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RESEARCH

Habitat Use by Breeding Waterbirds in Relation to Tidal Marsh Restoration in the San Francisco Bay Estuary

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ABSTRACT

The South Bay Salt Pond Restoration Project aims to restore many former salt production ponds, now managed for wildlife and water quality, to tidal marsh. However, because managed ponds support large densities of breeding waterbirds, reduction of pond habitat may influence breeding waterbird distribution and abundance. We investigated habitat use associated with breeding, feeding, and roosting behaviors during the breeding season for American Avocets (*Recurvirostra americana*), Black-necked Stilts (*Himantopus mexicanus*), Forster's Terns (*Sterna forsteri*), and Caspian Terns (*Hydroprogne caspia*) in south San Francisco Bay in 2019 after substantial tidal marsh restoration, and compared results to a 2001 survey (before restoration). In 2019, managed ponds (26% of currently available habitat) were selected by waterbirds engaged in breeding behaviors (> 39% of observations), foraging (> 42%), and roosting (> 73%). Waterbirds avoided tidal habitats (43% of available habitat), comprising < 17% of observations of breeding behavior, < 28% of foraging observations, and < 13% of roosting observations. Waterbird densities increased in managed ponds between 2001 and 2019, and decreased in active salt ponds, especially among feeding Avocets (92% decrease) and Stilts (100% decrease). Islands were important for waterbirds observed breeding and roosting (45% of Avocet and 53% of Tern observations). Avocets and Stilts fed primarily on wet bare ground (65% and 58%, respectively), whereas feeding Forster's Terns and Caspian Terns used mostly open water (82% and 93%, respectively). Within ponds, Avocets were associated with islands (131 m closer than expected). Stilts and Forster's Terns were also associated with islands (68 m and 161 m closer than expected), except when feeding (1 m closer and 90 m farther than expected). Avocets and Stilts were associated with pond levees (39 m and 41 m closer than expected), but Forster's Terns were not (9 m closer than

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expected). Our results emphasize the importance of managed ponds for breeding and foraging waterbirds, including islands for breeding and roosting and levees for foraging.

KEY WORDS

American Avocet, behavior, Black-necked Stilt, Black Skimmer, Caspian Tern, Forster's Tern, managed ponds, micro-habitat, nesting islands, tidal marsh restoration

INTRODUCTION

The San Francisco Bay has lost much of its historical tidal wetland habitat, approximately 140 km^2 of which was converted to commercial salt production ponds (Goals Project 1999). Many of these salt ponds (~60 km^2) were (1) transferred from Cargill Salt, Inc. (Newark, California) to the US Fish and Wildlife Service's (USFWS) Don Edwards San Francisco Bay National Wildlife Refuge and the California Department of Fish and Wildlife's (CDFW) Eden Landing Ecological Reserve in 2003, (2) taken out of salt production, and (3) managed as pond habitat for wildlife. Some of these managed ponds have since been restored to tidal action or designated for restoration to tidal marsh habitat as part of the South Bay Salt Pond (SBSP) Restoration Project (*www.southbayrestoration.org).* The restoration of tidal marsh habitat in south San Francisco Bay will provide habitat for tidal marsh-dependent species, including the endangered Ridgway's Rail (*Rallus obsoletus*) and salt marsh harvest mouse (*Reithrodontomys raviventris*), and could both improve water quality and mitigate flood risk (Goals Project 1999, 2015; USFWS and CDFW 2007). However, restoring managed pond habitat to tidal marsh will also reduce the amount of pond habitat available to other wildlife, especially migratory birds. These ponds—initially as commercial salt production ponds and more recently as managed ponds—have been a feature of the south San Francisco Bay wetland landscape for over 150 years. As the amount of natural wetland habitat around the south San Francisco Bay decreased, these ponds became critical breeding and wintering habitat for many waterbird species, and provided migration stop-over sites along the Pacific Flyway (Page et al. 1999; Takekawa et al. 2001; Stenzel et al. 2002; Warnock et al. 2002; Stralberg et al. 2009). To address this, the SBSP Restoration Project recommended that some former salt production ponds be maintained as managed pond habitat into the future (USFWS and CDFW 2007). Tidal marsh restoration is proceeding in phases using an adaptive management framework to monitor the ecological response, evaluate the progress of restoration targets, and ultimately determine how much managed pond habitat (10% to 50%) should remain on the landscape (Trulio et al. 2007; Stralberg et al. 2009). One of the restoration benchmarks influencing that decision is the maintenance of breeding populations of target species, including American Avocets (*Recurvirostra americana*), Black-necked Stilts (*Himantopus mexicanus*), Forster's Terns (*Sterna forsteri*), and Caspian Terns (*Hydroprogne caspia*). As tidal marsh restoration moves forward, loss of managed pond habitat will be offset by enhancement of the remaining managed ponds to maximize the numbers and reproductive success of target waterbird species (Trulio et al. 2007). Managed pond enhancements include active management of water flows, depth, and salinity, as well as construction of new nesting islands and the enhancement of existing islands (e.g., by the addition of gravel) to attract nesting birds (Ackerman, Hartman, Herzog et al. 2014).

Healthy waterbird populations require access to suitable nesting and brood-rearing habitat (often on islands or otherwise protected from predators), as well as nearby foraging habitat and roosting sites (Erwin et al. 1993; Law and Dickman 1998). Previous studies have demonstrated the importance of managed pond habitat (and especially islands) to waterbird species during the breeding season (Hickey et al. 2007; Ackerman et al. 2009; Hartman, Ackerman, Herzog et al. 2016; Hartman, Ackerman, Takekawa et al. 2016). For example, foraging Forster's Terns have been observed in both managed ponds and tidal marshes, but by far the largest percentage of foraging locations were in managed ponds, especially lower- salinity ponds (Ackerman et al.

2008; Bluso-Demers et al. 2016). American Avocets typically forage in the shallow areas at pond edges and are able to exploit prey in both high- and low-salinity ponds (Ackerman et al. 2007; Demers et al. 2008; Takekawa et al. 2009; Demers et al. 2010). Several studies have emphasized the importance for nesting waterbirds of islands within managed ponds (Strong et al. 2004a; Ackerman, Hartman, Herzog et al. 2014; Hartman, Ackerman, Herzog et al. 2016), and Black-necked Stilts are known to use more vegetated micro-habitat for nesting than American Avocets (Ackerman, Herzog, Takekawa et al. 2014).

A region-wide survey of distribution and habitat use in south San Francisco Bay was conducted in May 2001 for two waterbird species: American Avocets and Black-necked Stilts (Rintoul et al. 2003). Given the substantial landscape-level changes that have occurred since the 2001 study, the decline in the breeding populations of several waterbirds (Hartman et al. 2021), and the importance of wildlife population monitoring to the SBSP Restoration Project's adaptive management plan (Trulio et al. 2007), we replicated the May 2001 survey nearly 2 decades later in May 2019. This study is a companion paper to Hartman et al. (2021), which focused on overall distribution, habitat use, and population trends. The supporting data were also published by Hartman and Ackerman (2021). Herein, we investigated micro-habitat use associated with three primary behavior types to understand habitat needs for breeding activities, foraging, and roosting. Our study focused on three of the most numerous species of waterbirds breeding on the ponds (American Avocets, Black-necked Stilts, Forster's Terns), plus two less abundant species (Caspian Terns and Black Skimmers [*Rynchops niger*]), to understand their habitat use in this highly urbanized estuary that is undergoing large-scale tidal marsh restoration. Given previous research that has demonstrated the importance of islands for nesting sites, we predicted that waterbirds of all species exhibiting breeding behaviors would be found primarily in the vicinity of island nesting sites, with the possible exception of Black-necked Stilts, which often nest along vegetated shorelines in addition to islands (Ackerman, Herzog, Takekawa et al. 2014; Hartman et al. 2021). Further, we predicted that wading species (American Avocets and Black-necked Stilts) would primarily forage along island and mainland shorelines where water is shallower, and that the aerial foraging species (Forster's Terns and Caspian Terns) would forage in deeper water within ponds.

MATERIALS AND METHODS

Waterbird Population Survey

We surveyed all of the accessible wetland habitat adjacent to San Francisco Bay that was south of the San Mateo Bridge (Figures 1, A1) in 2019, replicating a previous study conducted in 2001 (Rintoul et al. 2003; Hartman et al. 2021). Densities of focal birds in the full area surveyed in each year are available in the Appendices (Tables A2 and A3). We divided the survey area into complexes based on existing divisions within the Don Edwards San Francisco Bay National Wildlife Refuge (USFWS) and Eden Landing Ecological Reserve (CDFW), as well as municipal boundaries (Figures 1, A1; Table 1). Complexes were then broken up into individual survey units (Figure A1), which could be completely surveyed in ≤1 day in most cases. We surveyed for five species (American Avocets, Black-necked Stilts, Forster's Terns, Caspian Terns, and Black Skimmers) over an 11-day period (May 14 through 24, 2019). Multiple teams surveyed different areas simultaneously, allowing us to cover a large area in the shortest time possible and minimize double-counting (Hartman et al. 2021). Individual observations consisted of one or a group of birds of the same species, within <3 m of one another, in the same habitat, and engaged in the same behavior. For each observation, we recorded species, number of individuals, behavior, main habitat (Table 2) and micro-habitat (Table 3), and we plotted the birds' location within the survey unit on a printed map. These locations were later digitized into a geographic information system (GIS; ArcMap 10.6.1; Environmental Research Systems Institute, Redlands, California) for mapping and spatial analysis (see "Habitat Data" section). We classified behaviors into four main categories:

