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RESEARCH

The Relative Importance of Agricultural and Wetland Habitats to Waterbirds in the Sacramento–San Joaquin River Delta of California

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ABSTRACT

Biodiversity loss from agricultural intensification underscores the urgent need for science-based conservation strategies to enhance the value of agro-ecosystems for birds and other wildlife. California's Central Valley, which has lost over 90% of its historical wetlands and currently is dominated by agriculture, still supports waterbird populations of continental importance. A better understanding of how waterbirds use available habitat is particularly needed in the Sacramento–San Joaquin Delta, an ecosystem under threat. From 2013 to 2015, we studied waterbird habitat associations in the Delta during fall migration and winter by conducting diurnal counts at random locations in key waterbird habitats throughout the Delta. Waterbird use of cover types (agricultural crops and managed wetlands) varied substantially among waterbird groups, by season, and among geographic sub-regions of the Delta. Overall, wetlands were particularly important to waterbirds in fall. In winter, wetlands and flooded

rice and corn were important to many waterbird groups, and non-flooded corn and irrigated pasture to geese and cranes. The factors that influenced waterbird abundance and distribution also varied substantially among groups and differed at various geographic scales. In both seasons, most groups had a positive association at the field level with flooded ground and open water, and a negative association with vegetation. Given the great uncertainty in the future extent and pace of habitat loss and degradation in the Delta, prioritizing the conservation actions needed to maintain robust waterbird populations in this region is urgent. For the Delta to retain its importance to waterbirds, a mosaic of wetlands and wildlife-friendly crops that accounts for the value of the surrounding landscape must be maintained. This includes restoring additional wetlands and maintaining corn, rice, alfalfa, and irrigated pasture, and ensuring that a substantial portion of corn and rice is flooded in winter.

KEY WORDS

Alfalfa, agro-ecosystems, Central Valley, corn, irrigated pasture, rice, waterbird conservation, waterbird habitat requirements

INTRODUCTION

Increased recognition of the scale of biodiversity loss from agricultural intensification highlights the urgent need for science-based conservation strategies to enhance species richness and abundance of birds and other wildlife in agro-ecosystems. In North America, agriculture is particularly intensive in California, where almost half of all the fruits, nuts, and vegetables in the United States are grown (NASS 2015). The heartland of California's agriculture is the Central Valley, which contains over 75% of the state's irrigated land (Shelton 1987).

Despite the loss of over 90% of its historic wetlands (Frayer et al. 1989; Kempka et al. 1991) and the current dominance of agriculture, the Central Valley remains one of the most important regions in the Pacific Flyway of North America for wintering and migratory birds (Shuford et al. 1998; Shuford 2014; Fleskes et al. 2018). The persistence of wetland-dependent birds reflects the restoration and enhancement of wetlands in recent decades, as well as the birds' use of certain crops that have offset the loss of the valley's historically flooded habitats to varying degrees (CVJV 2006). Post-harvest rice (*Oryza sativa*) and corn (*Zea mays*) are the most important agricultural habitats in the Sacramento Valley and Sacramento–San Joaquin River Delta (Delta), respectively, for migratory and wintering waterfowl and other waterbirds (CVJV 2006). In the Delta, other widespread wildlife-friendly crops are winter wheat (*Triticum* spp.; including triticale, a cross with rye [*Secale*]), irrigated pasture, and alfalfa (*Medicago sativa*), which are complemented by smaller amounts of rice and managed wetlands. Recent studies have documented the use of these crops and wetlands by Sandhill Cranes (*Antigone canadensis*) in broad areas of the Delta (Ivey 2015) and by various waterbird groups (waterfowl [geese, swans, and ducks], cranes, shorebirds, herons, and egrets, etc.) on a large individual Delta island (Shuford et al. 2013b, 2016b). But limited quantitative information exists on broad-scale patterns of crop use by various waterbirds across the entire Delta. Similarly, there is little information on how the location, extent, and juxtaposition of crops and wetlands affects the abundance and distribution of waterbirds at the landscape scale, as has been

demonstrated in the Sacramento Valley (Elphick 2008; Reiter et al. 2015b).

Understanding the drivers of the distribution and abundance of waterbirds is particularly needed to help guide conservation in the Delta, where environmental and societal problems are increasingly complex (Luoma et al. 2015). The Delta hosts a diverse assemblage of waterbird species, including large numbers of waterfowl (Fleskes et al. 2018), and is particularly important to wintering Sandhill Cranes, including the state threatened Greater Sandhill Crane (*Antigone canadensis tabida*) (Pogson and Lindstedt 1991; Ivey and Herziger 2003; Ivey et al. 2014), and to Long-billed Curlews (*Numenius americanus*) in fall (Shuford et al. 2009, 2013a). In the Delta's ever-changing environment (Cloern et al. 2011; Wiens et al. 2016), key threats to waterbirds—which also imperil the viability of the region's agriculture—include island inundation from catastrophic levee breaks during extreme flood events or earthquakes, rising sea level, increasing salinity, and further island subsidence (Mount and Twiss 2005; Deverel and Leighton 2010; Lund et al. 2010). Additional factors that put the region's waterbirds at risk include loss of wildlife-friendly crops from conversion to vineyards and orchards, or from urbanization (Ivey 2015). Waterbird populations are also likely to be affected, both positively and negatively, by the restoration of thousands of acres of riparian forest and wetland planned for the Delta (DSC 2013; CDFW 2017). Understanding the factors that influence waterbirds in the Delta may not only guide waterbird conservation in this region but also may provide insights applicable to similar efforts in other delta ecosystems around the globe that likewise are challenged with ongoing and impending environmental change and degradation (e.g., Vörösmarty et al. 2009; Renaud et al. 2013).

To help advance waterbird conservation in the Delta, we initiated a 2-year study in 2013 to assess the relative value of selected agricultural crops and wetlands for waterbirds during fall migration and winter (Shuford et al. 2016a). Our primary objectives were to quantify the relative bird use of a variety of crop types and managed wetlands throughout the Delta, and to evaluate the influence of local and landscape characteristics on the distribution and abundance of waterbirds. Here, we report patterns of

crop and wetland use by bird groups, evaluate which local factors may drive the observed differences among them, assess how different cover-type classes influence abundance at three landscape scales, and discuss how these findings may aid conservation planning and prioritization in the Delta.

STUDY AREA AND PERIOD

We defined our Delta study area to include all lands within the statutory or legal Delta boundaries (California Water Code Section 12220; CDWR c2001), except for small areas at the edge of Suisun Marsh and north of Interstate 80 near the Yolo Bypass Wildlife Area (Figure 1). We did, however, include a few survey points outside—but directly adjacent to—the legal boundary to improve sample sizes for cover types that were limited in extent.

