Project 1999). Former salt ponds provide breeding habitat for many waterbirds, especially avocets and terns, which along with California gulls (*Larus californicus*) are among the most numerous breeding waterbird species present. Islands within these ponds provide nesting habitat for 75% of avocets and 80% of terns breeding in South San Francisco Bay (Strong et al. 2004, Ackerman et al. 2013). These islands, many of which were constructed from dredge material, are composed of clay soils with little to moderate vegetation cover. We focused our study on 24 nesting islands within 9 former salt evaporation ponds of 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). These islands varied in size from 0.01 ha to 0.25 ha, whereas ponds varied in size from 62 ha to 277 ha. Elevation of island habitat ranged from 0 m to 1.5 m above the water surface and island topographies ranged from complex and bumpy to gradually sloping. Pickleweed (*Sarcocornia pacifica*) and alkali heath (*Frankenia salina*) were the dominant vegetation types on islands.

METHODS

Field Methods

We collected topographic data over the surface of 24 nesting islands. At each island, we collected Universal Transverse Mercator (UTM) coordinates (horizontal accuracy: ≤3.75 cm) and elevation above sea level data (vertical accuracy: ≤3.75 cm) using real-time kinematics (RTK; Leica Smart Rover GPS1200, Leica Geosystems, Atlanta, GA, USA) at each point along a predefined grid, where points were spaced by 1 m. We collected island topographic data in August and September 2011 (23 islands) and 2012 (1 island) after chicks had fledged. Using these data, we developed digital elevation models (DEMs) at a resolution of 1 m^2 for each island using inverse distance weighted (IDW) interpolation with the Spatial Analyst extension 10.2 for ArcMap 10.2 (Environmental Research Systems Institute, Redlands, CA, USA). From these DEMs, we calculated the maximum slope and corresponding aspect of each 1-m^2 island plot using the Spatial Analyst extension 10.2 for ArcMap 10.2. We calculated the elevation above the water surface of each plot by subtracting the water surface elevation of each pond (measured in early May) from the elevation above sea level generated from the DEMs. Additionally, we used RTK to trace each nesting island's perimeter at the water's edge in 2011. During the nesting season, water levels in salt ponds remained relatively static and were similar between 2011 and 2012. In ponds where water levels were different in 2012 than in 2011, we re-traced island perimeters. Using these island perimeters, we measured the distance to the water's edge of the centroid for each 1-m^2 island plot using the Near Geoprocessing Tool in ArcMap 10.2.

We monitored nests under the guidelines of the United States Geological Survey, Western Ecological Research Center's Animal Care and Use Committee. We entered avocet and tern nesting colonies once a week during the nesting season (Apr–Aug). We marked nests with a uniquely numbered aluminum tag placed outside the nest bowl. At each weekly visit, we recorded clutch size, floated eggs to estimate embryo age (Ackerman and Eagles-Smith 2010), and determined if each nest was active or inactive. We estimated nest initiation date by subtracting the clutch size and the average embryo age for eggs in the nest at the initial visit from the date of the initial visit. For each nest, we used a randomly generated azimuth (0–359°) and distance (1–10 m)

from the nest to obtain a paired random site representing available microhabitat, and marked it with a uniquely numbered aluminum tag. We placed a 1-m^2 frame centered on the nest bowl, or tag at a random site, so that the sides of the frame faced the cardinal directions. We visually estimated percent cover of vegetation and water to the nearest 1% over the entire 1-m^2 area and estimated the average vegetation height to the nearest 0.5 cm with a ruler. We divided the 1-m^2 frame into 9 equal cells (3 × 3 grid; each cell 0.33 m × 0.33 m) and visually estimated and recorded the dominant cover type within each cell. Dominant cover types included bare ground, water, litter, or species of vegetation.

After nesting had concluded, we returned to colony sites and centered the 1-m^2 frame at the same nest and random site locations. We recorded the UTM coordinates (accuracy: ≤3.75 cm), and elevation above sea level (accuracy: ≤3.75 cm) of the nest bowl or random site with RTK. At a subset of nests, we measured elevation at 16 points within the 1-m^2 frame to produce a microhabitat surface topographic profile around each nest and random site; points were spaced every 0.33 m and corresponded to the intersections of the 3 × 3 grid. Lastly, we measured elevation at the 2 highest and 2 lowest points within the 1-m^2 frame, with the restriction that only 1 high and 1 low point could be in any one of the 9 grid cells. Thus, for each nest and random site, we collected 21 data points: 1 at the nest or random site tag, 16 at the intersections of the 3×3 grid, 2 representing elevation maximums, and 2 representing elevation minimums.

Using 20 of these points (excluding the elevation at the nest or random site tag), we developed DEMs at a resolution of 0.33 m^2 around each nest and random site using IDW interpolation (Spatial Analyst extension 10.2 for ArcMap 10.2). Because avocets and terns sometimes build up their nests with vegetation and other materials, we elected to omit the elevation taken from the nest bowl when interpolating elevation because this point would create a high point in the center of the surface topography that did not exist at the time of nest-site selection. For consistency, we also omitted the elevation taken at the random site tag.

We calculated the maximum slope and corresponding aspect (Spatial Analyst extension 10.2 for ArcMap 10.2) from each nest- and random site-specific DEM. We quantified the ruggedness of the topography of each nest and random site by calculating a vector ruggedness measure (VRM) following Sappington et al. (2007), and using the Vector Ruggedness Measure script for ArcGIS. Briefly, VRM is a measure of terrain ruggedness that incorporates heterogeneity of slope and aspect. The primary advantage of VRM is that it allows ruggedness to be calculated more independently of slope than other methods such that steep rugged areas can be distinguished from areas that are steep but not rugged. The resulting VRM is a unitless value ranging from 0 (flat surface) to 1 (highly rugged surface; Sappington et al. 2007). We calculated the elevation above the pond's water surface for each nest and random site by subtracting the water surface elevation of each pond from the elevation of the nest and random site above sea level. We

measured the distance to water for each nest and random site using the island perimeters and the Near Geoprocessing Tool in ArcMap 10.2. Finally, using initiation dates and the dates when nests first became inactive (failed or hatched), we developed chronologies for each nest and then measured the distance of each nest, at the time of its initiation, to the closest active nest using the Near Geoprocessing Tool in ArcMap 10.2.