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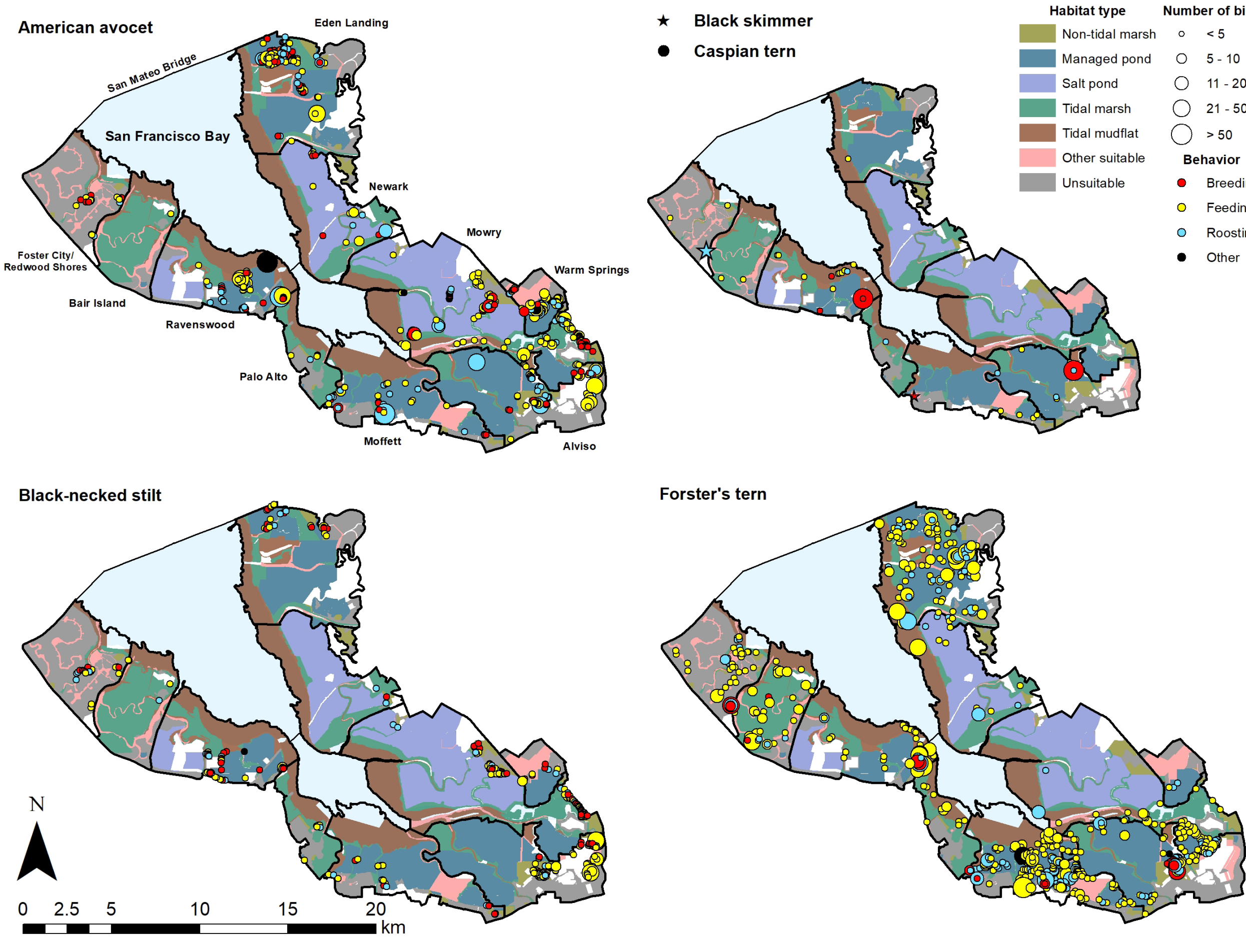

Figure 1 Bird observations and main habitat types in south San Francisco Bay during the May 2019 survey. Observation locations are *color-coded* based on the observed behavior. In cases where multiple behavior-types were recorded, we used a hierarchical approach that prioritized breeding behaviors > feeding > roosting > other. Habitat classifications were updated based on data from a GIS layer provided by the San Francisco Estuary Institute (1998). Pond complex designations are provided in the upper left map. Areas in *white* were not surveyed. The interior of San Francisco Bay is colored a *light blue* for clarity but was not surveyed.

1. **Feeding** (Avocets and Stilts: searching, probing, and dunking their bills in the water; Terns: diving, flying low with head facing down searching for prey);
2. **Roosting** (standing, sitting, preening);
3. **Breeding** (nest-building, incubating, brooding chicks, alarm calling, breeding display, copulation, or predator distraction display);
4. **Other** (walking, swimming, or flushing).

We excluded any birds observed flying over the survey units, since they could not be associated with any particular habitat. Behavioral observations were instantaneous, recording the behavior seen when the bird(s) were first observed. However, since an important goal of the survey was to identify breeding birds, more than one behavior was recorded if, for example, a bird that was originally observed feeding was also later observed engaged in a breeding behavior. In those cases, we recorded the original behavior and the breeding behavior. The survey period in May coincided with peak nesting for American Avocets and Black-necked Stilts in

Table 1 Distribution of waterbirds among wetland complexes in south San Francisco Bay in May 2019, showing percentage (*highest bolded*) of each species and behavior category that were using each complex. Habitat availability is the percentage of suitable habitat (see Table 2) surveyed that was within each complex. + indicates selection (used significantly more than expected based on availability); – indicates avoidance (used significantly less than expected based on availability) based on Fisher's exact tests. NA indicates not applicable because no birds were observed in that behavior category. The behavior category 'Other' was not included in models.

	Alviso	Bair Island	Eden Landing	Foster City/ Redwood Shores	Moffett	Mowry	Newark	Palo Alto	Ravenswood	Warm Springs	Total number of birds
American Avocet											
Breeding	9.5	0.0 –	22.4 +	4.3	5.0 –	**41.5 +**	3.8 –	0.0 –	6.4 –	6.9 +	419
Feeding	22.2 +	0.2 –	21.3 +	1.1 –	3.6 –	**25.2**	2.2 –	0.6 –	10.8	12.8 +	1079
Roosting	16.6 +	0.0 –	14.4	1.8	13.7	15.6 –	2.8 –	0.8 –	**24.9 +**	9.4 +	758
Other	2.2	0.0	0.7	2.9	1.5	5.9	0.0	0.0	**76.5**	10.3	136
Black-necked Stilt											
Breeding	23.8 +	0.0 –	8.3	8.3 +	7.1	**30.4**	1.2 –	0.0 –	17.3	3.6	168
Feeding	**47.0 +**	0.4 –	7.1 –	5.1	5.5 –	23.9	0.0 –	1.9	6.4 –	2.8	532
Roosting	24.3 +	0.7 –	2.7 –	14.2 +	10.8	**25.7**	2.7 –	5.4	12.2	1.4	148
Other	**50.0**	0.0	0.0	25	0.0	0.0	0.0	0.0	25	0.0	4
Forster's Tern											
Breeding	35.7 +	1.5 –	0.0 –	21.8 +	17.3 +	0.0 –	3.4 –	0.0 –	20.3 +	0.0 –	266
Feeding	4.1 –	9.0	27.3 +	4.1 +	**29.7 +**	7.3 –	4.0 –	1.5 –	13.0 +	0.1 –	1448
Roosting	12.1	0.7 –	19.6 +	7.2 +	**34.4 +**	6.2 –	2.7 –	0.0 –	16.8 +	0.4 –	745
Other	5.7	0.0	0.0	0.0	**94.3**	0.0	0.0	0.0	0.0	0.0	35
Caspian Tern											
Breeding	41.0 +	0.0 –	0.0 –	0.0	0.0 –	0.0 –	0.0 –	0.0	**59.0 +**	0.0	144
Feeding	13.8	10.3	3.4	6.9	13.8	0.0 –	0.0	0.0	**51.7 +**	0.0	29
Roosting	33.1 +	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.4 –	**66.5 +**	0.0 –	239
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Black Skimmer[a]											
Breeding	0.0	0.0	0.0	20.0	**80.0**	0.0	0.0	0.0	0.0	0.0	5
Feeding	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Roosting	0.0	0.0	0.0	**88.9**	11.1	0.0	0.0	0.0	0.0	0.0	54
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Habitat availability	10.9	8.4	14.5	2.6	10.8	22.0	13.9	6.7	10.5	2.7	

a. [a]Too few observations to compare statistically

south San Francisco Bay (Ackerman, Herzog, Takekawa et al. 2014). However, as Forster's Tern peak nesting occurs a few weeks later (Ackerman and Herzog 2012), breeding behaviors were less prevalent among Forster's Terns than they were for other species. See Hartman et al. (2021) for further details of survey methodology and habitat definitions.

Habitat Data

We entered all 2019 spatial data into ArcMap™ for mapping and spatial analysis. We mapped and quantified available habitat in each unit based on a published data layer (SFEI 1998), which we updated based on current aerial imagery and on-the-ground habitat assessments recorded during the 2019 survey. Habitat within each

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Table 2 Main habitat use of waterbirds in south San Francisco Bay in May 2019, showing percentage (*highest bolded*) of each species and behavior category that were using each main habitat type. Habitat availability is the percentage of total suitable habitat area surveyed that was composed of that habitat type. (+) indicates selection (used significantly more than expected based on availability); (–) indicates avoidance (used significantly less than expected based on availability) based on Fisher's exact tests. NA indicates not applicable because no birds were observed in that behavior category. The behavior category 'Other' was not included in models.

	Managed Pond	Salt Pond	Sewage/ holding Pond	Tidal Mudflat	Tidal Marsh	Non-tidal Marsh	Man-made Waterway	Bay	Channel	Vernal Pool	Total number of birds
American Avocet											
Breeding	**39.9 +**	20.3	1.7	2.6 –	13.8 –	16.9 +	1.2	0.0	0.2 –	3.3	419
Feeding	**50.2 +**	2.0 –	8.6 +	10.8 –	10.5 –	13.1 +	0.0 –	0.0	1.7 –	3.1 +	1079
Roosting	**73.4 +**	10.8 –	1.3	1.7 –	3.7 –	7.9 +	0.4	0.0	0.7 –	0.1 –	758
Other	14.0	5.1	0.0	**74.3**	5.1	1.5	0.0	0.0	0.0	0.0	136
Black-necked Stilt											
Breeding	30.4	0.0 –	8.9 +	0.0 –	10.7 –	**47.0 +**	0.0	0.0	0.0	3.0	168
Feeding	**42.5 +**	0.0 –	14.7 +	1.3 –	7.0 –	33.1 +	0.8	0.0	0.0 –	0.8	532
Roosting	33.1	3.4 –	3.4	0.0 –	19.6	**39.2 +**	0.0	0.0	1.4	0.0 –	148
Other	25.0	0.0	0.0	0.0	0.0	**75.0**	0.0	0.0	0.0	0.0	4
Forster's Tern											
Breeding	**56.4 +**	3.4 –	0.0	2.3 –	1.5 –	35.7 +	0.8	0.0	0.0 –	0.0	266
Feeding	**61.1 +**	0.8 –	0.3 –	17.7 –	9.3 –	2.3 –	2.1 +	0.1	6.4 +	0.0 –	1448
Roosting	**76.1 +**	2.8 –	0.0 –	11.0 –	1.5 –	6.0	1.6	0.1	0.8 –	0.0 –	745
Other	**94.3**	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0	35
Caspian Tern											
Breeding	**99.3 +**	0.0 –	0.0	0.7 –	0.0 –	0.0 –	0.0	0.0	0.0	0.0	144
Feeding	17.2	0.0 –	0.0	**44.8**	24.1	3.4	0.0	0.0	10.3	0.0	29
Roosting	**99.2 +**	0.0 –	0.0	0.8 –	0.0 –	0.0 –	0.0	0.0	0.0 –	0.0	239
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Black Skimmer[a]											
Breeding	20.0	0.0	0.0	0.0	0.0	0.0	**80.0**	0.0	0.0	0.0	5
Feeding	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Roosting	**88.9**	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	54
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Habitat availability	25.8	20.6	1.5	21.6	21.3	3.8	0.9	0.2	3.1	1.2	

a. Too few observations to compare statistically.

survey unit was classified into the following main habitat categories (see Table 2):

1. **Managed pond:** most of which were formerly used for salt production, but which USFWS and CDFW currently manage for wildlife;
2. **Salt pond:** currently used for salt production or till owned and managed by commercial salt producers;
3. **Sewage/holding pond;**
4. **Tidal mudflat;**
5. **Tidal marsh;**
6. **Non-tidal marsh;**
7. **Other wetland habitat:** bay, vernal pool, large tidal channel, other man-made waterways;

Table 3 Micro-habitat use of waterbirds in the south San Francisco Bay in May 2019, showing percentage (*highest bolded*) of each species and behavior category that were using each micro-habitat type. Note: row totals may sum to >100% because not all micro-habitat categories are mutually exclusive. Availability of micro-habitats in the study area was not measured. NA indicates not applicable because no birds were observed in that behavior category.