Historically, the Delta was a maze of sloughs and swampy islands, but now an extensive levee system protects many large islands or tracts from floods and tidal surges. Agriculture is the region's dominant land use, and, because of aeration of the Delta's peat soils, most of the islands have subsided to below sea level (Lund et al. 2010). The Delta's climate is hot and dry in the summer, and cool and wet in the winter, when it is often foggy. In Stockton, the largest city in the Delta, annual average precipitation is 45.3 cm, which falls as rain mainly from October to April, and average high temperatures are 33.5 °C in July and 13.2 °C in January (<http://www.usclimatedata.com/climate/>). Annual variability for these climate factors, however, can be very high, and our 2013–2015 study period coincided with a period of extreme drought and above-average winter temperatures in the Delta's catchment (Dettinger and Cayan 2014; <http://droughtmonitor.unl.edu/Maps.aspx>). This drought reduced waterbird habitat throughout the Central Valley (Reiter et al. 2018).

We evaluated waterbird use of crops and wetlands over 2 years from July 2013 to March 2015. We conducted field surveys within two seasonal periods: fall (mid-July to mid-November) and winter (mid-November to early March). We defined the limits of these seasons on the basis of knowledge of waterbirds' patterns of seasonal occurrence in the Delta—knowing these vary considerably among groups (and species)—as well as the timing of crop

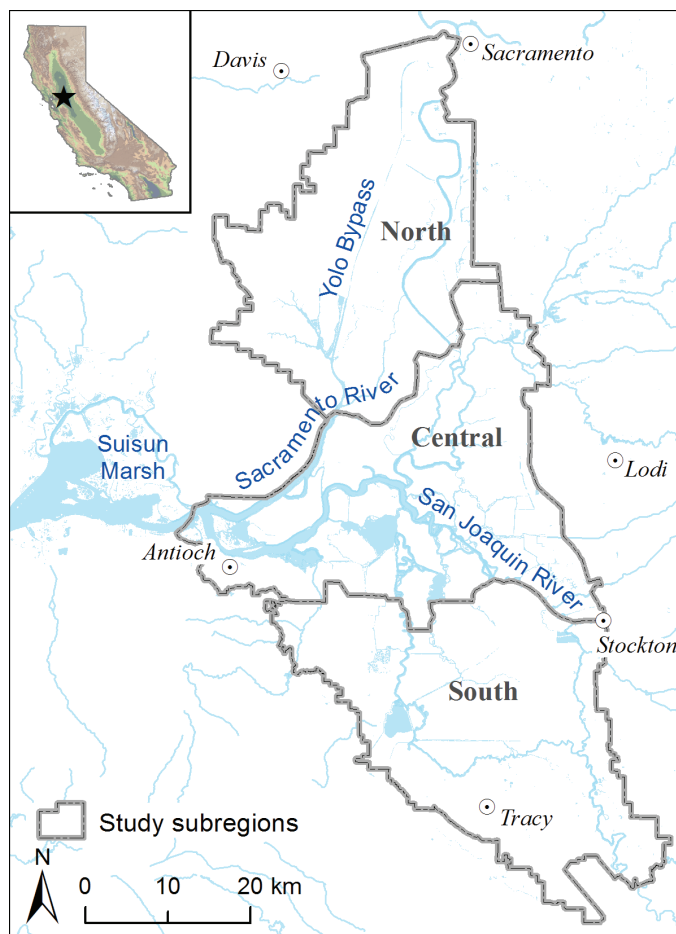


Figure 1 The Delta study region within California's Central Valley, showing three sub-regions used for implementing the sampling design

harvest and subsequent availability of habitat for waterbirds.

METHODS

Focal Cover Types

From the literature and extensive field experience, we identified eight combinations of cover types and management practices (hereafter, cover types) particularly suitable for waterbirds in the Delta. The availability of these cover types varied by season. Fall cover types included alfalfa, irrigated pasture, flooded managed wetlands, and growing rice. Winter cover types included alfalfa, irrigated pasture, flooded managed wetlands, flooded post-harvest rice, flooded post-harvest corn, non-flooded post-harvest corn, and growing winter wheat.

In the Delta, alfalfa and irrigated pasture provide waterbird habitat year round, but both are irrigated mainly during the hot, dry period from April through September or October; during this time, alfalfa fields are harvested six to seven times. Corn fields are not suitable for waterbirds until harvested in September and October, with some fields flooded from October or November into February. Post-harvest practices in corn fields vary across the Delta, but those fields not deeply plowed provide waste grain for cranes and waterfowl (particularly geese). Research on Staten Island, a large island in the central sub-region of the Delta, indicates that the majority of waste corn is depleted by early December (Conservation Farms and Ranches and The Nature Conservancy 2016, unpublished data, see “Notes”). Post-harvest corn was available during the latter part of our fall survey period, but the sample size was small, particularly for flooded corn, and therefore not included in our fall analyses. Growing rice was flooded and available to some waterbirds early in our fall survey period, although the standing crop can be quite dense. After harvest in September and October, some rice fields are plowed and others are left untilled and provide waste grain for waterbirds. When post-harvest rice is flooded, water is applied anywhere from October to December and held into February. As with post-harvest corn, sample sizes for post-harvest rice available in the later part of our fall survey period were too small to include in our fall analyses. Winter wheat is planted from November to January, and the growing crop was included in our winter surveys. Winter wheat is harvested in June or July, but many waterbirds do not use such fields in the fall unless they are flooded. Given that very little post-harvest wheat is flooded in the Delta (and mainly on Staten Island), we did not include it in our study. Some permanent wetlands are available year round; flooding of seasonal wetlands typically begins in mid-September, with peak availability of wetlands generally from November through at least early March.

Sampling Design

CropScape spatial data layers (NASS c2010–2014) of the distribution of focal cover types (including wetlands) within the Delta formed the foundation for selecting our sampling design and defining our

sampling frame at a coarse scale. As detailed below, we later refined these data layers for use in assessing and mapping the total extent of key crops and wetlands within the Delta during our survey period and in analyses of landscape variables that might influence waterbird abundance.

We used two sampling strategies to select survey locations for cover types, achieve good spatial distribution for landscape analyses, and limit logistical constraints for field surveys. First, we used a two-stage cluster design (Cochran 1977) to sample widespread crop types throughout the sampling frame within the study region. We defined our first-stage clusters to be the 108 Delta islands and tracts defined by the California Department of Water Resources (CDWR) for water management. Within each potential cluster (island/tract), we wanted to be able to survey as many cover types as possible. To ensure adequate crop coverage to sample on each tract, we identified tracts with >100 ha each of corn, wheat, and alfalfa, the most widespread “waterbird-friendly” crops in the Delta region. Of the 108 islands/tracts, 30 met this criterion in at least 1 of the 3 years (2010–2012) of CropScape data just before starting the study and were considered “primary tracts.” We defined three sub-regions (North, Central, and South) within the Delta to ensure the selected primary tracts were adequately distributed spatially, given their low sample size (but did not stratify our sample by these regions). This also ensured that selected primary tracts were well distributed relative to variation in the extent of flooding (open surface water) in the Delta, which tends to be concentrated in the central sub-region (Reiter et al. 2015a). We randomly selected a first-stage sample of 8 of the 30 primary tracts (three in North Delta, two in Central Delta, and three in South Delta) using generalized random tessellation stratified sampling (Stevens and Olsen 2004) so we could replace tracts, by region, if they were determined inaccessible. We strategically included Staten Island as a third tract in our surveys in the central sub-region because it included a large landscape of flooded habitat and multiple cover types (Shuford et al. 2016b), ensuring that we had adequate spatial distribution and sample sizes.