Statistical Analyses

Nest–site selection at the island plot scale.—Using nest coordinates, we assigned each 1-m^2 island plot as used or not used by nesting avocets and used or not used by nesting terns in each breeding season and developed resource selection probability functions (RSPFs; Manly et al. 2002) to model avocet and tern probability of nesting according to topographic features and social factors.

We used generalized linear mixed models (PROC GLIMMIX, SAS/STAT software, release 9.4, SAS Institute, Cary, NC, USA), with a binomial distribution and logit link function to model the probability that an island plot was used for nesting by avocets or terns. We evaluated the class variable year and 4 physical characteristic variables of island plots: elevation above the water surface, slope, aspect (analyzed using the cosine of aspect in radians), and distance to the water's edge from the plot centroid. We used 4 social factor variables to describe the presence and abundance of nearby nesting birds: number of bordering plots (0–8) that were used by nesting conspecifics, number of bordering plots (0–8) that were used by nesting avocets or terns, number of conspecific nests initiated in bordering plots, and number of avocet and tern nests initiated in bordering plots. By evaluating these 4 social factor variables, we could examine if the presence and abundance of nesting conspecifics only had more or less of an influence on nesting probability than the presence and abundance of any waterbird nest (avocet or tern). Because these 4 social factor variables were highly correlated ($r^2 = 0.51$–0.97), we allowed only 1 to be included in any given model. Allowing for this restriction, we built a balanced set of candidate models based on all combinations of the class variable year, and linear and quadratic terms for the physical characteristic variables, and quadratic terms for each of the 4 social factor variables, plus the null model (810 candidate models). In all models, we included nesting island as a random effect. Because avocets and terns did not always nest on the same islands, we conducted separate analyses for each species.

Nest–site selection at the microhabitat scale.—At the microhabitat scale, we used conditional logistic regression for matched-pairs data (PROC LOGISTIC, SAS/STAT software) to model microhabitat vegetation and topographic characteristics affecting nest-site selection. We matched individual nests and their corresponding random site with the strata option. We used a binomial distribution and logit link function to model the probability that a site was a nest rather than a random site. Unlike the used-versus-unused design in our island plot scale analysis, this used-versus-available design does not yield the true probability of use but

Table 1. Model selection results for logistic regression mixed models for the probability that an island plot was used for nesting by American avocets or Forster's terns in South San Francisco Bay, California, USA, 2011 and 2012. All models include nesting island as a random effect. Only the top models that represented 0.75 cumulative model weights, and the null model are presented.

Model	K^a	$-2LogL$	AIC_c^b	ΔAIC_c^c	w_i^d	Evidence ratio[e]
American avocets						
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific nests + no. bordering conspecific nests^2 + slope	10	2,888.3	2,908.3	0.0	0.30	1.00
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific nests + no. bordering conspecific nests^2 + slope + slope^2	11	2,887.8	2,909.8	1.5	0.14	2.14
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope	10	2,890.2	2,910.2	1.9	0.12	2.58
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific nests + no. bordering conspecific nests^2 + slope + aspect	11	2,888.2	2,910.2	2.0	0.11	2.65
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific nests + no. bordering conspecific nests^2 + slope + aspect + aspect^2	12	2,887.2	2,911.2	2.9	0.07	4.27
Year + elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope + slope^2	11	2,889.7	2,911.7	3.4	0.05	5.56
Null	2	3,062.8	3,066.8	158.5	1.14×10^{-35}	2.61×10^{34}
Forster's terns						
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2	8	2,220.0	2,236.0	0.0	0.09	1.00
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2	7	2,222.1	2,236.1	0.1	0.09	1.04
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + aspect	9	2,219.0	2,237.0	1.0	0.06	1.67
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + aspect	8	2,221.3	2,237.3	1.3	0.05	1.88
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + year	8	2,221.4	2,237.5	1.5	0.05	2.07
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + year	9	2,219.5	2,237.5	1.5	0.04	2.10
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope + slope^2	9	2,219.6	2,237.6	1.6	0.04	2.21
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + aspect + aspect^2	10	2,217.6	2,237.7	1.7	0.04	2.28
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + aspect + aspect^2	9	2,219.8	2,237.9	1.9	0.04	2.53
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope	9	2,220.0	2,238.0	2.0	0.03	2.72
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope + slope^2	10	2,218.0	2,238.1	2.0	0.03	2.78
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope	8	2,222.1	2,238.1	2.1	0.03	2.82
Elevation + elevation^2 + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + year + aspect	10	2,218.5	2,238.5	2.5	0.03	3.47
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + year + aspect	9	2,220.6	2,238.6	2.6	0.03	3.70
Elevation + distance to water + distance to water^2 + no. bordering conspecific plots + no. bordering conspecific plots^2 + slope + slope^2 + aspect	10	2,218.7	2,238.7	2.7	0.02	3.84

(*Continued*)

Table 1. (*Continued*)

Model	K^a	−2LogL	AIC_c^b	ΔAIC_c^c	w_i^d	Evidence ratio[e]
Elevation + distance to water + distance to water² + no. bordering conspecific plots + no. bordering conspecific plots² + slope + slope² + aspect + aspect²	11	2,216.9	2,238.9	2.9	0.02	4.30
Elevation + distance to water + distance to water² + no. bordering conspecific plots + no. bordering conspecific plots² + slope + slope² + year	10	2,218.9	2,239.0	3.0	0.02	4.41
Elevation + elevation² + distance to water + distance to water² + no. bordering conspecific plots + no. bordering conspecific plots² + slope + slope² + aspect	11	2,217.0	2,239.0	3.0	0.02	4.50
Null	2	2,982.3	2,986.3	750.3	1.14×10^{-164}	8.28×10^{162}

[a] The no. parameters in the model.
[b] Akaike's Information Criterion corrected for small sample size.
[c] The difference in the AIC_c values of the current model and the model with the lowest AIC_c.
[d] Akaike model weight. The likelihood of the model given the data, relative to other models in the candidate set.
[e] The weight of evidence that the model with the lowest AIC_c value is better than the current model.

rather yields the relative probability of microhabitat use (Manly et al. 2002).