	Channel	Dry pond bottom	Island	Island shoreline	Levee	Levee island	Levee island shoreline	Mainland shoreline	Wet bare ground	Structure	Vegetated	Water	Total number of birds
American Avocet													
Breeding	0.5	9.1	31.3	7.4	5.0	0.0	0.2	17.5	19.6	0.0	21.8	0.7	418
Feeding	2.3	0.7	1.0	3.7	0.3	0.0	2.3	14.2	**64.6**	0.0	9.0	7.6	1079
Roosting	0.5	7.1	8.0	3.3	5.4	0.0	0.5	18.1	**33.0**	0.3	6.6	19.8	758
Other	0.0	1.5	0.7	0.0	0.7	0.0	0.0	6.6	**83.1**	1.5	4.4	1.5	136
Black-necked Stilt													
Breeding	1.8	8.3	2.4	0.0	2.4	0.0	0.0	25.0	16.1	0.0	**63.1**	2.4	168
Feeding	2.1	1.7	0.9	0.6	0.0	0.0	0.0	19.0	**58.3**	0.0	27.6	1.7	532
Roosting	4.7	6.1	0.7	1.4	0.0	0.0	0.0	29.7	23.6	0.0	**45.9**	0.0	148
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**50.0**	0.0	0.0	**50.0**	0.0	4
Forster's Tern													
Breeding	0.0	0.0	**48.5**	4.1	0.0	3.4	0.0	5.3	1.5	0.0	38.0	1.5	266
Feeding	5.7	0.0	0.0	0.0	0.0	0.0	0.0	9.7	2.7	0.0	0.1	81.8	1448
Roosting	0.0	0.0	20.8	2.3	0.0	3.2	0.3	0.1	17.2	52.1	3.4	0.8	745
Other	0.0	0.0	**74.3**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	25.7	35
Caspian Tern													
Breeding	0.7	0.0	98.6	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	144
Feeding	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	**93.1**	29
Roosting	0.0	0.0	**96.7**	0.0	0.8	0.0	0.0	0.0	2.1	0.0	0.0	0.4	239
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Black Skimmer													
Breeding	0.0	0.0	**80.0**	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5
Feeding	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
Roosting	0.0	0.0	40.7	**59.3**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54
Other	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0

8. **Unsuitable habitat**: urban, landfill, grassland, beach.

Salt ponds comprised a wider range of salinities than managed ponds and included very-high-salinity (>250 ppt) crystallizer ponds. For the inter-year comparison, we mapped habitat available in 2001 in the same way as the 2019 data, using historical aerial imagery (Google Earth© Pro 7.3.3.7692 2020) taken as close as possible to when the 2001 survey was conducted.

Within the main habitat categories defined above, we also defined micro-habitat categories per Hartman et al. (2021):

- **Channel:** channel or small slough, within any of the main habitat types;
- **Dry pond bottom:** dry ground within a pond;
- **Island:** dry island substrate > 15 cm from the water's edge;
- **Island shoreline:** in the water ≤3 m from an island or on dry ground on an island ≤15 cm from the water's edge;
- **Levee:** top or side of a levee or dike;

- **Levee island:** dry levee that has been cut to form an island, >15 cm from the water's edge;
- **Levee island shoreline:** in the water ≤3 m from a levee island or on dry ground on a levee island ≤15 cm from the water's edge;
- **Mainland shoreline:** in the water ≤3 m from mainland or on mainland ≤15 cm from the water's edge;
- **Wet bare ground:** exposed mudflats or shallow water ≤10 cm deep, within any of the main habitat types. (This category includes some less permanent, low-lying islands occasionally used for nesting.);
- **Structure:** artificial structure (e.g., wooden duck blind, boardwalk, post);
- **Vegetated:** within or ≤3 m from a vegetated area;
- **Water:** open water >10 cm deep, within any of the main habitat types;

All micro-habitat classifications were mutually exclusive, except for "vegetated," which could be used in addition to another category (e.g., a micro-habitat could be both "island" and "vegetated").

Analysis

We expanded on analyses of bird distribution in the study area reported previously (Hartman et al. 2021) by focusing on habitat use and examining each behavioral category separately, which allowed us to obtain a more complete picture of how these species used the different pond complexes and how they used main habitats and micro-habitats. First, we considered a main habitat type or pond complex to be selected if it was used by a greater number of birds than would be expected based on its availability alone and avoided if it was used less than expected based on its availability. We calculated expected values based on the area of available habitat (area of suitable habitat surveyed in that category × total number of birds / total area of suitable habitat surveyed). To determine selection or avoidance, we performed Pearson's chi-squared tests on the full contingency table for each species and behavior (e.g., feeding Avocets), with p-values simulated based on 2,000 iterations. Significant chi-squared tests ($\alpha = 0.05$) were investigated further with Fisher's exact tests to examine each complex or main habitat type individually (Shan and Gerstenberger 2017). Chi-squared tests assumed that individuals selected locations independently of the presence of other individuals, and p-values should be interpreted with that in mind. Second, we report bird use of micro-habitat by behavior, based on a field assessment of the micro-habitat in the immediate vicinity of each bird observation (Table 3). However, because it was not practical to map micro-habitat in the field during the survey, or to use aerial imagery after the fact (the area of micro-habitat available was too variable over time, depending on tidal stage, management of water levels, etc.), we did not compare bird use to availability for micro-habitats.

Inter-Year Comparisons of Waterbird Distribution and Habitat Use, 2001-2019

To examine changes in distribution and habitat use of birds by behavioral category over time (American Avocets and Black-necked Stilts only), we used the raw data from the 2001 survey reported in Rintoul et al. (2003), which we re-processed to match our 2019 behavior and habitat definitions (Hartman et al. 2021). Because the areas surveyed were not identical in both years (we surveyed a larger area in 2019), all inter-year comparisons were conducted using only data from areas that were surveyed in both 2001 and 2019 (Figure A1). Between 2001 and 2019, availability of certain habitat types changed. For example, approximately 54 km^2 of salt ponds within the study area were converted to managed ponds, and approximately 8 km^2 of managed pond habitat was subsequently converted to tidally-influenced habitat. To compare survey years while controlling for changes in habitat availability, we calculated the percent change in bird densities (number of birds / area of suitable habitat surveyed) between 2001 and 2019 (Table 4).

Waterbird Space Use in Relation to Habitat Features, 2019
We evaluated the influence of habitat features on bird use and distribution within managed pond habitat in 2019 by conducting a detailed spatial analysis that examined the distribution of birds within pond survey units in relation to key habitat features for three focal species: American Avocets, Black-necked Stilts, and Forster's Terns. For this analysis, we used a subset of ponds (including both managed ponds and salt ponds) that (1) contained at least one bird observation in the 2019 survey, (2) were flooded at the time of the 2019 survey (not completely dried out), and (3) for which we could obtain clear enough imagery to delineate all habitat features of interest in 2019. The three main habitat features of interest (selected for their importance to managers) were defined as follows:

1. **Islands:** created purposefully as bird habitat, created as wind break islands to protect levees, or created from dredge spoil accumulation that resulted from ditch construction. We did not include low-lying mud-flat types of islands that were temporarily present as a result of fluctuating water levels which exposed the topography of the pond bottom. Although they may provide useful habitat for birds, availability of such mud-flat islands varies substantially with water levels among and within years, and they are not considered permanent features of these ponds.

2. **Levees:** built-up embankments forming current or former pond boundaries (external and internal).

3. **Levee Islands:** a subset of levees, these islands still form part of the surrounding levee boundaries of ponds, but they have been deliberately breached in at least one place to increase water flow between ponds. Levee cutting is a typical management action to increase water connectivity. Smaller, older, and highly eroded portions of former levees were considered as islands rather than levee islands if they were broken-up to the point that they no longer possessed the characteristic structure of a levee (i.e., long linear shape with steep sides).

We used aerial imagery (Google Earth© Pro 7.3.3.7692 2020) from May 29, 2019 and June 20, 2019 (as close to the 2019 survey window as possible) to delineate all habitat features. In the case of one pond unit (Pond E2; Figure A2), clear images from these dates were not available so we used imagery from the previous year (May 9, 2018), after confirming with managers that there had been no substantial changes to habitat between years. Island features were traced as polygons directly over imagery in Google Earth© Pro, which were then imported into ArcMap™ for analysis. Levee features, because they are larger and less variable over time, were digitized as line features directly in ArcMap™, with reference to the appropriate aerial imagery to ensure that locations of levee breaches were accurate for the time of the survey. To convert levee lines into polygons for spatial analysis, we split lines into segments of similar width, measured the distance from the center line to the water's edge for each segment (at least five measurements were used per segment and then averaged), and used that value as the radius to draw a buffer around the line using the Buffer tool in ArcMap™. In cases where there was no defined levee center through which to draw the line, we traced the shoreline instead, and used a buffer of zero.