After choosing a first-stage sample of tracts, we selected a second-stage sample by establishing a random set of survey locations (each separated by

at least 0.8 km [0.5 mi], when possible) within each tract. We attempted to establish at least five survey locations per cover type per tract, for a minimum total of 40 survey locations per cover type across the Delta; we met these goals except for cover types with limited distributions. For the latter cover types (rice, managed wetlands, and irrigated pasture), we found we could not adequately sample these using the two-stage cluster design. Consequently, we augmented our initial sample of these cover types by selecting additional tracts with concentrations of these cover types and then establishing a random set of survey locations (similar to above) within each tract. For some cover types, more than eight tracts were required to get 40 samples.

In the second year of the study, we attempted to select a new random set of tracts and a new set of survey locations. For cover types with limited availability and restricted distribution in the Delta, however, neither was always feasible. For tracts used in both years, in the second year we selected new survey locations whenever possible. In 2013–2014 and 2014–2015, respectively, we established 119 and

Table 1 Number of survey areas and number of surveys, in parentheses, by cover type within three sub-regions of the Delta (N = North, C = Central, S = South) in the fall (July 16 – November 15) and winter (November 17 – March 5), 2013–14 and 2014–15 combined

Treatment	Fall ^a			Winter ^a		
	N	C	S	N	C	S
Alfalfa	41 (702)	23 (395)	46 (753)	42 (332)	23 (184)	43 (340)
Irrigated pasture	52 (900)	31 (523)	8 (135)	51 (407)	31 (248)	8 (64)
Wetland, flooded	20 (166)	15 (196)	0	51 (354)	21 (150)	0
Rice, growing	14 (147)	15 (150)	0	—	—	—
Rice, flooded	—	—	—	14 (107)	14 (112)	0
Rice, non-flooded	—	—	—	0	0	0
Corn, flooded	—	—	—	0	61 (428)	21 (158)
Corn, non-flooded	—	—	—	15 (117)	23 (172)	12 (86)
Winter wheat	—	—	—	25 (155)	17 (113)	33 (240)
Total	127 (1,915)	84 (1,264)	54 (888)	198 (1,472)	190 (1,407)	117 (888)

a. “0” indicates no cover type sampled or available in a region; “—” indicates cover type not present seasonally or just starting to be available at the end of a season.

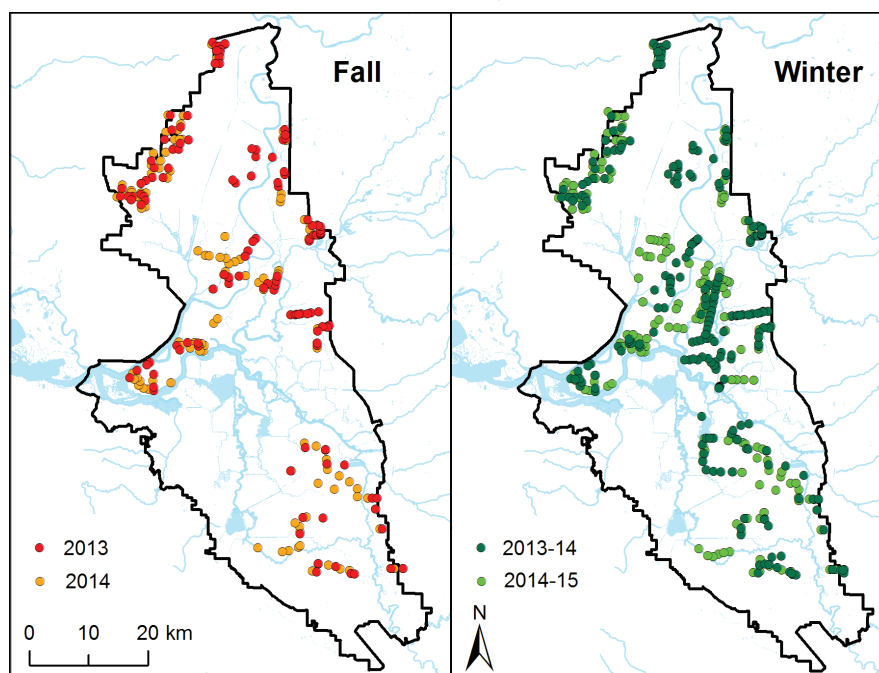


Figure 2 Location of sampling locations in the Delta in fall (July 16 – November 15) and winter (November 17 – March 5), 2013–15

146 survey locations in the fall period, and 243 and 262 in the winter period (Table 1; Figure 2).

Field Surveys

Four different observers surveyed waterbirds, using a protocol designed to maximize the probability of detecting birds and minimize other potential sources of bias. In both years of the study, observers collected data on bird abundance and local site characteristics at each established survey area about once a week in fall (July 16 – November 15), when bird numbers can change rapidly during migration, and once every other week in winter (November 17 – March 5), when bird populations are typically more stable. In 2013–2014 and 2014–2015, respectively, we completed 1,792 and 2,275 sampling events in the fall period, and 1,828 and 1,939 in the winter period (Table 1).

At each survey location, observers surveyed waterbirds from a predetermined point at the edge of each selected field. To reduce bias from diminishing detection of birds with increasing distance, counts were restricted to the (survey) area within a 200-m semi-circle arc from the field boundary at the survey point (sometimes constrained further when the arc was truncated by other field edges). Given the generally very open habitats and the relatively small sampling areas in fields, it seems unlikely that inter-observer bias contributed much to variation in waterbird counts. To minimize the effects of time of day on waterbird counts, observers attempted to start surveys in the early morning and varied the order in which they visited survey areas among survey dates; surveys were conducted between 0635 to 1930 hrs. Over the course of the study, this provided data on the overall daytime habitat use patterns of waterbird groups (and species). Observers did not survey during high winds (>20 mph), steady rain, or dense fog. Observers used binoculars and spotting scopes to scan each survey area for at least 2 minutes or until they counted all birds (excluding flyovers).

To boost our sample sizes for wetlands, we included additional survey data from Stone Lakes National Wildlife Refuge and the Sacramento Regional Bufferlands collected concurrently with our study. At regular intervals (once a week and once every other week at the two sites, respectively), their biologists counted all waterbirds within each of the

flooded wetland impoundments along predetermined survey routes. This enabled waterbird densities to be estimated by wetland units, a sample of which we used in our analyses.