We evaluated 11 microhabitat variables: 1) vegetation presence (yes or no); 2) percent vegetation cover; 3) percent water cover; 4) average vegetation height; 5) slope; 6) aspect; 7) surface ruggedness; 8) distance to water; 9) elevation above the water surface; 10) distance to the nearest active conspecific nest; and 11) distance to the nearest active avocet or tern nest. Again, because of strong correlations among the cover variables vegetation presence, percent vegetation cover, percent water cover, and average vegetation height, we allowed only 1 of these variables to be included in any given model. Similarly, because of strong correlation between distance to the nearest active conspecific nest and distance to the nearest active nest, we allowed only 1 of these 2 variables to be included in any given model. Allowing for these restrictions, we evaluated a balanced set of additive models that incorporated all linear combinations of the 11 predictor variables (479 candidate models).

We used an information-theoretic approach and second-order Akaike Information Criterion (AIC_c; Burnham and Anderson 2002) to rank models. 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 best 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 the beta parameters of the variables 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 of the models in the candidate set. We used evidence ratios to compare the relative weight of support between models. Furthermore, we used evidence ratios to determine the importance of each variable in the best model, by comparing the likelihood of the best model to the same model structure but with one of the variables omitted. At the microhabitat scale, we used standardized odds ratios calculated from the model-averaged parameter estimates to further evaluate the effect size for each variable. We standardized odds ratios for continuous variables by calculating them at the first and third quartile

values of the random site data (Harrell 2001). In this way, we scaled odds ratios for each variable relative to the amount of variability of that variable across the study area, thereby allowing for direct comparison of effect size among variables.

We also investigated potential differences in the distribution of vegetation around nests relative to random sites. We constructed a 2×2 contingency table with the number of nests and random sites where the cell was dominated by vegetation, and the number of nests and random sites where the cell was not dominated by vegetation (i.e., dominated by bare ground or water) separately for each of the 9 microhabitat grid cells (each cell $0.33 \text{ m} \times 0.33 \text{ m}$). We used McNemar's test (Zar 1999) for matched pairs with a χ^2 statistic to test for differences in vegetation cover between nests and random sites in each grid cell. We considered differences significant at $P \leq 0.05$.

RESULTS

Nest-Site Selection at the Island Plot Scale
We recorded locations of 345 avocet nests (2011: $n = 263$, 2012: $n = 82$) and 1,022 tern nests (2011: $n = 506$, 2012: $n = 516$). Avocets initiated nests between 24 March and 19 July ($\bar{x} \pm 1$ SD: 19 May ± 27 days, $n = 340$), whereas terns initiated nests between 25 April and 22 July ($\bar{x} \pm 1$ SD: 17 June ± 14 days, $n = 1,001$). However, whereas avocets nested within all ponds where terns nested, terns did not nest within all avocet-nesting ponds. Considering only ponds where both avocets and terns nested, avocets initiated nests between 4 April and 19 July ($\bar{x} \pm 1$ SD: 29 May ± 22 days, $n = 192$). Avocets nested on 23 islands in 8 ponds in 2011 and 9 islands in 5 ponds in 2012 (24 different islands), and terns nested on 10 islands in 5 ponds in 2011 and 8 islands in 4 ponds in 2012 (11 different islands). Islands used by nesting avocets contained 29,513 1-m² island plots, whereas islands used by nesting terns contained 3,701 island plots.

The probability that avocets nested within an island plot was best explained by a model that included year, a linear term for plot slope, and quadratic terms for plot elevation, distance to water, and number of conspecific nests initiated in

bordering plots; the model had an Akaike weight of 0.30 and was 2.14 times more likely than the next best model (Table 1). Two other models were competitive (ΔAIC_c < 2.0) and similar to the best model but included either a quadratic term for plot slope, or the number of bordering plots with nesting conspecifics rather than the number of conspecific nests in bordering plots. All models that contained the variables in the best model had a cumulative weight of 0.70. Using evidence ratios, we estimated that the best model was 2.29×10^8 times more likely than the best model without plot elevation, 9.48×10^7 times more likely

than the best model without year, 1.70×10^5 times more likely than the best model without plot distance to water, 3,500 times more likely than the best model without the number of conspecific nests initiated in bordering plots, and 27 times more likely than the best model without plot slope.