We measured the distance from each bird observation to the nearest island, levee, and levee island within the same pond using the Near tool in ArcMap™. All ponds in the analysis contained levees, but not all ponds contained islands or levee islands. Therefore, for analyses involving these habitat features, we limited the data to only the subset of ponds that contained the specific feature(s) of interest (i.e., we only measured the distance from bird locations to the nearest feature in the same pond unit, and removed ponds from analyses that did not contain the specific feature being evaluated). If a bird was observed *on* the habitat feature (i.e., standing on an island or a levee), the distance to that habitat feature was recorded as 0 m. To compare a habitat feature's use to its availability, we used a systematic

Table 4 Percent change in American Avocet and Black-necked Stilt density (number of birds per square kilometer of suitable habitat) by main habitat type (**A**) and wetland complex (**B**) in south San Francisco Bay between 2001 and 2019. Comparison includes only areas that were surveyed in both 2001 and 2019 and excludes areas of unsuitable habitat for waterbirds (e.g., urban areas). Percent change in density was not calculated if the habitat was not represented in the 2001 survey (vernal pools) or if the 2001 density was zero. Note: some of the larger percent increases in density result from very low use in 2001.

	American Avocet				Black-necked Stilt			
	Overall density for all behaviors in 2019 (birds km^{-2})	Percent change in density 2001–2019			Overall density for all behaviors in 2019 (birds km^{-2})	Percent change in density 2001–2019		
		Breeding	Feeding	Roosting		Breeding	Feeding	Roosting
A								
Managed pond	22.5	–58%	+468%	+965%	5.4	+53%	+102%	—
Salt pond	5.4	–70%	–91%	–59%	0.1	–100%	–100%	–90%
Sewage/holding pond	23.2	—	—	+251%	18.6	—	+2062%	+17%
Tidal mudflat	6.5	–3%	+13%	–43%	0.2	—	+238%	—
Tidal marsh	6.0	+269%	+34%	+118%	2.3	–82%	–28%	–15%
Non-tidal marsh	35.5	+18%	+11%	–28%	38.2	+8%	–7%	–27%
Man-made waterway	15.8	—	—	—	2.0	—	—	—
Bay	0.0	—	—	—	0.0	—	—	—
Channel	4.2	—	+105%	—	0.4	—	–100%	—
Vernal pool	60.2	—	—	—	11.5	—	—	—
Overall density for study area in 2019 (birds km^{-2})	13.1	2.3	6.0	4.2	4.3	0.8	2.8	0.8
B								
Alviso	15.8	–74%	+79%	–44%	12.2	–42%	+1%	–69%
Bair Island	0.0	–100%	–100%	–100%	0.0	—	–100%	—
Eden Landing	14.0	–74%	–34%	–23%	1.7	–81%	–59%	–82%
Foster City/Redwood Shores	20.3	—	—	—	23.4	—	—	—
Moffett	7.1	–45%	–59%	+122%	2.1	+176%	–10%	+434%
Mowry	15.6	+347%	+145%	+72%	5.9	+99%	+169%	+468%
Newark	2.1	–94%	–82%	–74%	0.2	–99%	–100%	–89%
Palo Alto	1.6	—	–90%	+5%	2.3	–100%	–12%	+68%
Ravenswood	35.0	+1643%	+2771%	—	5.5	+61%	–28%	+285%
Warm Springs	107.5	–68%	+275%	+49%	5.0	—	—	—
Overall density for study area in 2019 (birds km^{-2})	13.1	2.3	6.0	4.2	4.3	0.9	2.8	0.8

approach to measure available habitat, rather than using a random sampling of locations to estimate availability (Benson 2013). We overlayed a 10-m × 10-m grid (using the Create Fishnet tool in ArcMap™) onto the whole study area, placed points in the center of each cell, and clipped the resulting layer to the extent of each pond unit in the analysis. We then measured nearest distances from each of these "available grid points" to the nearest habitat feature, just as we did for bird locations. We chose a 10-m × 10-m grid size to sample habitat at a scale appropriate to (1) the size of the habitat features of interest and (2) the spatial resolution of the bird location data, which were mapped based on a visual estimation of their position in the unit by the surveyor in the field.

Previous research has shown that water depth is a significant driver of bird use of managed wetlands, with deeper areas mostly unavailable to wading birds (Elphick and Oring 1998; Isola et al. 2000; Takekawa et al. 2009). However, because we lacked detailed topographic data for 87 pond bottoms, we could not directly incorporate water depth in our evaluation of habitat use. Instead, we examined the distance to the managed habitat features that are associated with shallower water (islands and levees). This enabled us to test if breeding, feeding, or roosting behaviors were associated with these managed habitat features.

We conducted statistical analyses in the program R v. 3.6.0 (R Core Team 2019) using linear mixed-effect models with type II Wald chi-squared tests (R packages *lme4*, Bates et al. 2015; *car*, Fox and Weisberg 2019). Distance measurements were right-skewed, so we $\log_e$-transformed the distance data to improve normality of the response variable. Because distances of 0 m were recorded when the bird was directly *on* the feature (e.g., standing on an island), we added a constant value (c) equal to one-half of the minimum non-zero value in the subset of data being tested before transformation. Because each observation consisted of one or more birds (range: 1 to 136 individual birds per observed group of birds), we weighted each observation by the square root of the number of birds in the group so that larger groups provided more weight in the analysis, but without too much influence by the largest groups. Uniform grid points that represented availability were all weighted equally, equivalent to one individual at each location. To compare bird use vs. availability, we conducted models separately for each of the three species we focused on by comparing distances to habitat features from bird locations with distances from uniform grid points. In all models, pond unit was included as a random effect, which nested individual bird (used) and grid center (available) locations within each pond unit: ln(distance to habitat feature + c) ~ location type + pond unit (random), where location type was used or available. We ran separate models for each habitat feature, examining distance to the nearest (1) island, (2) levee (encompassed the whole pond perimeter, which in some cases included levee islands), and (3) levee island. Because some observations included multiple behavior types (for example, if a breeding behavior were observed after a non-breeding behavior), we first ran analyses on the full data set (for each species separately), not including behavior in the models. We then investigated the potential role of behavior in habitat selection by using a hierarchical classification system (breeding > feeding > roosting; with other behaviors [< 2% of birds] excluded) to ensure that each observation was assigned to a single behavior category. We then re-ran models with behavior included as a factor. When data were subset to include only ponds with levee islands, most behavior categories contained too few bird locations to produce meaningful results. We used model-estimated least squares means (R package *emmeans*; Lenth 2020) for post-hoc comparisons among factor levels and for data visualization (means and standard errors were back-transformed using the delta method for standard errors; Seber 1982).

RESULTS

During the 2019 survey, we observed 2,357 American Avocets, 819 Black-necked Stilts, 2,492 Forster's Terns, 412 Caspian Terns, and 59 Black Skimmers (excluding flyovers; Figure 1). Among American Avocets, 18% were engaged in breeding behaviors, 46% were feeding, and 32% were roosting. Among Black-necked Stilts, 21% were engaged in breeding behaviors, 65% were feeding, and 18% were roosting. Among Forster's Terns, 11% were engaged in breeding behaviors, 58% were feeding, and 30% were roosting. Among Caspian Terns, 35% were engaged in breeding behaviors, 7% were feeding, and 58% were roosting. Finally, among Black Skimmers, 8% were engaged in breeding behaviors, 0% were feeding, and 92% were roosting. Note that because some birds were engaged in multiple behaviors concurrently (e.g., feeding while brooding chicks), percentages may sum to more than 100.

Waterbird Habitat Use by Behavior

Suitable habitat for waterbirds in the area during the 2019 survey was composed primarily of

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managed ponds (26%), tidal mudflats (22%), tidal marshes (21%), and salt ponds (21%), with all other categories < 5% each (Table 2). The overall density of focal species throughout the study area was 10.6 American Avocets km^{-2}, 3.7 Black-necked Stilts km^{-2}, and 11.3 Forster's Terns km^{-2} (Table A2). We observed Black Skimmers engaged in breeding behaviors and roosting at only two study locations: at breeding colonies within a managed pond at Foster City/Redwood Shores and within a man-made lake at Moffett (Figure 1). We did not observe any Black Skimmers feeding during this survey.

Pond Habitats

Managed ponds were selected (used more than would be expected by availability alone) by American Avocets ($p < 0.001$; density 22.3 birds km^{-2}; Table A2) and Forster's Terns ($p < 0.001$; density 28.6 birds km^{-2}; Table A2) regardless of behavior (Figure 2; Table 2). A large percentage (30% to 42%, depending on behavior) of Black-necked Stilts used managed ponds, although they were present in lower numbers than other species (density 5.5 birds km^{-2}; Table A2) and Stilts selected managed pond habitat only when observed feeding ($p < 0.001$; Figure 2; Table 2). Caspian Terns that were observed roosting or engaged in breeding behaviors were located almost exclusively in managed ponds (99%, the majority of which were at breeding colonies in just two pond units). All species avoided salt ponds (relative to availability of habitat) regardless of behavior ($p < 0.03$; densities 0.1 to 4.2 birds km^{-2}; Table A2), with the exception of Avocets engaged in breeding behaviors ($p > 0.99$; Figure 2; Table 2).

Non-Tidal Marshes

Non-tidal marshes (such as New Chicago Marsh, which hosted a large mixed-species nesting colony; Figure A2) accounted for only 4% of the entire study area, but were selected by American Avocets ($p < 0.001$; density 31.8 birds km^{-2}; Table A2) and Black-necked Stilts ($p < 0.001$; density 35.4 birds km^{-2}; Table A2) for breeding, foraging, and roosting (Figure 2). The largest percentage of Stilt breeding behaviors was observed in non-tidal marshes (47%). Non-

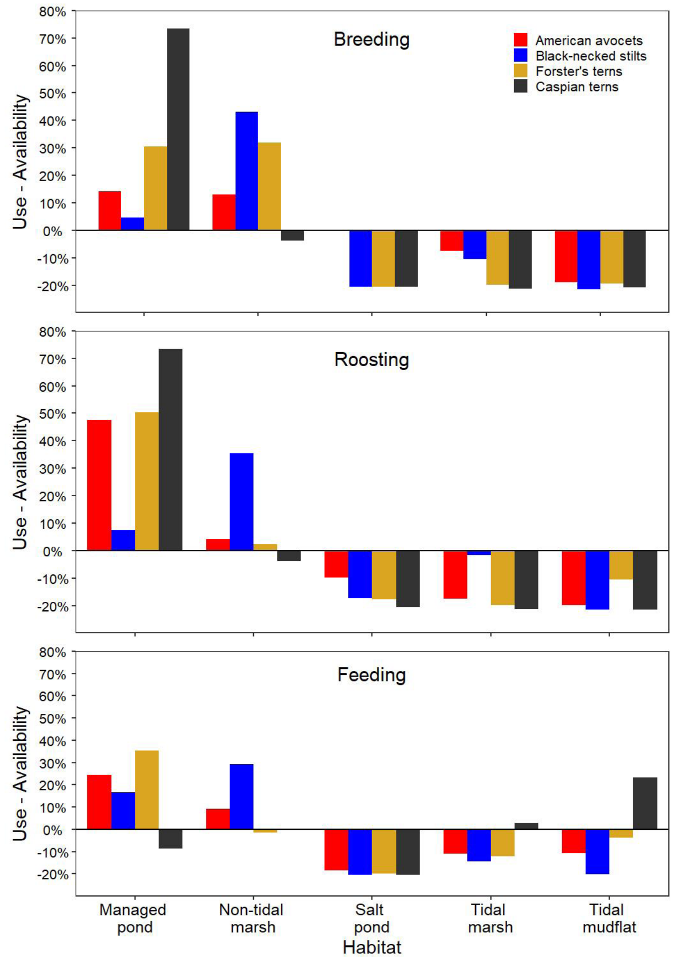

Figure 2 Main habitats used by waterbirds relative to their availability in south San Francisco Bay in May 2019. The y-axis shows the percentage of birds engaged in that behavior relative to the habitats' availability within the study area. *Positive numbers* indicate habitats that were used more than expected based on availability, and *negative numbers* indicated habitats that were used less than expected.

tidal marshes were also used at high densities (20.3 birds km^{-2}; Table A2) by Forster's Terns. Non-tidal marshes were selected by Forster's Terns engaged in breeding behaviors ($p < 0.001$) and avoided by Forster's Terns observed foraging ($p = 0.02$; Figure 2; Table 2).