With few exceptions, observers identified all individual waterbirds to species. Species included were those within the following taxonomic groups: waterfowl [ducks, geese, and swans; Anatidae]; grebes [Podicipedidae]; rails, gallinules, and coots [Rallidae]; cranes [Gruidae]; shorebirds [Recurvirostridae, Chardriidae, Scolopacidae]; gulls and terns [Laridae]; cormorants [Phalacrocoracidae]; pelicans [Pelecanidae]; herons, bitterns, and allies [Ardeidae]; and ibis [Threskiornithidae]. When possible, observers also distinguished between the Lesser (*Antigone canadensis canadensis*) and Greater subspecies of the Sandhill Crane. Taxonomy follows that of the American Ornithologists' Union's *Check-list of North American Birds*, 7th edition, through its 58th supplement (2017; <http://checklist.aou.org/>); scientific names are included in Table A1.

Over the 2-year study, observers recorded a total of 67 species of waterbirds (Table A1). Of these, 55 waterbird species were assorted for analyses into 11 groups (four of which included only one species). Although members of many of these groups have strong taxonomic affinities, we assigned species to these 11 groups largely on the basis of similarity of niche requirements, including water-depth preferences, use of flooded or dry habitats (or a combination of the two), foraging style, and diet. Several species or species groups were excluded from analyses (see Table A1) because of small sample sizes. These included marsh birds (four species) and gulls and terns (five species), though the latter included one numerous species, the Ring-billed Gull. The American Coot was excluded because many individuals also grazed extensively in grassy areas between fields and roads, making it difficult to determine if birds' preferences pertained to the surveyed cover type, the adjacent grassy edges, or a combination of the two.

To assess local factors that might influence bird use (e.g., Strum et al. 2013; Shuford et al. 2016b), at the end of each bird survey (including at Stone Lakes and the Bufferlands), observers visually estimated water conditions as the proportion of each survey

area that was flooded, moist, or dry, and cover conditions as the proportion that consisted of crop residue (cut and standing or lying on the ground), green vegetative growth, bare ground, or open water. Our assessment of the cover condition “open water” represents vegetation-free areas of standing water, whereas the water condition “flooded” may include areas that are heavily vegetated but have water below the vegetation.

Data Analyses

Waterbird Density by Cover Type

To quantify relative bird use, we generated model-fitted density estimates for each of 11 waterbird groups (Tables A2 and A3) among the 12 cover type/season combinations; this was not possible for some groups when data were limited in a particular season. Given the nested study design and the high degree of over-dispersion in our count data, we used a Poisson generalized mixed-model (Gelman and Hill 2007) with a random effect of tract (primary sampling unit) and an observation-level random effect (akin to the over-dispersion parameter in a negative binomial model) (Elston et al. 2001). For each season, we used the total count summed across multiple visits to a survey area as the response variable to further reduce zero-inflation and auto-correlation from repeated surveys of the same location. We included the natural logarithm of the total area surveyed (survey area [ha] × number of visits) as an offset term to account for varying survey area sizes. We calculated the area (ha) of each survey area using the National Agriculture Imagery Program’s 2012 aerial imagery (www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/) and ArcGIS Version 10.2.1 (© 1995–2014 ESRI Inc.).

We fit four models to the data for each season: (1) an intercept-only, (2) a cover-type-only, (3) a cover type + year, and (4) a cover type × year interaction model. To help with model convergence and to reduce zero-inflation, we removed from model fitting for a waterbird group any cover types that had <0.5% of the total birds observed within a season or had a <1% probability of bird occurrence. As a result, some species included only one cover type and, hence, we fitted only two models, given that the intercept-only and cover-type-only models were equivalent.

We ranked these models using Akaike’s information criterion (AIC; Burnham and Anderson 2002) and then used the model with the lowest AIC to estimate the density and 95% confidence interval (CI) for the density estimate for each cover type. A stratified, non-parametric bootstrap procedure was used to complete 5,000 fits of the best-supported model using re-samples of the original data to estimate the mean density (birds ha⁻¹; median of the fitted means from the bootstrap distribution) and 95% CIs for the fitted mean values using the 125th and 4875th ranked values of the 5,000 fitted means. We considered estimated densities with 95% CIs that did not overlap between cover types to be significantly different. For some species or groups with very few data, we had problems with model convergence, so we estimated the mean and 95% CIs of the density of each waterbird group on the basis of simple bootstrapping of the mean and the percentile method, respectively (Manly 2007). For two groups (Sandhill Crane, diving ducks) that did not arrive in the Delta until partway through the fall season, we excluded data from modeling efforts from *all* surveys conducted before their first detection (August 10 for Sandhill Crane; September 22 for diving ducks).

Drivers of Use

Local Factors. We examined local site conditions that may influence the use of different cover types by each waterbird group in each season. Covariates considered in single-factor models included the percentage of the survey area that was flooded, moist or dry (water conditions), and the percentage that was covered in open water, vegetation, crop residue, or bare ground (cover conditions) (Tables A4 and A5). From knowledge of the ecology of the species and previous studies at Staten Island in the Delta (Shuford et al. 2016b) and in the Sacramento Valley (Strum et al. 2013; Sesser et al. 2016), we expected the following associations: dabbling ducks positively with the amount of the survey area flooded, and negatively with crop residue; diving ducks positively with flooding, and negatively with crop residue and moist or dry soil; long-legged waders positively with flooding; cranes positively with crop residue (itself associated with dry fields); and shorebirds positively with the amount of moist soil.

Landscape Factors. We also examined variables (cover-type classes) within the surrounding landscape that may influence the abundance of each waterbird group at 2-, 5-, and 10-km scales. These cover-type classes included all grain (total area of rice, corn, wheat, and other grains), flooded grain (the proportion of open water in all grain types combined), flooded rice (proportion of open water in rice), hay/pasture (total area of alfalfa, irrigated pasture, and dryland pasture), flooded wetlands (proportion of open water in freshwater emergent wetlands, managed wetlands, and woody wetlands), and fallow (all fallow/idle cropland).

We aggregated crop and wetland cover types in the Delta study area used for landscape analyses from various finer categories in the 2013 and 2014 NASS CropScape data sets for California (<http://nassgeodata.gmu.edu/CropScape/>), with refinements for irrigated pasture and managed wetlands (Table A6), and further grouped these into fewer cover-type classes (e.g., hay/pasture) for landscape analyses. We supplemented CropScape data for irrigated pasture with additional data for that cover type (The Nature Conservancy 2015, unpublished data, see “Notes”). For managed wetlands, we used the Central Valley Joint Venture’s wetlands layer produced by Ducks Unlimited (Petrik et al. 2014).