Model-averaged predictions indicated that avocet nesting probability increased with plot elevation up to a peak 0.8 m above the water surface and decreased thereafter (Fig. 1a). Similarly, avocet nesting probability increased with plot distance to the water's edge up to a peak of 7 m and then decreased thereafter (Fig. 1b). Moreover, avocet nesting
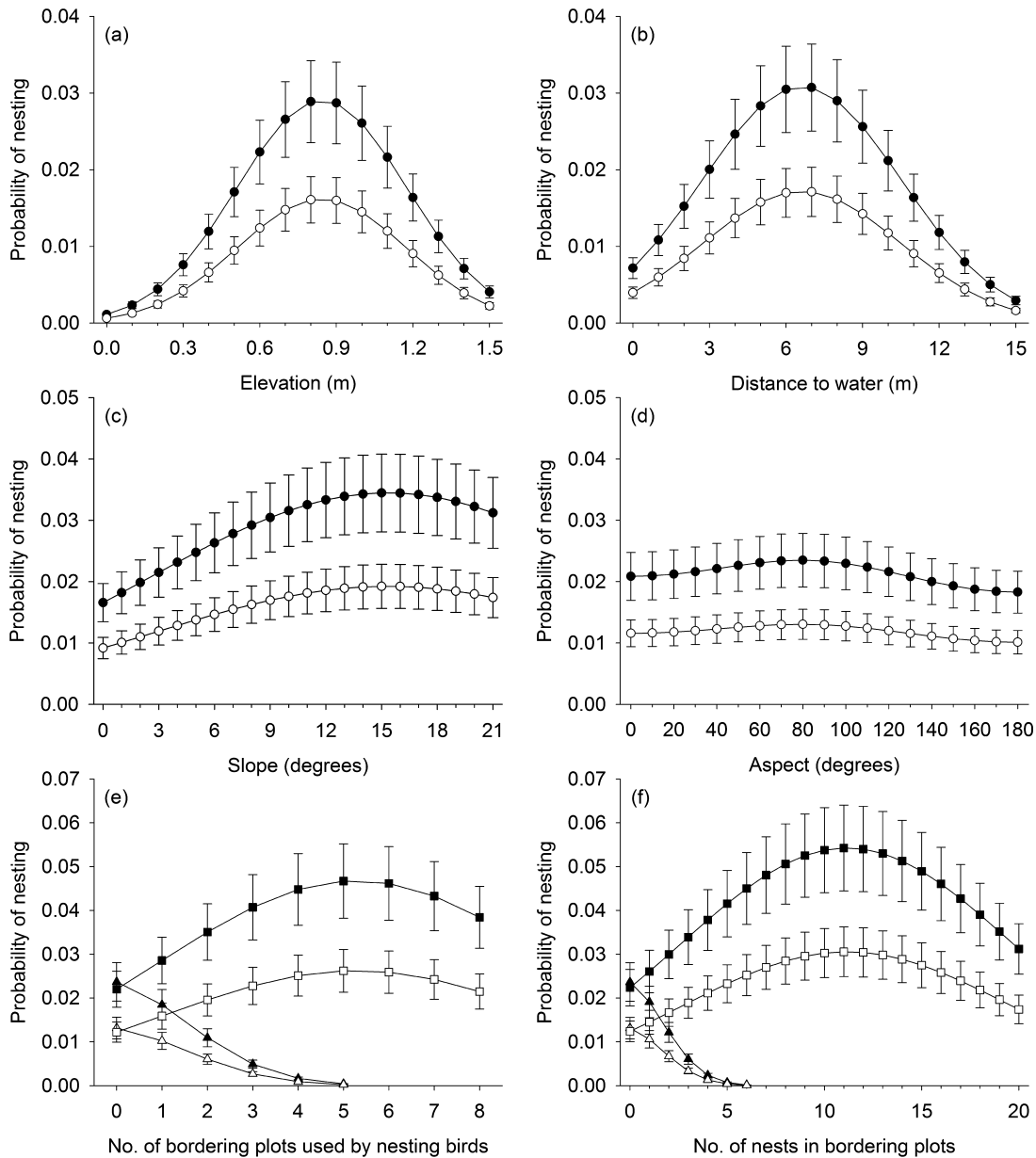

Figure 1. Probability ($\bar{x} \pm$ 95% CI) of American avocets nesting on island plots in South San Francisco Bay, California, USA, 2011 (filled markers) and 2012 (unfilled markers): (a) peaked at an elevation of 0.8 m, (b) peaked at a distance of 7 m from the water's edge, (c) increased as slope increased up to a peak of approximately 15°, (d) was relatively constant among aspect orientations (values 180–360° were converted to 0–180° for presentation), (e) decreased as the number of bordering plots used by avocets (triangles) increased yet increased as the number of bordering plots used by avocet and terns (squares) increased up to a peak of 5 plots, decreasing thereafter, and (f) decreased as the number of bordering avocet nests (triangles) increased, yet increased as the number of bordering avocet and tern nests (squares) increased up to a peak of 11 nests, decreasing thereafter. Each relationship with probability of nesting is displayed at the mean values for all other variables.

probability increased with plot slope, showing that avocets preferred to nest in plots with more steep terrain up to a peak of 15° (Fig. 1c). Conversely, there was little effect of plot aspect on avocet nesting probability (Fig. 1d). Finally, avocet nesting probability decreased with the number of bordering plots used by nesting avocets (Fig. 1e) and the number of avocet nests initiated in bordering plots (Fig. 1f). In contrast, avocet nesting probability increased with the number of bordering plots used for nesting by avocets and terns, and the number of avocet and tern nests initiated in bordering plots up to a peak of approximately 5 bordering plots and 11 bordering nests, decreasing thereafter (Fig. 1e and f).

The probability that terns nested within an island plot was best explained by a model that included quadratic terms for plot elevation, distance to water, and number of bordering plots used by nesting terns; the model had an Akaike weight of 0.09 and was 1.04 times more likely than the next best model, which was similar to the top model but included a linear rather than a quadratic term for plot elevation (Table 1). Eight other models were competitive ($\Delta AIC_c < 2.0$), and each was similar to the best model but included the variables year, plot aspect, plot slope, or had a linear term for plot elevation instead of a quadratic term. However, year, plot aspect, and plot slope did not improve model fit and were considered to be uninformative parameters. Models that contained plot elevation, plot distance to water, and the number of bordering plots used by nesting terns had a cumulative weight of 1.00. The best model was 2.67×10^{56} times more likely than the best model without number of bordering plots used by nesting terns, 8.85×10^{12} times more likely than the best model without plot distance to water, and 2.14×10^7 times more likely than the best model without plot elevation.

Model-averaged predictions indicated that tern nesting probability increased with plot elevation (Fig. 2a), and increased with plot distance to the water's edge up to a peak approximately 2 m from the water's edge, decreasing thereafter (Fig. 2b). In contrast to avocets, terns were slightly more likely to nest in plots with flat to shallow slopes (Fig. 2c), but similar to avocets, plot aspect had little effect on tern nesting probability (Fig. 2d). Tern nesting probability increased as the number of bordering plots used by terns, and bordering plots used by avocets and terns, increased (Fig. 2e). Tern nesting probability also increased as the number of tern nests and the number of avocet and tern nests initiated in bordering plots increased, up to a peak of approximately 10 tern nests and 12 avocet and tern nests, and decreased thereafter (Fig. 2f).

Nest-Site Selection at the Microhabitat Scale

We collected 11 microhabitat variables at the nest site and at a paired random site for 229 avocet nests (2011: $n = 161$, 2012: $n = 68$) and 433 tern nests (2011: $n = 202$, 2012: $n = 231$). The most parsimonious model describing avocet nest microhabitat included the variables vegetation presence, distance to nearest active conspecific nest, and aspect; the model had an Akaike weight of 0.16, and was 2.26 times more likely than the next best model (Table 2). Two other

models were competitive ($\Delta AIC_c < 2.0$), and similar to the best model but also included either surface ruggedness or distance to water. However, surface ruggedness and distance to water did not improve model fit and were considered to be uninformative parameters. Models that contained vegetation presence, distance to nearest active conspecific nest, and aspect had a cumulative weight of 0.86. The best model was 6.09×10^{11} times more likely than the best model without vegetation presence, 408 times more likely than the best model without distance to nearest active conspecific nest, and 2.9 times more likely than the best model without aspect.