Tidal Habitats

Species densities were generally low in tidal marshes (4.3 Avocets km^{-2}, 1.6 Stilts km^{-2}, 3.1 Forster's Terns km^{-2}; Table A2) and tidal mudflats (4.9 Avocets km^{-2}, 0.1 Stilts km^{-2}, 7.2 Forster's Terns km^{-2}; Table A2). Feeding Avocets, Stilts, and Forster's Terns avoided tidal marsh and tidal mudflat habitats ($p < 0.02$; Figure 2; Table 2). Avocets were observed feeding in tidal marshes 51% less than expected based on availability and in tidal mudflats 50% less than expected (Figure 2) based on availability. Stilts were observed feeding in tidal marshes 67% less than expected and in tidal mudflats 94% less than expected (Figure 2). Forster's Terns were observed feeding in tidal marshes 57% less than expected and in tidal mudflats 18% less than expected (Figure 2). Only 7% (29 of 412) of Caspian Terns recorded during the survey were observed feeding. These were located primarily in tidal mudflats (45%) and tidal marshes (24%); use was proportional to habitat availability ($p > 0.09$; Figure 2; Table 2). Only Forster's Terns selected channels and man-made waterways for feeding ($p < 0.02$; Table 2).

Waterbird Micro-habitat Use

Overall, most birds were observed on islands, along mainland shorelines (defined as in the water ≤ 3 m from the mainland or on dry ground ≤ 15 cm from the water's edge), in open water, in vegetation, or on wet bare ground, with relatively few birds observed using channels, dry pond bottoms, and levees (> 15 cm from water's edge; Table 3).

Breeding Behaviors

When engaged in breeding behaviors, American Avocets (31%), Forster's Terns (48%), Caspian Terns (99%), and Black Skimmers (80%) were primarily observed on islands (defined as island interiors > 15 cm from water's edge, with island shorelines in a separate category defined as in the water ≤ 3 m from an island or on an island ≤ 15 cm from water's edge; Hartman et al. 2021). This was not the case for Black-necked Stilts, the majority of which were in vegetated areas (63%), along mainland shorelines (25%), or on wet bare ground (16%) when observed engaged in breeding behavior. Vegetated habitat was also used by a large percentage of Avocets (22%) and Forster's Terns (38%) engaged in breeding behaviors, although much of this was driven by a large nesting colony in dense vegetation in the New Chicago Marsh unit of the Alviso complex (Table 3; Figure A2). Most Avocets engaged in nest-related behaviors (nest building and incubation) were observed on islands (36%) and wet bare ground (17%; a category that includes less permanent, low-lying islands occasionally used for nesting). Most Avocet chick brooding was observed along mainland shorelines (49%). Vegetated habitat was frequently used for both nesting and chick-brooding Stilts (72% and 63%, respectively), but mainland shorelines were used by Stilts for chick brooding only (49% of brooding observations, 4% of nesting observations). Note that the category of "vegetated" is not mutually exclusive with other micro-habitat categories.

Feeding Behaviors

When observed feeding, Avocets and Stilts were located primarily on wet bare ground (65% and 58%, respectively), whereas feeding Forster's and Caspian Terns used mostly open water (82% and 93%, respectively), with smaller numbers in channels (both species), along mainland shorelines (Forster's Terns), and over wet bare ground (Caspian Terns; Table 3).

Roosting Behaviors

Forster's Terns were the only species observed commonly making use of structures (e.g., wood pilings) for roosting (Table 3). Most roosting was observed on islands (97% of roosting Caspian Terns, 21% of roosting Forster's Terns), wet bare ground (33% of roosting Avocets, 24% of roosting Stilts, 17% of roosting Forster's Terns), mainland shorelines (18% of roosting Avocets, 30% of roosting Stilts), structures (52% of roosting Forster's Terns), and in vegetation (46% of roosting Stilts; Table 3).

Change in Waterbird Habitat Use by Behavior (2001 vs. 2019)

Forster's Terns, Caspian Terns, and Black Skimmers were not counted in the 2001 survey, so all inter-year comparisons were only made for American Avocets and Black-necked Stilts. Considering the re-classification of approximately 54 km^2 of former salt ponds to managed ponds between 2001 and 2019, American Avocet density in managed ponds increased by 468% for feeding (Table 4A) and 965% for roosting (Table 4A). Use of managed ponds by Black-necked Stilts also increased in 2019 compared to 2001, with the greatest increase occurring for feeding birds (102% increase in density; Table 4A). Over the same time-period, use of the remaining salt pond habitat decreased (even when taking into account the reduced area available), and both Avocets and Stilts avoided salt pond habitats in 2019 (Figure 2, Table 2). The largest decrease in salt pond use was among feeding Avocets (91% decrease in density; Table 4A) and Stilts (100% decrease in density; Table 4A), very few of which were found in salt pond habitats in 2019 (Table 2). Use of tidal mudflats and tidal marshes increased from 2001 to 2019 in some behavior categories as restoration projects increased the availability of those habitats (Table 4A), but in 2019 these habitats were used in proportion to (roosting Black-necked Stilts in tidal marshes) or below (all other categories) what would be expected based on availability alone (Figure 2, Table 2). Table 4 uses densities calculated based on only the area surveyed in both 2001 and 2019. Densities of focal birds in the full area surveyed in each year are available in the appendices (Tables A2 and A3).

Waterbird Space Use in Relation to Habitat Features

Approximately 46% of the suitable habitat surveyed in 2019 consisted of managed ponds and salt ponds. Of the 87 pond units surveyed in 2019, 58 contained at least one of the three species of focus. Of those, 43 pond units fit our criteria for functional pond habitat, which we defined as consisting primarily of open water surrounded by levees and experiencing little or no tidal influence—thereby excluding restored ponds, dry ponds, and ponds that were so shallowly flooded that they contained a large amount of exposed mudflat at the time of the survey. Twenty-five of those pond units contained islands (58%) and 10 units contained levee islands (23%). The ponds included in this spatial analysis contained 817 American Avocets, 59 Black-necked Stilts, and 1,287 Forster's Terns during the 2019 survey (excluding flyovers). Of these, 18% of Avocets, 22% of Stilts, and 3% of Forster's Terns were observed on or within 5 m of a levee, and 22% of Avocets, 14% of Stilts, and 19% of Forster's Terns were observed on or within 5 m of an island.

Overall Space Use

When individuals engaged in all behaviors were grouped together, we found that American Avocets were located significantly closer to islands (mean distance: 4 m, 163 m closer than available grid points; $X^2_1 = 2062.2$, $p < 0.001$, $n = 206$ bird locations; Figure 3A), levee islands (mean distance: 136 m, 131 m closer than available grid points; $X^2_1 = 8.9$, $p < 0.01$, $n = 12$ bird locations; Figure 3B), and levees (mean distance: 13 m, 39 m closer than available grid points; $X^2_1 = 157.8$, $p < 0.001$, $n = 256$ bird locations; Figure 3C) than expected based on availability. Black-necked Stilts were closer than expected to islands (mean distance: 5 m, 68 m closer than available grid points; $X^2_1 = 61.0$, $p < 0.001$, $n = 19$ bird locations; Figure 3D) and levees (mean distance: 8 m, 41 m closer than available grid points; $X^2_1 = 41.3$, $p < 0.001$, $n = 37$ bird locations; Figure 3F), but not levee islands (mean distance: 61 m; 53 m closer than available grid points $F_1 = 0.9$, $p = 0.86$, $n = 3$ bird locations; Figure 3E). Forster's Terns were closer than expected to islands (mean distance: 28 m, 161 m closer than available grid points; $X^2_1 = 630.4$, $p < 0.001$, $n = 160$ bird locations; Figure 3G) and levee islands (mean distance: 214 m, 226 m closer than available grid points; $X^2_1 = 43.6$, $p < 0.001$, $n = 50$ bird locations; Figure 3H), but not levees (mean distance: 65 m, 9 m farther than available grid points; $X^2_1 = 3.2$, $p = 0.07$, $n = 332$ bird locations; Figure 3I). Note that the levee island models were based on smaller sample sizes because there were fewer ponds with levee islands and fewer observations of birds in those ponds.