We calculated the proportion of each of the cover types that had open water by overlaying cover type and seasonal water layers, the latter estimated for the 2 years of this study using the methods described in Reiter et al. (2015a). We first calculated the probability of open water as the average of water occurrence for each pixel across the months in each season; imagery dates spanned July 15 to November 15 for fall, and December 15 to February 28 for winter. Averaging the water data across months limited the influence of cloud cover in our estimates. We then summed those probabilities to estimate the average proportion of open water within the landscape buffers in each season. Because our water layers did not cover the full extent of the Delta (missing piece in the southwest), for survey locations that had landscape buffers that fell outside of our water layers, we assumed that the proportion flooded in the unobserved part of the buffer was equal to that in the observed area.

From the known ecology of the species as well as prior studies, we evaluated one to four cover-type classes per season that we expected would be positively associated with each bird group (Tables A7 and A8). For Sandhill Cranes, we also included distance to the closest known nighttime roost site (The Nature Conservancy and Ivey 2015, unpublished data, see “Notes”), which is thought to influence their distribution (Ivey et al. 2015). We predicted that larger distances would result in fewer Sandhill Cranes, and thus a negative association between abundance of Sandhill Cranes and the distance to a known nighttime roost.

For all assessments of local and landscape associations with bird abundance, we used the same generalized linear mixed-model framework as described above. We evaluated residual plots of all models for evidence of lack of fit, and tested residuals of the best fitted cover-type model for evidence of over-dispersion (Cochran 1977). We conducted all analyses in the statistical program R version 3.2.0 or 3.2.1 (R Development Core Team 2013).

RESULTS

Relative Abundance of Cover Types and Waterbird Groups

Overall, the distribution and extent of the various cover types available to waterbirds in the Delta varied substantially (Figure 3, Table 2). In the 2-year study period, however, there was limited between-year variation in the extent of each cover type and the proportion of each that had open water (Figures 3 and 4, Table 2). Of the individual cover types, corn and alfalfa exhibited the greatest between-year variation in their extent (Table 2). Within and between seasons, the abundance of waterbirds varied substantially among groups (Table 3) and among the species within groups (Table A1).

In some cases, numbers for one species dominated the total number of individuals recorded for a group with multiple species (Table A1). In such cases, the density estimates or other model results presented below are likely more representative of the dominant species than of the group as a whole. For fall and winter, respectively, Killdeer accounted for 98% and 87% of all plovers, Great Egrets for 62% and 71% of

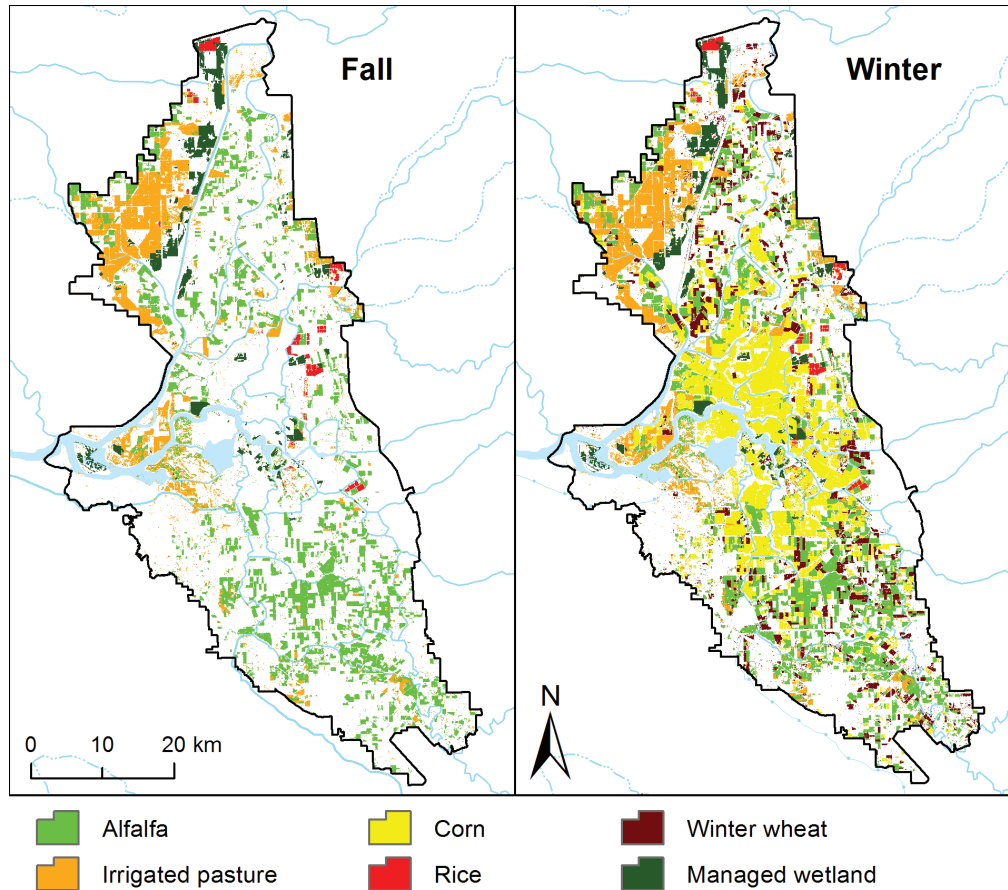


Figure 3 Distribution of four focal cover types widely available to waterbirds in the Delta in the fall, 2013, and six in the winter, 2013–14 (for data sources, see “Methods”). In the following year, the extent of alfalfa substantially increased and the extent of corn substantially decreased (Table 2), but their general patterns of distribution remained much the same.

Table 2 The extent (ha) of six focal cover types in the Delta study area in the fall and winter periods of 2013 and 2014 and the proportion of each of these that had open water (in parentheses)

Cover type	Fall 2013 ^a	Fall 2014 ^a	Winter 2013	Winter 2014
Corn	—	—	42,072 (0.09)	30,284 (0.18)
Rice	1,936 (0.03)	1,769 (0.05)	1,936 (0.34)	1,769 (0.20)
Winter wheat	—	—	14,793 (0.01)	15,534 (0.09)
Irrigated pasture	21,522 (0.01)	20,901 (0.04)	21,522 (0.01)	20,901 (0.03)
Alfalfa	36,334 (0.00)	43,908 (0.02)	36,334 (0.00)	43,908 (0.05)
Managed wetlands	7,665 (0.21)	7,665 (0.20)	7,665 (0.48)	7,665 (0.31)

a. “—” indicates cover type suitable for waterbirds of limited occurrence in the Delta overall (flooded winter wheat) or just starting to be widely available at the end of the fall period (post-harvest, particularly flooded, corn; see “Methods”).