Standardized odds ratios indicated that distance to nearest conspecific nest had the greatest effect size among variables, followed by distance to nearest nest of either species, vegetation presence or absence, percent vegetation cover, aspect, and average vegetation height (Table 3). A microhabitat located 3.7 m from the nearest active avocet nest was 5.9 times more likely to be used for nesting by an avocet than a microhabitat 20.6 m from the nearest active avocet nest. In addition, avocet nest sites were 4.1 times more likely to have vegetation present than random sites. Lastly, a microhabitat with a more southern aspect (138°) was 1.6 times more likely to be used by nesting avocets than a microhabitat with a more northern aspect (53°).

The most parsimonious model describing tern nest microhabitat included the variables percent vegetation cover, elevation, distance to nearest active conspecific nest, and aspect; the model had an Akaike weight of 0.20, and was 1.69 times more likely than the next best model (Table 2). Three other models were competitive ($\Delta AIC_c < 2.0$), and similar to the best model but also included slope, surface ruggedness, or both. However, slope and surface ruggedness did not improve model fit and were considered to be uninformative parameters. Models that contained percent vegetation cover, elevation, distance to nearest active conspecific nest, and aspect had a cumulative weight of 0.66. The best model was 860 times more likely than the best model without percent vegetation cover, 240 times more likely than the best model without elevation, 23 times more likely than the best model without distance to nearest active conspecific nest, and 6 times more likely than the best model without aspect.

Standardized odds ratios indicated that percent vegetation cover had the greatest effect size among variables, followed by elevation, vegetation presence, aspect, and distance to nearest conspecific nest (Table 3). A microhabitat with 75% vegetation cover was 2.6 times more likely to be used for nesting by terns than a microhabitat with 0% vegetation cover. Similarly, microhabitats at an elevation of 0.72 m were 2.5 times more likely to be used for nesting by terns than a microhabitat at an elevation of 0.37 m. Tern nest sites were 1.6 times more likely to have vegetation present than random sites, and microhabitats with a more southern aspect (141°) were 1.4 times more likely to be used by nesting terns than a microhabitat with a more northern aspect (48°). Finally, a microhabitat located 0.6 m from the nearest active tern nest was 1.3 times more likely to be used for nesting by terns than a microhabitat 2.1 m from the nearest active tern nest.
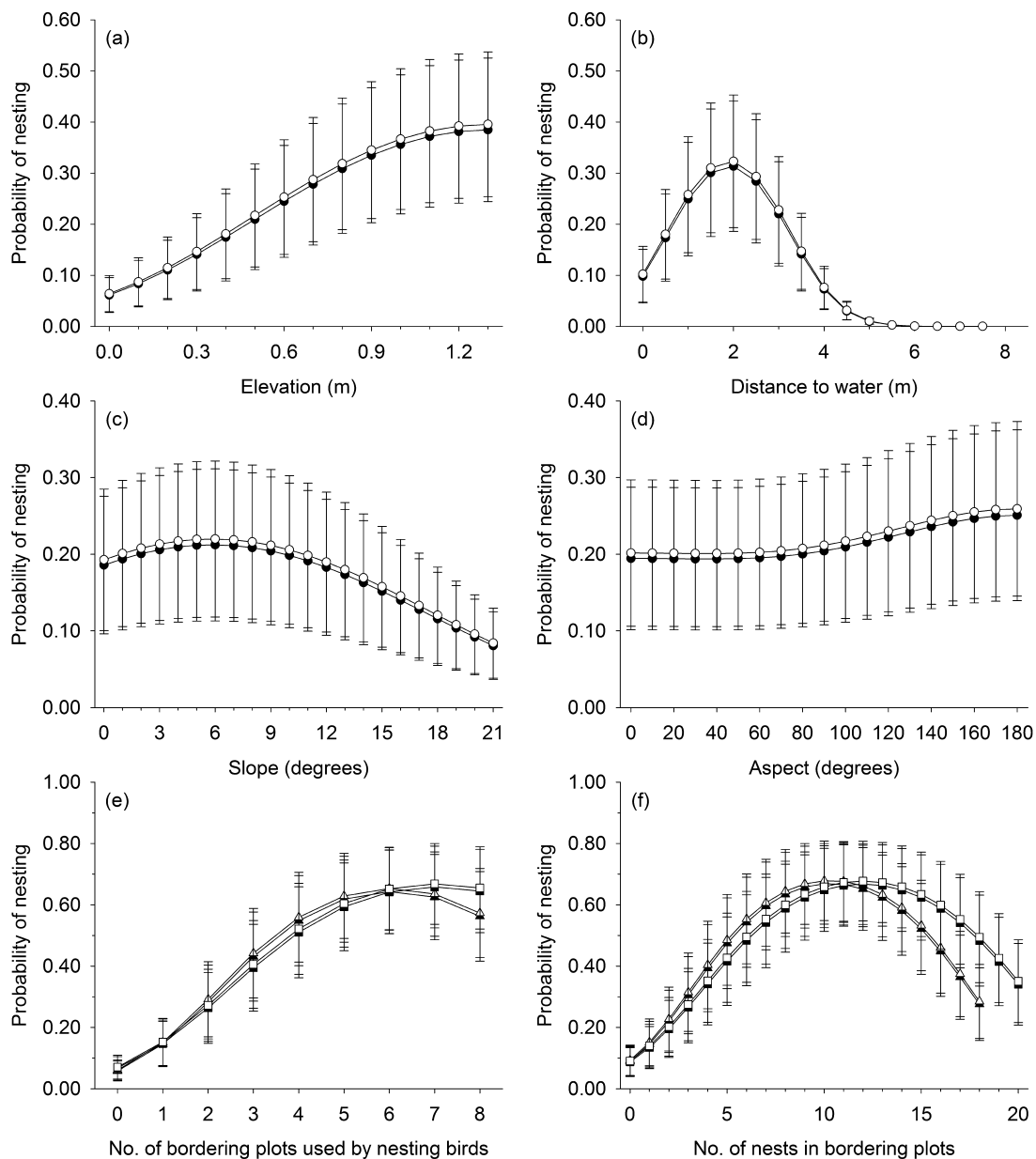
Figure 2. Probability ($\bar{x} \pm 95\%$ CI) of Forster's terns nesting on island plots in South San Francisco Bay, California, USA, 2011 (filled markers) and 2012 (unfilled markers): (a) increased with greater elevation, (b) peaked at a distance of 2 m from the water's edge, (c) decreased slightly as slope increased beyond approximately 10°, (d) was relatively constant among aspect orientations (values 180–360° were converted to 0–180° for presentation), (e) increased as more bordering plots were used by nesting terns (triangles) and nesting terns and avocets (squares), and (f) increased as the number of bordering tern nests (triangles), and avocet and tern nests (squares) increased up to a peak of 10 tern nests and 12 avocet and tern nests, decreasing thereafter. Each relationship with probability of nesting is displayed at the mean values for all other variables.