American Avocets by Behavior

When behavior was included as a factor in the model, American Avocets in all behavior categories were located >90 m closer to islands than expected ($z > 9.0$, $p < 0.001$, $n = 213$ bird locations), with significant differences among all behaviors (breeding vs. feeding: $z = 26.0$, $p < 0.001$; breeding vs. roosting: $z = 14.5$, $p < 0.001$; roosting vs. feeding: $z = 13.1$, $p < 0.001$; Figure 4A). Avocets engaged in breeding behaviors were closest to islands (mean distance: 0 m, 168 m closer than available grid points), followed by birds observed roosting (mean distance: 4 m, 144 m closer than

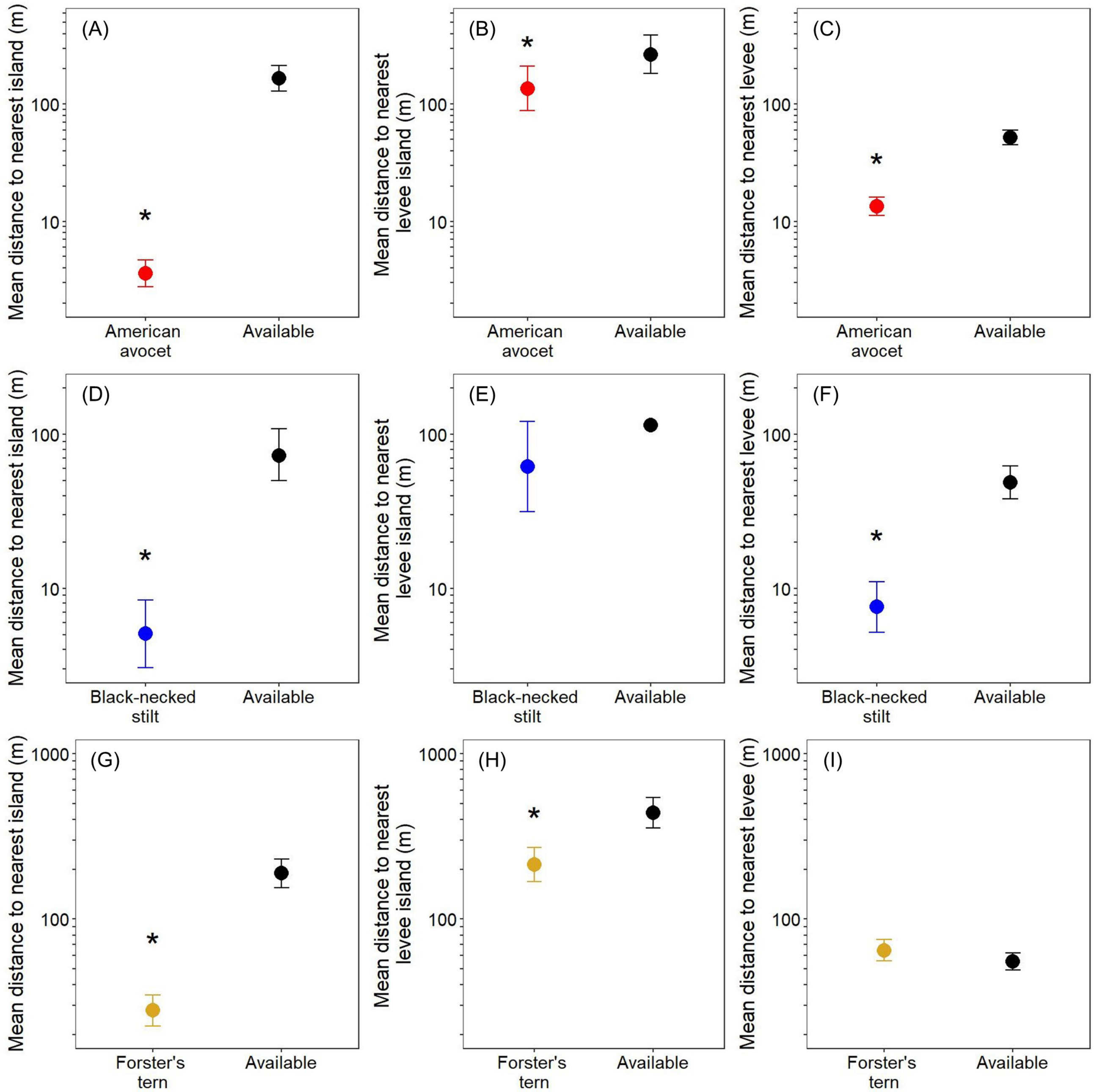

Figure 3 Distance between observed bird locations and specific habitat features within south San Francisco Bay managed ponds and salt ponds in the May 2019 survey, compared to a uniform grid (10 m × 10 m) of locations that represent all available habitat in the same pond unit. Model-estimated least squares means are presented on a log-scale, with standard errors back-transformed using the delta method. *Asterisks* indicate statistically significant differences ($\alpha = 0.05$) between bird locations and available locations.

available grid points), and birds observed feeding (mean distance: 46 m, 91 m closer than available grid points; Figure 4A). American Avocets in all behavior categories were located > 26 m closer to levees than available grid points ($z > 3.4$, $p < 0.01$, $n = 263$ bird locations), with significant differences between birds observed feeding and roosting ($z = 3.8$, $p < 0.01$; Figure 4B). Avocets engaged in breeding behaviors (mean distance: 15 m, 34 m closer than available grid points) and

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roosting (mean distance: 9 m, 40 m closer than available grid points) were closest to levees, followed by Avocets observed feeding (mean distance: 25 m, 27 m closer than available grid points; Figure 4B).

Black-necked Stilts by Behavior

Black-necked Stilts (n = 19 bird locations) engaged in breeding behaviors (mean distance: 0 m, 79 m closer than available grid points; $z = 9.3$, $p < 0.001$) or roosting (mean distance: 0 m, 67 m closer than available grid points; $z = 6.7$, $p < 0.001$) were located > 66 m closer to islands than expected, but Stilts observed feeding were not (mean distance: 74 m, 1 m closer than available grid points; $z = 0.03$, $p > 0.99$; Figure 4A). Black-necked Stilts in all behavior categories (mean distances: 7 to 9 m) were located > 37 m closer to levees than available grid points ($z > 2.8$, $p < 0.03$, n = 37 bird locations), and there were no differences among behavior categories ($z < 0.4$, $p > 0.9$; Figure 4B).

Forster's Terns by Behavior

Forster's Terns engaged in breeding and roosting behaviors were located > 100 m closer to islands than expected ($z > 19.7$, $p < 0.001$, n = 158 bird locations), with significant differences between birds observed breeding and roosting ($z = 20.8$, $p < 0.001$; Figure 4A). Forster's Terns engaged in breeding behaviors were closest to islands (mean distance: 0 m, 110 m closer than available grid points), followed by birds observed roosting (mean distance: 18 m, 156 m closer than available grid points; Figure 4A). Forster's Terns observed feeding did not differ from available grid points in distance to islands (mean distance: 192 m, 90 m farther from than available grid points; $z = 0.1$, $p > 0.99$; Figure 4A). Forster's Terns showed no differences in distance to levees among behaviors (mean distances: 43 m to 72 m; $z < 1.5$, $p > 0.4$) and none differed significantly from the distribution of available locations ($z < 2.0$, $p > 0.2$, n = 328 bird locations; Figure 4B).

Waterbird Distribution by Behavior

For the most part, the distribution of waterbirds in the study area was similar among behaviors, with exceptions (Figure 1, Table 1). Birds were not evenly distributed within complexes (Table A1), but were often concentrated in smaller areas

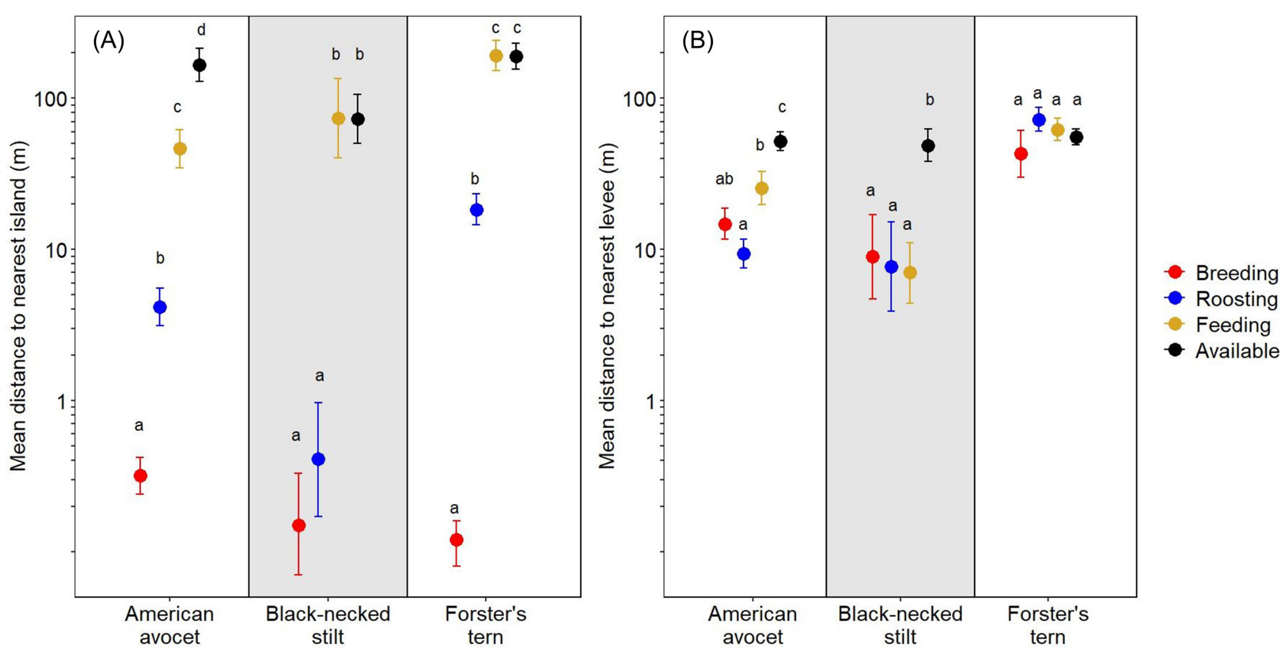

Figure 4 Distance between observed bird locations and the nearest (**A**) island or (**B**) levee within south San Francisco Bay managed ponds and salt ponds in the May 2019 survey, compared to a uniform grid (10 m × 10 m) of locations that represent all available habitat in the same pond unit. Model-estimated least squares means are presented on a log-scale, with standard errors back-transformed using the delta method. Each species was modeled separately, and different letters (a through d) denote groups that were significantly different within each model ($\alpha = 0.05$).

(e.g., eastern Alviso and eastern Ravenswood, which both hosted large multi-species breeding colonies). Densities are presented in Table A2.

Change in Waterbird Distribution by Behavior (2001 vs. 2019)

Changes in the distribution of American Avocets and Black-necked Stilts were generally similar in magnitude and direction across behaviors (Tables 4B, A2). Densities of Avocets and Stilts in Alviso when observed roosting or engaged in breeding behaviors decreased by a range of 42% to 74% between survey periods, but densities of Avocets observed feeding increased by 79%, whereas use by feeding Black-necked Stilts remained similar (Table 4B). These changes were not distributed evenly throughout the complex. Use of western Alviso (specifically use of Ponds A7 and A8; Figure A2) decreased to almost zero in 2019, regardless of species and behavior, after these ponds were opened to tidal influence on their way to tidal marsh restoration (although still functionally considered managed pond habitat for the purposes of this study).