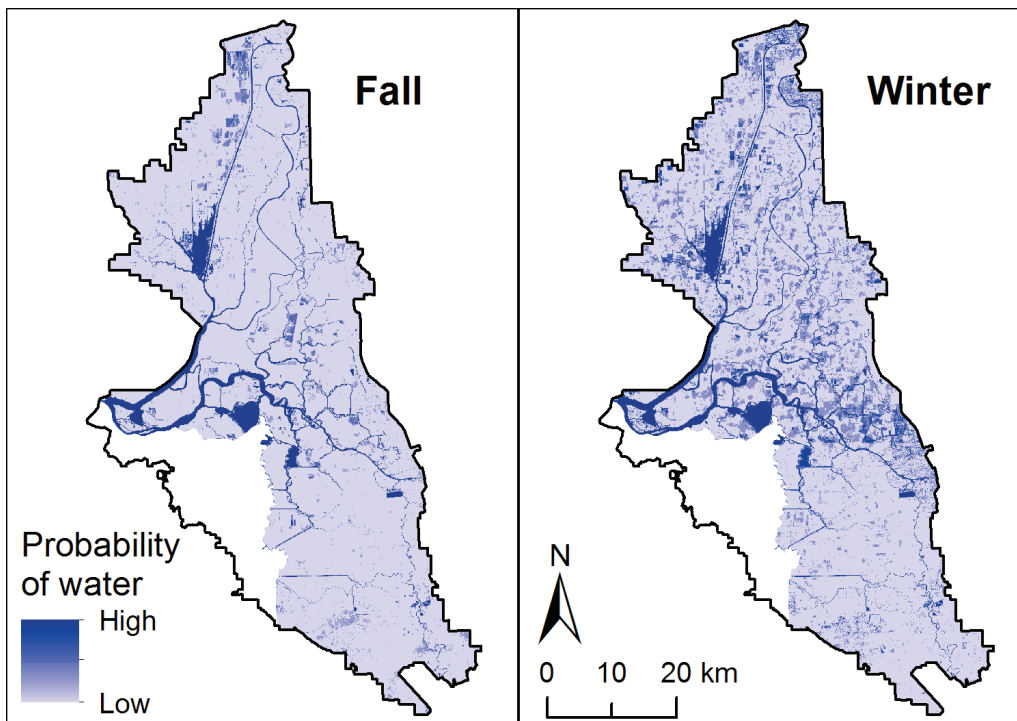


Figure 4 The probability of open water in the Delta study region for fall and winter developed using the methods described in Reiter et al. (2015a). This probability is the average of water occurrence for each pixel across the months in each season, 2013 and 2014 combined; imagery dates spanned July 15 to November 15 for fall and December 15 to February 28 for winter. Data were unavailable for estimating water probability in the southwest section of the Delta.

Table 3 Relative abundance (total individuals) by waterbird group summed over all sampling surveys across the Delta in each season: fall (July 16–November 15), winter (November 17–March 5), and fall–winter combined (July 16–March 5), 2013–14 and 2014–15. Abundance should not be compared between seasons because of unequal sampling effort.

Group (number of species) ^a	Fall	Winter	Fall–Winter
Geese (5)	25,765	45,920	71,685
Tundra Swan (1)	16	4,272	4,288
Dabbling ducks (10)	23,956	92,028	115,984
Diving ducks (9)	251	13,390	13,641
Other divers (7)	413	2,407	2,820
Sandhill Crane (1; 2 subspecies)	5,544	4,013	9,557
Plovers (2)	1,865	3,590	5,455
Long-billed Curlew (1)	2,584	513	3,097
Other shorebirds (12)	15,596	12,628	28,224
Long-legged waders (6)	1,217	618	1,835
White-faced Ibis (1)	3,132	34	3,166

a. See Table A2 for the species included in each waterbird group, including those groups not included in analyses.

long-legged waders, and Long-billed Dowitchers for 79% and 52% of other shorebirds. Similarly, Cackling Geese accounted for 89% of all geese in fall, and Ring-necked Ducks for 70% of all diving ducks in winter.

Density Estimate Models

The best-supported models for estimating density varied among bird groups and by season, and in some cases certain models—particularly interaction models—would not converge (Table A9). In the fall, the cover-type-only model (or equivalent intercept-only model for groups with only one cover type in the model) was the best supported, on the basis of AIC, for cranes, dabbling ducks, diving ducks, geese, plovers, and other shorebirds, and was used to estimate model-fitted density and 95% CIs. For long-legged waders and other divers, the best-supported model included year and cover type; whereas for the Long-billed Curlew, the intercept-only model was best supported, suggesting no

difference in density among cover types. However, we used the cover-type-only model (<2 AIC from top model) to explore the variation in density of the Long-billed Curlew across cover types. Models for the White-faced Ibis would not converge, so we used standard bootstrapping of the mean to estimate density variation across cover types. In the winter, the cover-type-only model was the best supported for geese, Tundra Swans, diving ducks, Sandhill Cranes, plovers, and other shorebirds. For diving ducks, the cover-type-only and cover-type-interaction-with-year models were equally supported, on the basis of AIC, so we used the simpler model to estimate model-fitted density and 95% CIs. The cover-type-plus-year model was the best supported for long-legged waders, and the cover-type-interaction-with-year model was best supported for dabbling ducks. Both subspecies of the Sandhill Crane plus other divers and the Long-billed Curlew required standard bootstrapping of the mean. Model residuals for all bird groups in both seasons indicated no major violations of distribution assumptions, and there was no residual over-dispersion ($P > 0.05$).

Patterns of Bird Use in Fall

Use by Cover Types

In fall, densities of individual waterbird groups varied among the four cover types analyzed, and, hence, particular cover types varied in their importance to various groups and to waterbirds overall (Figure 5; Table A2). Dabbling ducks, diving ducks, other divers, and other shorebirds had their highest densities in managed wetlands, where they occurred almost exclusively in fall. Three groups primarily used two cover types: geese (irrigated pasture, wetlands), long-legged waders (growing rice, wetlands), and Long-billed Curlew (irrigated pasture, alfalfa). Long-legged waders had significantly higher densities in the two primary cover types than in alfalfa and irrigated pasture. Sandhill Cranes and plovers (almost entirely Killdeer) showed no significant differences in densities among the cover types they used, but both groups had much higher mean densities (but broad confidence intervals) in managed wetlands than in irrigated pasture and alfalfa.

In alfalfa, the Sandhill Crane and White-faced Ibis had the highest mean densities of five bird groups,

but the only significant difference when comparing among groups was a higher density of cranes than of long-legged waders. In irrigated pasture, geese (mostly Cackling Geese) had a significantly higher density than the six other groups that used pasture. Growing rice held relatively few waterbirds of any kind, with long-legged waders and White-faced Ibis being the only groups with numbers high enough for density calculations. In wetlands, the three groups with the highest mean densities (dabbling ducks, other shorebirds, and geese) did not differ significantly from each other in density. Densities for dabbling ducks and shorebirds, however, were significantly higher than for five other groups, as was the case for geese relative to three other groups.