We compared dominant cover between nests and random sites in each of the 9 (3×3 grid; each cell 0.33 m $\times$ 0.33 m) microhabitat grid cells for 316 avocet and 648 tern nests. Vegetation, primarily pickleweed and alkali heath, was the dominant cover in the center microhabitat grid cell (the cell where the nest bowl was located) in 30% of avocet nests compared to only 21% of random sites ($\chi^2 = 27.16$, $P < 0.001$; Fig. 3a). Vegetation also was more likely to be the dominant cover type in cells north ($\chi^2 = 9.99$, $P = 0.002$) and east ($\chi^2 = 4.50$, $P = 0.03$) of the center microhabitat cell at avocet nests sites relative to random sites (Fig. 3a). Among terns, vegetation was more likely to be the dominant cover

type within each of the 9 microhabitat grid cells at nest sites relative to random sites (all $\chi^2 \geq 15.20$, $P < 0.001$; Fig. 3b).

DISCUSSION

Our results demonstrate key differences in nest-site selection between co-occurring avocets and terns, and indicate the effects of physical characteristics and social factors on selection of nesting habitat are dependent on the spatial scale. At the larger, island plot scale, avocet and tern nesting probability was most influenced by the physical characteristics elevation above the water surface, distance to the water's edge, and slope. At the smaller, microhabitat scale,

Table 2. Model selection results for conditional logistic regression models evaluating differences between nest microhabitat and the microhabitat of a paired random site for American avocet or Forster's tern nests in South San Francisco Bay, California, USA, 2011 and 2012. Only the top models that represented 0.75 cumulative model weights are presented.

Model	K^a	$-2LogL$	AIC_c^b	ΔAIC_c^c	w_i^d	Evidence ratio[e]
American avocet						
Vegetation presence + distance to conspecific nest + aspect	3	246.1	252.2	0.0	0.16	1.00
Vegetation presence + distance to conspecific nest + aspect + ruggedness	4	245.7	253.8	1.6	0.07	2.26
Vegetation presence + distance to conspecific nest + aspect + distance to water	4	245.8	253.9	1.8	0.06	2.41
Vegetation presence + distance to conspecific nest + aspect + slope	4	246.1	254.1	2.0	0.06	2.69
Vegetation presence + distance to conspecific nest + aspect + elevation	4	246.1	254.2	2.0	0.06	2.76
Vegetation presence + distance to conspecific nest	2	250.3	254.3	2.1	0.05	2.87
Vegetation presence + distance to conspecific nest + aspect + ruggedness + slope	5	245.1	255.2	3.0	0.03	4.51
Vegetation presence + distance to conspecific nest + slope	3	249.3	255.3	3.2	0.03	4.84
Vegetation presence + distance to conspecific nest + aspect + ruggedness + distance to water	5	245.5	255.6	3.4	0.03	5.52
Vegetation presence + distance to conspecific nest + distance to water	3	249.8	255.8	3.6	0.03	6.17
Vegetation presence + distance to conspecific nest + aspect + ruggedness + elevation	5	245.7	255.8	3.7	0.02	6.27
Vegetation presence + distance to nest + aspect	3	249.8	255.8	3.7	0.02	6.27
Vegetation presence + distance to conspecific nest + aspect + distance to water + slope	5	245.8	255.9	3.8	0.02	6.51
Vegetation presence + distance to conspecific nest + aspect + distance to water + elevation	5	245.8	256.0	3.8	0.02	6.63
Vegetation presence + distance to conspecific nest + aspect + slope + elevation	5	246.1	256.2	4.0	0.02	7.46
Vegetation presence + distance to conspecific nest + elevation	3	250.2	256.2	4.1	0.02	7.62
Vegetation presence + distance to conspecific nest + ruggedness	3	250.3	256.3	4.1	0.02	7.90
Vegetation presence + distance to conspecific nest + ruggedness + slope	4	248.4	256.5	4.3	0.02	8.55
Forster's tern						
Vegetation cover + elevation + distance to conspecific nest + aspect	4	546.9	554.9	0.0	0.20	1.00
Vegetation cover + elevation + distance to conspecific nest + aspect + slope	5	545.9	556.0	1.1	0.12	1.69
Vegetation cover + elevation + distance to conspecific nest + aspect + slope + ruggedness	6	544.4	556.5	1.6	0.09	2.21
Vegetation cover + elevation + distance to conspecific nest + aspect + ruggedness	5	546.6	556.7	1.8	0.08	2.41
Vegetation cover + elevation + distance to conspecific nest + aspect + distance to water	5	546.8	556.9	2.0	0.07	2.70
Vegetation cover + elevation + distance to conspecific nest + aspect + slope + distance to water	6	545.8	557.9	3.0	0.04	4.56
Vegetation cover + elevation + distance to conspecific nest	3	552.4	558.5	3.6	0.03	5.94
Vegetation cover + elevation + distance to conspecific nest + aspect + slope + ruggedness + distance to water	7	544.3	558.5	3.6	0.03	5.95
Vegetation cover + elevation + distance to conspecific nest + aspect + ruggedness + distance to water	6	546.5	558.6	3.7	0.03	6.36
Vegetation cover + elevation + distance to conspecific nest + slope	4	550.8	558.8	3.9	0.03	7.04
Vegetation presence + elevation + distance to conspecific nest + aspect	4	551.0	559.0	4.1	0.03	7.81
Vegetation cover + elevation + distance to conspecific nest + distance to water	4	552.0	560.0	5.1	0.02	12.92

[a] The no. parameters in the model.
[b] Akaike's Information Criterion corrected for small sample size.
[c] The difference in the AIC_c values of the current model and the model with the lowest AIC_c.
[d] Akaike model weight. The likelihood of the model given the data, relative to other models in the candidate set.
[e] The weight of evidence that the model with the lowest AIC_c value is better than the current model.