DISCUSSION

Since 2001, approximately 8 km^2 of managed pond (former salt pond) habitat has been restored to tidal influence in south San Francisco Bay. This region lost approximately 140 km^2 of its historical wetlands between the 1860s and the 1950s (Goals Project 1999). Restored tidal areas are expected to provide habitat for marsh-dependent endangered species (e.g., Ridgway's Rail and salt marsh harvest mouse), as well as ecosystem services in the form of improved water quality and buffering against storm surge and sea level rise (USFWS and CDFG 2007; Goals Project 2015). Over the last 150 years, some species have come to depend on the managed wetland habitat provided by current and former salt production ponds. Despite the overall decrease in availability, managed ponds remained of high importance to the waterbirds surveyed in this study, hosting the largest percentage of individuals feeding or engaged in breeding behaviors for most species studied (Table 2), and supporting among the highest densities of American Avocets (22.3 Avocets km^{-2}) and Forster's Terns (28.6 Terns km^{-2}) in the study area (Table A2). Use of tidal marsh habitat increased between 2001 and 2019 for American Avocets (34% to 269% increase in density, depending on behavior; Table 4), but 2019 densities (4.3 Avocets km^{-2} and 1.6 Black-necked Stilts km^{-2}) remained low compared to more selected habitats (e.g., 31.8 Avocets km^{-2} and 35.4 Stilts km^{-2} in non-tidal marshes; Table A2). Moreover, new tidal-marsh and tidal-mudflat habitats appeared to provide lower foraging habitat value for birds breeding in nearby managed ponds because Avocets, Stilts, and Forster's Terns fed primarily in managed ponds (42% to 61% of feeding birds observed) compared to tidal marsh and mudflats combined (8% to 27%). Only Caspian Terns fed in tidal wetland habitat more than expected (although differences were not statistically significant), with 45% of feeding observations occurring in tidal mudflats that made up 22% of available habitat (Table 2). However, only 7% of Caspian Terns were observed feeding during the 2019 survey, and it is possible that those birds were foraging opportunistically while in transit from nesting colonies in managed ponds to the bay, where they were likely feeding farther offshore than we were able to record in this survey (Lyons et al. 2005). Overall, the distribution of feeding birds among habitats was similar to the distribution of breeding and roosting birds (Table 2), suggesting that most waterbirds were feeding in proximity to where they nested (Bluso-Demers et al. 2008; Demers et al. 2008).

The 2001 and 2019 surveys were conducted during a short, 2-week time-period to reduce the potential of double-counting mobile birds. Consequently, we did not control survey times to account for tidal stages, but rather surveyed throughout the day to ensure that all habitat types were surveyed during low and high tides, and to avoid any systematic bias in the actual availability of tidal habitat to wading shorebirds caused by fluctuations in water depths. In using this approach, tidal habitat availability may have been overestimated in some of our calculations; however, because surveys in both years were conducted randomly with respect to tides, the

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inter-year comparisons would not be affected. Furthermore, species-specific models designed to evaluate the factors that drive use of managed ponds and salt ponds took into account tidal stage and found no effect of tidal stage on Forster's Tern or American Avocet use of ponds, but the number of Black-necked Stilts found in managed ponds increased with tide level (Hartman et al. 2021). In contrast to the majority of the species studied here, the influence of tidal stage on tidal marsh availability for some other shorebird species, such as Western Sandpipers (*Calidris mauri*), would be expected to play a larger role in their habitat use (Warnock and Takekawa 1995). Importantly, the central management question for this study is whether focal waterbird species make greater use of tidal marsh or managed pond habitat, so the scale of our interpretation seems appropriate.

We found substantial differences in the use of managed ponds and salt ponds between 2001 and 2019. Since 2001, a large proportion of salt pond habitat (50 of 91 units, approximately 54 km^2) has been converted from salt ponds to managed pond habitat. Taking these changes into account, waterbird use of managed ponds increased relative to availability and use of salt ponds decreased, especially among feeding birds (59% to 100% decrease in density of feeding Avocets and Stilts; Table 4). Although some of this shift in use may be the result of enhancements made to managed ponds, the large decreases observed in the use of specific salt ponds (Hartman et al. 2021) suggest that changes were more likely driven by a reduction in the habitat value of the remaining salt ponds, many of which are high-salinity ponds (>120 ppt at the time of the 2019 survey) and are still used for salt production. High-salinity ponds can support abundant populations of invertebrate prey (*Ephydra* brine flies and *Artemia* brine shrimp) that often are exploited by American Avocets, Black-necked Stilts, and California Gulls (*Larus californicus*; Carpelan 1957; Herbst 2006; Takekawa et al. 2009); however, those ponds are generally above the salinity tolerance of the fish on which Terns feed, which are limited to low- and medium-salinity ponds (Carpelan 1957; Mejia et al. 2008; Peterson et al. 2018; Riensche et al. 2018). Forster's Terns have been shown to preferentially forage in lower-salinity pond habitat (Bluso-Demers et al. 2016), and salinity was an important factor that determined overall pond use for both Forster's Terns and American Avocets (Hartman et al. 2021). Most of the remaining lower-salinity salt ponds are in the Newark complex (Figure A2) where California Gull populations have been increasing (Burns et al. 2018; Hartman et al. 2021). As a major predator of waterbird eggs and chicks in the south San Francisco Bay (Herring et al. 2011; Ackerman, Hartman, Herzog, et al. 2014; Ackerman, Herzog, Hartman et al. 2014), California Gulls may contribute to declining waterbird use in ponds near large Gull breeding colonies.

As expected, micro-habitat use by feeding waterbirds reflected differences in feeding ecology between the terns (which forage aerially and mainly feed on fish) and the wading shorebirds (which feed mainly on invertebrates in the ground). American Avocets and Black-necked Stilts foraged primarily on wet bare ground (65% and 58%, respectively), a category that included exposed mudflats and shallow water (<10 cm), whereas Caspian and Forster's Terns foraged over deeper water (82% and 93%, respectively; Table 3) and made greater use of channels and man-made waterways (Table 2). These results indicate that providing variability in water depths within or among managed ponds may increase waterbird diversity. Similar conclusions have been drawn for other types of wetlands, such as flooded rice fields, where research has shown that different depths attract different waterbird species (Elphick and Oring 1998; Strum et al. 2013). Our results also confirmed the importance of islands for breeding American Avocets, Forster's Terns, and Caspian Terns, which has been demonstrated in previous studies (Strong et al. 2004; Ackerman, Hartman, Herzog et al. 2014; Hartman, Ackerman, Herzog et al. 2016), and the importance of vegetated marshes for breeding Black-necked Stilts (Ackerman, Herzog, Takekawa et al. 2014). These observations are consistent with the results of pond-level modeling, which found that the presence of islands was a significant predictor of Forster's Tern and American Avocet abundance, but not of Black-necked Stilt abundance (Hartman et al. 2021). The importance of islands and pond edges was further demonstrated by a spatial analysis of the 2019 survey data. Forster's Terns, American Avocets, and Black-necked Stilts were disproportionately clustered near islands, 4 to 28 m away, which was more than 60 m closer to islands than would be expected by chance (Figure 3). The association with islands was stronger for breeding and roosting birds than for feeding birds, but Avocets were also found closer to islands than expected when feeding, likely because islands were constructed to provide shallow foraging areas around their perimeter as they slope down to the pond bottom (Figure 4A). Additionally, Avocets and Stilts were clustered near levees, located more than 25 m closer to levees than expected by chance (Figure 4B). Like islands, these levee edges provide areas of shallower topography for wading birds within relatively deep ponds. We observed no American Avocets or Black-necked Stilts and few Forster's Terns using levee islands during the 2019 survey (Table 3), and these habitat features did not appear to be functionally or structurally equivalent to the other, much smaller islands in the south San Francisco Bay. Detailed analyses of nest sites showed that these species more commonly nested < 10 m from the water's edge, < 1.5 m above the water's surface, and on flat to moderate slopes, and had higher reproductive success on islands that were farther from the nearest levee (Hartman, Ackerman, Herzog et al. 2016; Hartman, Ackerman, Takekawa et al. 2016). Levee islands retain the steep sides characteristic of levees and are often separated from other (mainland) levees by relatively narrow channels, which may not completely eliminate access by mammalian predators and disturbance from people using trails around the ponds, potentially making them less attractive for nesting. Many of the larger levee islands in the south San Francisco Bay also host large California Gull breeding colonies (Burns et al. 2018), which would be a strong deterrent for other nesting waterbirds.

Case Studies: Waterbird Response to Tidal Restoration or Enhancement of Former Salt Ponds

Many former salt pond units have changed between the 2001 and 2019 surveys, including those that were restored to tidal influence and those that were converted to managed ponds and enhanced by the construction of new breeding islands. These units allow us to directly compare waterbird communities before and after management actions associated with the SBSP Restoration Project.

Enhanced Ponds

Within three managed ponds, extensive new island construction occurred between 2001 and 2019 (Figure 5). American Avocets increased at two of the three enhanced ponds, but Black-necked Stilt numbers remained relatively low (Table A4).

- **Pond A16** (Alviso; Table A4; Figures 5, A2): Despite construction of additional islands between 2001 (4 historical islands) and 2019 (16 new islands; 20 total islands), American Avocets declined by 79% and Black-necked Stilts by 93%. However, despite the relatively low number of American Avocets recorded during the 2019 survey (33, compared to 160 in 2001), in a separate study 156 Avocet nests were found in Pond A16 in 2019 (a number that could include re-nesting by some pairs, as well as nests of individuals that were not identified as breeding birds in these surveys due to the snapshot approach used (2022 in-person communication between J. T. Ackerman, and C. R. Schacter, unreferenced, see "Notes"). Additionally, island construction, combined with social attraction efforts, have led to the establishment of a large Caspian Tern breeding colony and re-establishment of Forster's Tern nesting at this site (Hartman et al. 2019, 2020).