Drivers of Use

Local Factors. In the fall, significant associations with local site (water and cover) conditions in single-factor models were similar among many waterbird groups (Table 4; Table A4). Of the 10 groups evaluated, six had a significant positive association with the proportion of flooded ground; five of the six had a significant negative association with the proportion of the survey area that was dry. Each of a separate, but similar, set of six groups had a significant positive association with open water and a significant negative association with vegetation. Only one group—plovers, dominated by Killdeer—had a significant association with moist or bare ground, and in each case it was positive. Diving ducks, Long-billed Curlew, and White-faced Ibis did not show any significant relationships with water or cover conditions.

Landscape Factors. In landscape models, the magnitude and direction of associations with the extent of different crop classes and the proportion flooded varied substantially among waterbird groups and at various scales in the fall (Figure 6, Table A7). The Sandhill Crane and other shorebirds were negatively associated with hay/pasture at all three scales, whereas the Long-billed Curlew was positively associated with this crop class at all three scales. These patterns for hay/pasture associations at landscape scales correspond with patterns of group use of cover types at the field level. Negative associations of the Sandhill Crane and other shorebirds with hay/pasture at all landscape scales

was consistent with the very low densities of both groups in alfalfa and irrigated pasture, and their high densities in wetlands (Figure 5). By contrast, the Long-billed Curlew's positive association with hay/pasture at all scales was consistent with its almost exclusive use of alfalfa and irrigated pasture at the field level. The only significant associations

with the proportion of flooded rice were positive ones for long-legged waders at all three scales. This group also had a positive association with wetlands at two scales; long-legged waders predominantly used two cover types at the field level: growing rice and wetlands (Figure 5). Significant associations with the proportion of flooded wetlands were mixed

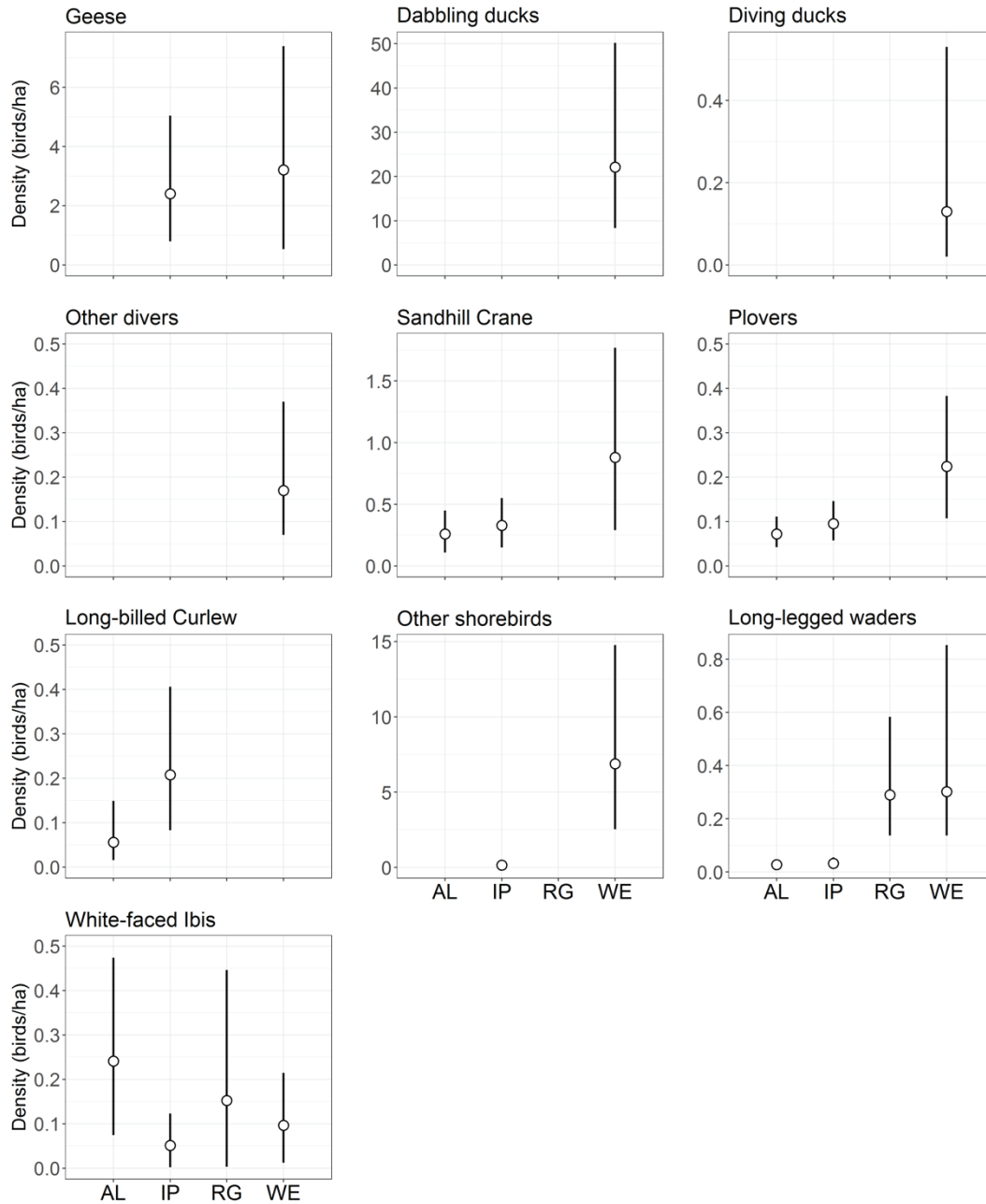


Figure 5 Mean density (birds ha⁻¹) and 95% CI for 10 waterbird groups in areas surveyed in the Delta in fall (July 16 – November 15) 2013 and 2014. Cover types: AL = alfalfa, IP = irrigated pasture, RG = rice (growing), WE = wetland.

Table 4 Significant positive and negative associations of 10 waterbird groups with various water and cover conditions from single-factor models fit to fall (July 16 – November 15) waterbird survey data in the Delta, 2013 and 2014. Magnitude of positive and negative parameter value estimates, respectively: “+,” <5; “++,” 5–10; “+++,” >10 and “-,” > -5; “--,” -5–10; “---,” < -10. Blank cells indicate no significant association (see Table A4 for full set of results).

Group	Water conditions			Cover conditions		
	Flooded	Moist	Dry	Open water	Vegetation	Bare ground
Geese	+++		--	+++	---	
Dabbling ducks				+	-	
Diving ducks						
Other divers	+		-	+	-	
Sandhill Crane	+			++	--	
Plovers	+	+	-	+	-	+++
Long-billed Curlew						
Other shorebirds	++		--	+++	---	
Long-legged waders	+		-			
White-faced Ibis						

with respect to bird groups and landscape scales (Figure 6, Table A7). Overall, the strongest effects were the negative association of the Sandhill Crane with hay/pasture at the 2-km scale, and the positive association of long-legged waders with flooded rice, also at the 2-km scale (Figure 6, Table A7).