Table 3. Model-averaged parameter estimates, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits, and standardized odds ratios for variables examined for differences between nest and random site microhabitat of American avocets and Forster's terns in South San Francisco Bay, California, USA, 2011 and 2012.

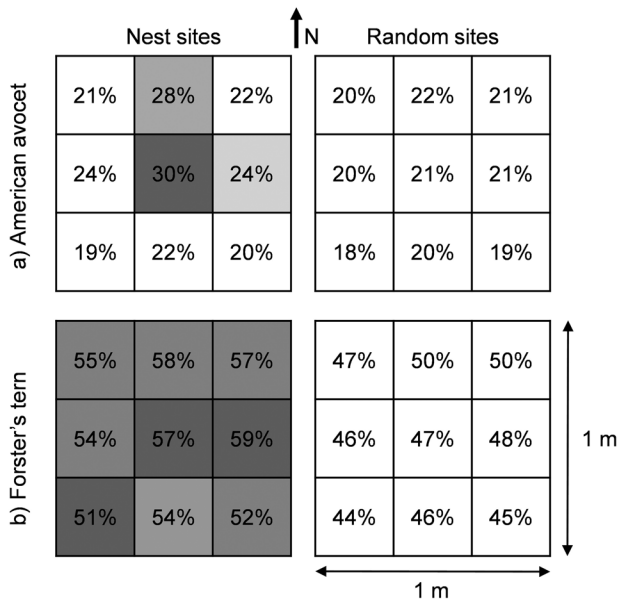| Species	Variable	Estimate	SE	LCL	UCL	Odds ratio
American avocet	Elevation (m)	0.03	0.86	−1.65	1.72	1.02
	Distance to water (m)	0.04	0.07	−0.10	0.18	1.18
	Distance to conspecific nest (m)	−0.10	0.04	−0.18	−0.02	5.86
	Distance to nest (m)	−0.11	0.04	−0.19	−0.02	5.74
	Slope	−0.01	0.02	−0.06	0.03	1.10
	Ruggedness	17.40	25.60	−32.78	67.57	1.03
	Vegetation cover	1.76	0.56	0.66	2.85	2.13
	Vegetation height (cm)	0.06	0.03	0.01	0.11	1.51
	Water cover	−3.05	2.03	−7.01	0.92	1.00
	Aspect	−0.35	0.18	−0.70	0.00	1.60
	Vegetation presence	1.42	0.27	0.88	1.96	4.14
Forster's tern	Elevation (m)	2.55	0.76	1.06	4.03	2.47
	Distance to water (m)	0.00	0.15	−0.30	0.29	1.00
	Distance to conspecific nest (m)	−0.15	0.07	−0.29	−0.02	1.27
	Distance to nest (m)	−0.05	0.06	−0.18	0.07	1.06
	Slope	−0.01	0.01	−0.04	0.01	1.15
	Ruggedness	7.38	9.48	−11.20	25.95	1.04
	Vegetation cover	1.27	0.34	0.61	1.94	2.60
	Vegetation height (cm)	0.01	0.02	−0.02	0.04	1.08
	Water cover	−1.73	1.05	−3.78	0.32	1.05
	Aspect	−0.25	0.11	−0.47	−0.03	1.43
	Vegetation presence	0.44	0.14	0.17	0.71	1.56

Figure 3. The proportion of each nest and random site microhabitat grid cell in which vegetation was the dominant cover type among (a) American avocets and (b) Forster's terns in South San Francisco, California, USA, 2011–2012. More (30%) avocet nests had vegetation cover in the center grid cell, where the nest bowl was located, compared to random sites (21%). More avocet nests had vegetation cover north (28%) and east (24%) of the nest bowl, compared to random sites (22% and 21%, respectively). A greater number of tern nests had vegetation cover within each of the 9 microhabitat grid cells relative to random sites. Shading denotes microhabitat cells in which a significantly ($P \leq 0.05$) greater number of nest sites had vegetation cover than random sites. Darker shading indicates greater differences between microhabitat cells at nest sites and random sites.

vegetation presence, percent vegetation cover, and aspect were most important in distinguishing avocet and tern nest sites from random sites. Lastly, the number, distribution, and proximity of nesting conspecifics and heterospecifics influenced nest-site selection by both species.

Physical Characteristics of Island Plots Used for Nesting

Avocets and terns preferred island plots elevated above the water surface, and near, but not adjacent to, the water's edge. Many waterbirds avoid low elevation, near-water nest sites susceptible to flooding (Storey et al. 1988, Lauro and Burger 1989), and nests at higher elevations often exhibit greater nest success (Rounds et al. 2004, Owen and Pierce 2013). In our study, variability in water management and wave action from high winds often inundated low-lying island areas, particular those on the windward side of islands, and flooding accounted for ≤60% of avocet nest failures in some ponds (Ackerman et al. 2013). Avoidance of low-lying, near-water areas by avocets and terns may reduce the likelihood of nest flooding.

The probability of avocet and tern nesting within island plots also varied according to slope. Avocets preferred steeper slopes, whereas terns preferred flat to shallow slopes. Previous studies reported slope to be a determinant of nest-site selection in terns and shorebirds (Whittingham et al. 2002, Anteau et al. 2012), with these birds typically selecting flatter areas for nesting. Nesting in flatter areas may aid in predator detection and prevent eggs from rolling away during strong winds.