- **Pond SF2** (Ravenswood; Table A4; Figures 5, A2): Thirty islands were constructed in SF2 in 2010. No American Avocets or Black-necked Stilts were observed in this unit during the 2001 survey, at which point the pond was mostly dry. In 2019, there was a small increase in Stilts (8, all feeding), and a large increase in Avocets (163 total, of which 24 were feeding, 1 was engaged in breeding behavior, and 138 were roosting). Additionally, social attraction

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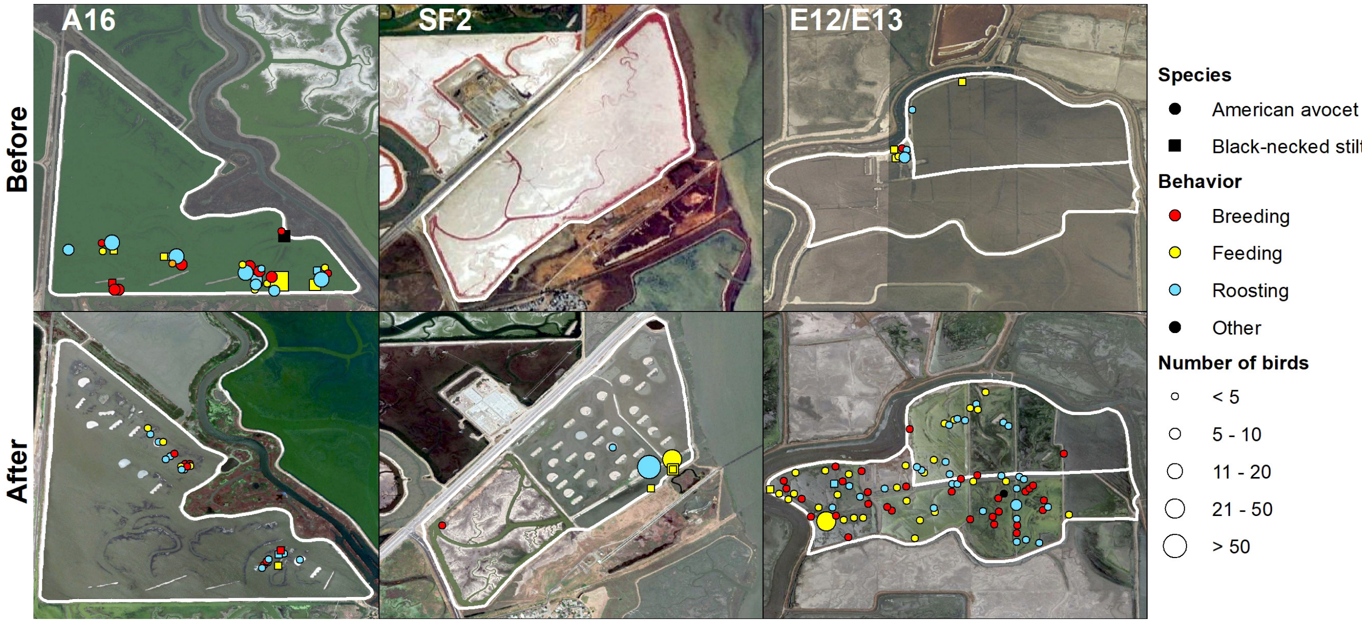

Figure 5 Case studies of managed ponds enhanced by island construction. Within three managed ponds, new island construction occurred between 2001 (*above*) and 2019 (*below*). American Avocets increased at two of these three enhanced managed ponds, whereas Black-necked Stilt numbers remained relatively low. Background imagery was taken from Google Earth© (Google Earth© Pro 7.3.3.7692 2020) as close as possible to the time of each survey.

efforts at this site during 2015–2017 established the second-largest Caspian Tern colony in San Francisco Bay (Hartman et al. 2019).

- **Ponds E12 and E13** (Eden Landing; Table A4; Figures 5, A2): Six islands and numerous mounds for roosting and foraging were constructed in 2015. These managed ponds were used by small numbers of Black-necked Stilts (all observed feeding) and American Avocets (mostly observed roosting) in 2001. During 2019, the number of Stilts observed was still low (5 in 2001, 3 in 2019), but we found large increases in the number of Avocets in all behavior categories (13 in 2001, 163 in 2019).

Ponds Restored to Tidal Influence

Of the 14 former salt ponds that were breached to allow varying degrees of tidal flow between 2001 and 2019, three had fewer than five observations of American Avocets and Black-necked Stilts in either survey (Hartman et al. 2021). Of the remaining 11 units, use by American Avocets and Black-necked Stilts increased in four units (A17, A19, MECM, MECMM; Table A4; Figure A2) and decreased in seven units (A8, A21, E8A, E8X, E9, E10X, NCM[1]; Table A4; Figure A2) between 2001 and 2019. We discuss five units in more detail as examples below.

- **Pond A8/A8S** (Alviso; Figure 6; Table A4; Figure A2): Pond A8 was breached in 2011 with tidal flow from Alviso Slough managed by large water-control structures. Interior levees that connected ponds A8, A8S, A7, and A5 were also breached to provide increased connectivity to the entire pond complex; however, tidal action was muted. The units were much deeper in 2019 than historically, completely submerging the former nesting islands and some internal levees. Pond A8/A8S was used by some American Avocets (84) in 2001 and was historically a major breeding site for Avocets and Forster's Terns (Ackerman and Herzog 2012; Hartman et al. 2021). In 2019, no Avocets were observed, and the 17 Forster's Terns observed were feeding or roosting.

- **Pond A17** (Alviso; Figure 6; Table A4; Figure A2): Pond A17 was breached in 2012 and consisted

1 Note that NCM is a former pond unit in the Eden Landing complex, not to be confused with New Chicago Marsh in Alviso.

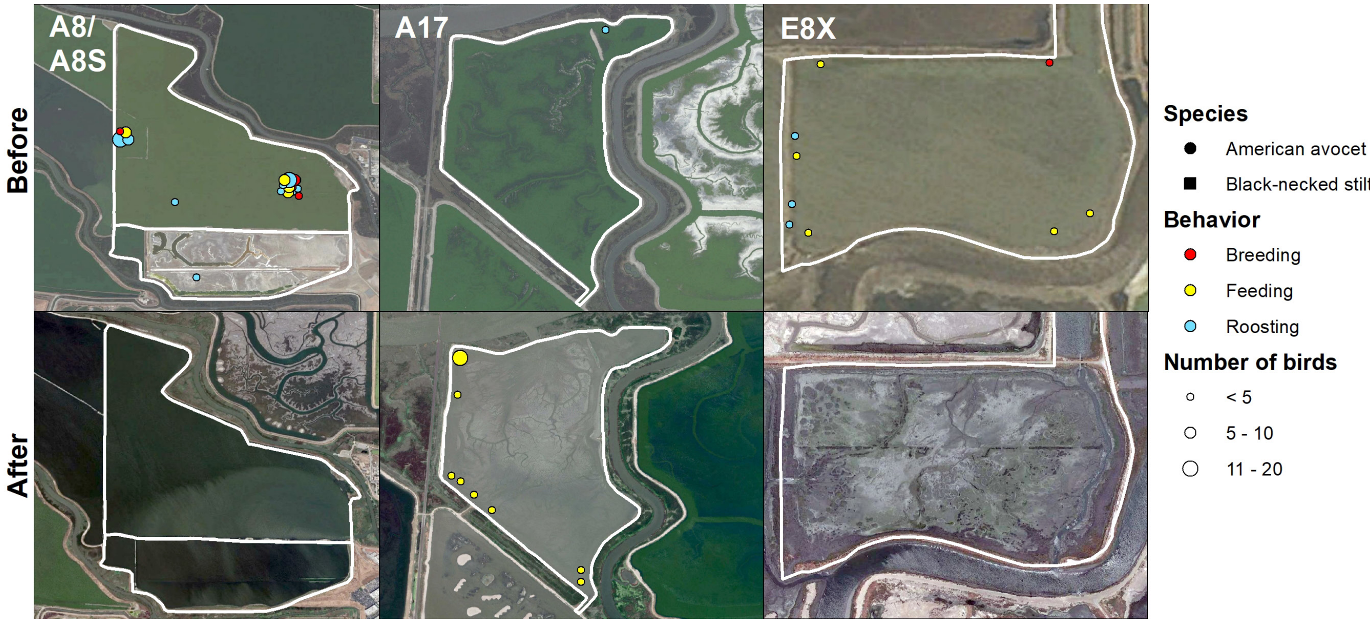

Figure 6 Case studies of managed ponds restored to tidal habitat. Of the 14 former salt pond units that were breached to allow varying degrees of tidal flow between 2001 (*above*) and 2019 (*below*), three units had fewer than five observations of American Avocets and Black-necked Stilts in either survey (Hartman et al. 2021). Of the remaining 11 units, use by American Avocets and Black-necked Stilts increased in four ponds and decreased in seven ponds between 2001 and 2019. Of these 11 restored ponds, we present three as case studies. Background imagery was taken from Google Earth© (Google Earth© Pro 7.3.3.7692 2020) as close as possible to the time of each survey.

entirely of tidal mudflat habitat during the 2019 survey. Black-necked Stilts were not observed in either survey, but American Avocet use increased between 2001 (2) and 2019 (26), all but one of which were observed feeding.

- **Pond A19** (Mowry; Table A4; Figure A2): Pond A19 was breached in 2006 and by 2019 consisted entirely of tidal mudflat and tidal marsh habitat. We observed no Black-necked Stilts in this pond during either the 2001 or the 2019 survey. American Avocet numbers increased from 0 in 2001 to 21 in 2019, 18 of which were feeding.

- **Pond E8X** (Eden Landing; Figure 6; Table A4; Figure A2): Pond E8X was breached in 2011 and by 2019 comprised a large southern area of tidal marsh habitat, and a smaller northern portion that remained a managed pond. Numbers of American Avocets and Black-necked Stilts using the unit in 2001 were relatively low (14 and 8, respectively) but included 3 American Avocets engaged in breeding behavior. We observed no birds of either species in 2019. The only birds we observed using the unit in 2019 that were focal to our study were 7 Forster's Terns feeding in the managed pond portion.

- **Pond E10X** (Eden Landing; Table A4; Figure A2): Pond E10X was breached in 2006 and by 2019 consisted primarily of tidal marsh habitat. This unit was used by 29 American Avocets and 9 Black-necked Stilts in 2001 (feeding, roosting, or engaged in breeding behavior), but only 7 feeding American Avocets were observed in 2019.

CONCLUSIONS

Our results emphasize the importance of managed pond habitat in the south San Francisco Bay for both nesting and foraging waterbird habitat, and the relatively low use by waterbirds of recently restored ponds and older tidal-marsh habitats. We found no evidence that tidal

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habitats in the south San Francisco Bay provided suitable breeding habitat for the waterbird species we examined. Additionally, these tidal habitats were used much less by feeding birds than their availability would predict. Identifying specific managed ponds that are most beneficial to breeding waterbirds—and enhancing the remaining managed ponds with islands for nesting and a varied topography suitable for foraging habitat—could benefit the adaptive management approach being used by the South Bay Salt Pond Restoration Project to arrest the current decline in breeding waterbird populations (Hartman et al. 2021) while restoring some areas to tidal marsh habitat (USFWS and CDFW 2007).

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