Physical Characteristics of Nest Microhabitat

Vegetation presence, percent vegetation cover, and distribution around the nest were all characteristics influencing avocet and tern nest microhabitat selection. However,

notable difference existed between the species. First, tern nesting areas were more vegetated than avocet nesting areas; 67% of tern random sites contained some vegetation. In contrast, only 43% of avocet random sites contained vegetation. Indeed, many of the islands that were used exclusively by avocets contained very little vegetation. Second, microhabitat at avocet and tern nests was more likely to have vegetation than were the random sites. However, the presence of vegetation most distinguished microhabitat of avocet nests from random sites, whereas a greater amount of vegetation cover most distinguished microhabitat of tern nests from random sites. Thus, although both species preferred microhabitats with some vegetation, a higher degree of vegetation cover (>50%) was more important to nesting terns than avocets. Third, for terns, there appeared to be little if any preference for the distribution of vegetation around the nest; compared to random sites, tern nests were more likely to have vegetation present throughout the microhabitat area. Conversely, avocet nests were only more likely to have vegetation present in the center of the microhabitat area (where the nest bowl was located), and immediately north and east of the nest bowl. Some shorebirds, including avocets, often place their nest immediately adjacent to conspicuous objects, such as livestock dung piles, rocks, and dirt mounds (Grover and Knopf 1982, Colwell and Oring 1990), a behavior that may make the incubating bird less conspicuous to predators, particularly in areas with little vegetation cover (Allen 1980). Selection for vegetation next to the nest bowl may reflect avocets' preference for nesting near conspicuous objects. Furthermore, selection for vegetation immediately north of the nest bowl may protect the nest from northerly winds, which predominate in the region.

Avocet and tern nest microhabitat selection also was affected by aspect; both species' nests were more likely to have south-facing than north-facing slopes relative to random sites. This result is in contrast with our island plot scale analysis where aspect was a relatively unimportant determinant of nest-site selection. Our results suggest that after settling in specific island areas with little or no concern for aspect, smaller-scale nest microhabitats with south-facing slopes are then chosen, an orientation that may afford some protection to nests from northerly winds. Finally, surface ruggedness at the microhabitat scale did not vary between nests and random sites, indicating that avocet and tern nest microhabitats were no more smooth or rugged than available sites.

Conspecific and Heterospecific Interactions on Nest-Site Selection

Nest-site selection was greatly influenced by the number, distribution, and proximity of conspecific and heterospecific nests. The probability that avocets nested in an island plot decreased as the number of bordering plots used by nesting avocets increased, and as the number of avocet nests initiated in bordering plots increased. Thus, avocets appeared to avoid, or were excluded from, island areas immediately adjacent to those used by other nesting avocets. During incubation, avocets defend an area directly surrounding the nest from conspecifics (Gibson 1971). Intraspecific territoriality may explain why avocets were less likely to nest in plots immediately adjacent to plots used by other nesting avocets. At the same time, the probability that avocets nested in a plot increased as the number of bordering plots used by both nesting terns and avocets increased and as the number of tern and avocet nests initiated in bordering plots increased. This result suggests that the potential territoriality expressed by nesting avocets toward conspecifics does not extend to heterospecific terns, and, instead, avocets are more likely to choose nest sites located next to terns. Indeed, previous work reported that nearest neighbor distances for avocets were greater among conspecifics than they were among heterospecifics, including Forster's terns and black-necked stilts (*Himantopus mexicanus*; Ackerman et al. 2013).

The probability that terns nested in an island plot increased with the number of bordering plots used by nesting terns and the number of tern nests initiated in bordering plots over the nesting season. Conspecific attraction to nesting sites has been documented in many colonial waterbird species and has been used to great effect in restoration of seabird breeding colonies (Jones and Kress 2012). Unlike avocets, which are semi-colonial, terns appear more tolerant of closer nearest-neighbor distances of conspecifics. The presence of many conspecifics may signal to individual terns a high-quality breeding site. Furthermore, like many tern species, Forster's terns display aggressive predator mobbing behaviors (McNicholl et al. 2001). In San Francisco Bay, California gulls are important waterbird chick predators, accounting for >50% of Forster's tern and American avocet chick deaths (Ackerman et al. 2014*a*, *b*). By choosing to nest immediately adjacent to many other terns, individual terns and avocets may reduce the probability that their eggs or chicks are depredated, through greater communal mobbing of predators by terns, and predator satiation and dilution (Götmark and Andersson 1984).

Comparison of nest sites and random sites at the microhabitat scale also revealed that proximity to the nearest active nest had a large effect on nesting. At the island plot scale, avocets avoided immediately adjacent plots with conspecific nests; at the microhabitat scale, avocets were more likely to nest nearer to other active avocet nests. This apparent dichotomy suggests that beyond an immediate buffer area of 1–2 m, where intraspecific territoriality may limit or even prevent other avocets from nesting too closely, avocets seek out nest locations close to other avocet nests. Overall, a microhabitat became less likely to be used by nesting avocets or terns as it became farther from the nearest active conspecific nest (in the case of avocets and terns) or heterospecific nest (in the case of avocets). These results demonstrate that avocets and terns have great affinity for nesting near conspecifics, and that avocets also have an affinity for nesting near terns.

MANAGEMENT IMPLICATIONS

We identified optimal characteristics of island habitat for nesting waterbirds that can be used in island construction for

restoration. First, nesting islands should have abundant area between 0.5 m and 1.5 m above the water surface because this range encompasses the preferred elevations of both avocets and terns. Second, both avocets and terns selected island plots close to the water's edge, with nesting probability peaking at 7 m and 2 m from the water's edge for avocets and terns, respectively. This suggests that construction of long and narrow islands 10–15 m wide would maximize habitat within the preferred proximity to water, whereas large, rounded islands would contain more of less preferred habitat farther from the water's edge. Third, orienting linear islands in an east-to-west direction would maximize the amount of area with south-facing slopes preferred by nesting avocets and terns. Fourth, islands with a mix of areas with moderately steep terrain and flatter surfaces would accommodate preferred slopes of both avocets and terns. Finally, avocets and terns were more likely to select nest microhabitats with vegetation; however, tern nests often had greater amounts of vegetation cover, whereas many avocet nests were sparsely vegetated. This suggests that islands with complete vegetation cover would limit nesting by avocets.

ACKNOWLEDGMENTS

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