Patterns of Bird Use in Winter

Densities by Cover Types

Similar to the fall, waterbird densities in winter varied among groups and cover types (Figure 7, Table A3). Tundra Swans, dabbling ducks, diving ducks, other divers, and other shorebirds were concentrated mainly in wetlands and flooded post-harvest crops of rice and corn. Geese, Sandhill Cranes, plovers, and long-legged waders were more widely spread among flooded and non-flooded crops and wetlands. Although the highest mean densities of geese, dabbling ducks, diving ducks, plovers and other shorebirds were in either flooded post-harvest rice or wetlands, because of the large variation around the means for those cover types there were no significant differences in densities among any of the cover types used by the respective groups. The Long-billed Curlew had the most distinctive pattern of use, being mainly in alfalfa and irrigated pasture.

In alfalfa, each of five waterbird groups represented had a relatively low density, with the most use by the Lesser subspecies of the Sandhill Crane, plovers, and other shorebirds. Statistically significant patterns in alfalfa were a higher density for plovers than for long-legged waders, and for the Lesser than for the Greater subspecies of the Sandhill Crane. In irrigated pasture, densities were relatively low for all six groups represented, except for geese, which had a significantly higher mean density than for all of the other groups. Other significant relationships in irrigated pasture were higher densities for the Sandhill Crane and plovers than for long-legged waders, and for the Lesser than for the Greater subspecies of the Sandhill Crane.

In flooded corn, six of the nine groups represented had relatively high densities; in particular, geese and dabbling ducks had significantly higher densities than for each of the remaining seven groups. Four groups used non-flooded corn; geese had a significantly higher mean density than for long-legged waders and plovers, as did the Sandhill Crane in comparison to long-legged waders. In flooded rice, dabbling ducks and geese had the highest mean densities, which, respectively, were significantly higher than for six and three other groups.

Of the nine waterbird groups represented in wetlands, four had relatively high densities. Of those, dabbling

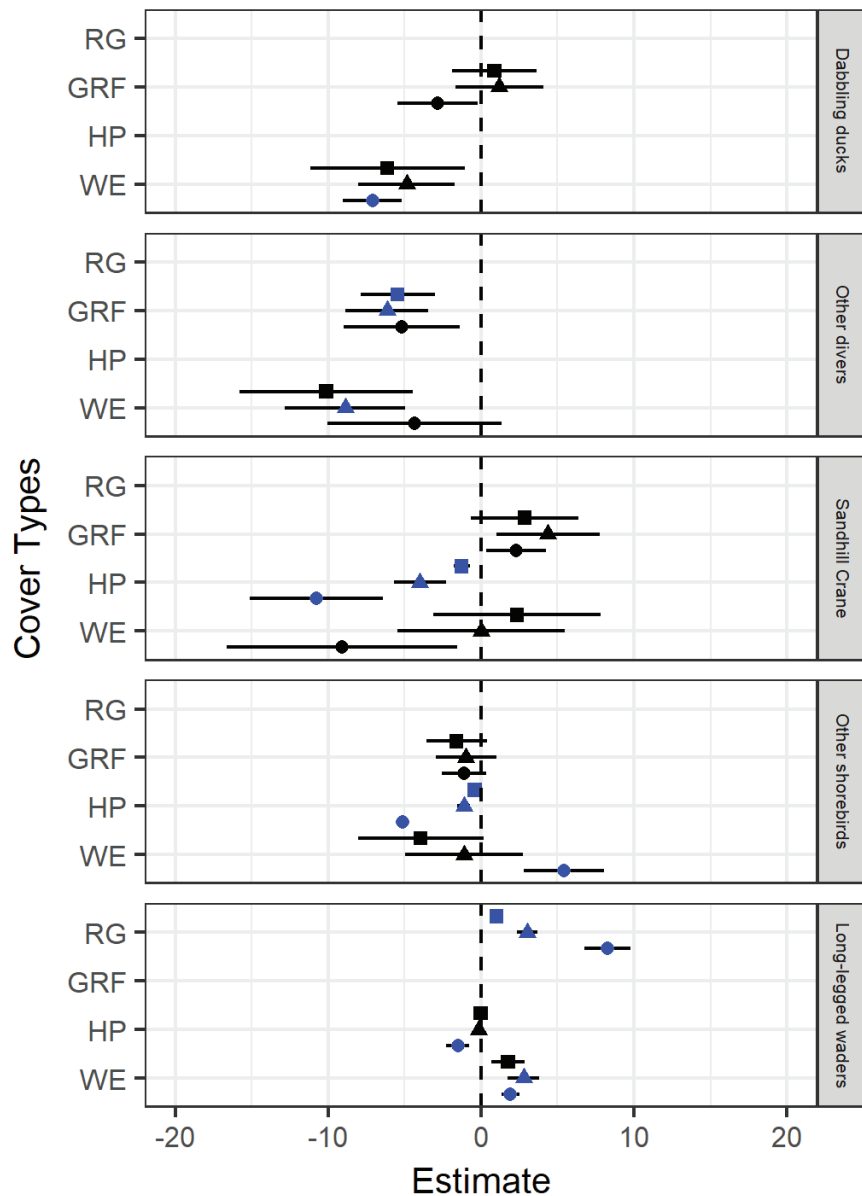


Figure 6 Summary of parameter estimates for landscape models fit to fall (July 16 – November 15) waterbird survey data in the Delta, 2013 and 2014, quantifying the associations between the amount of specific cover types and bird abundance. Each cover type was evaluated for buffers at three scales (■ = 10 km, ▲ = 5 km, ● = 2 km). Blue symbols are significant ($P < 0.05$). Data presented only for bird groups with at least one significant result (full set of results in Table A7). Cover types: RG = rice (growing), GRF = flooded grain crops, HP = hay/pastures, WE = wetlands.

ducks had significantly higher densities than for all of the other eight groups. Finally, in winter wheat, the highest mean density was for geese, followed by those for Sandhill Crane and plovers, all three of which were significantly higher than for long-legged waders.

Drivers of Use

Local Factors. In the winter, significant associations with local site (water and cover) conditions in single-factor models were similar for many but not all waterbird groups (Table 5; Table A5). Overall,

eight of 10 groups evaluated had a significant positive association with open water. Of the eight, six also had a significant positive association with flooded ground, and five had a significant negative association with dry ground. The Sandhill Crane and Long-billed Curlew were the only groups that lacked a significant positive association with the extent of either open water or flooded ground. Of the six groups with significant associations with both open water and flooded area, four had a negative association with the percent of vegetated area. The Sandhill Crane was the only other group with a negative association with the amount of vegetation.

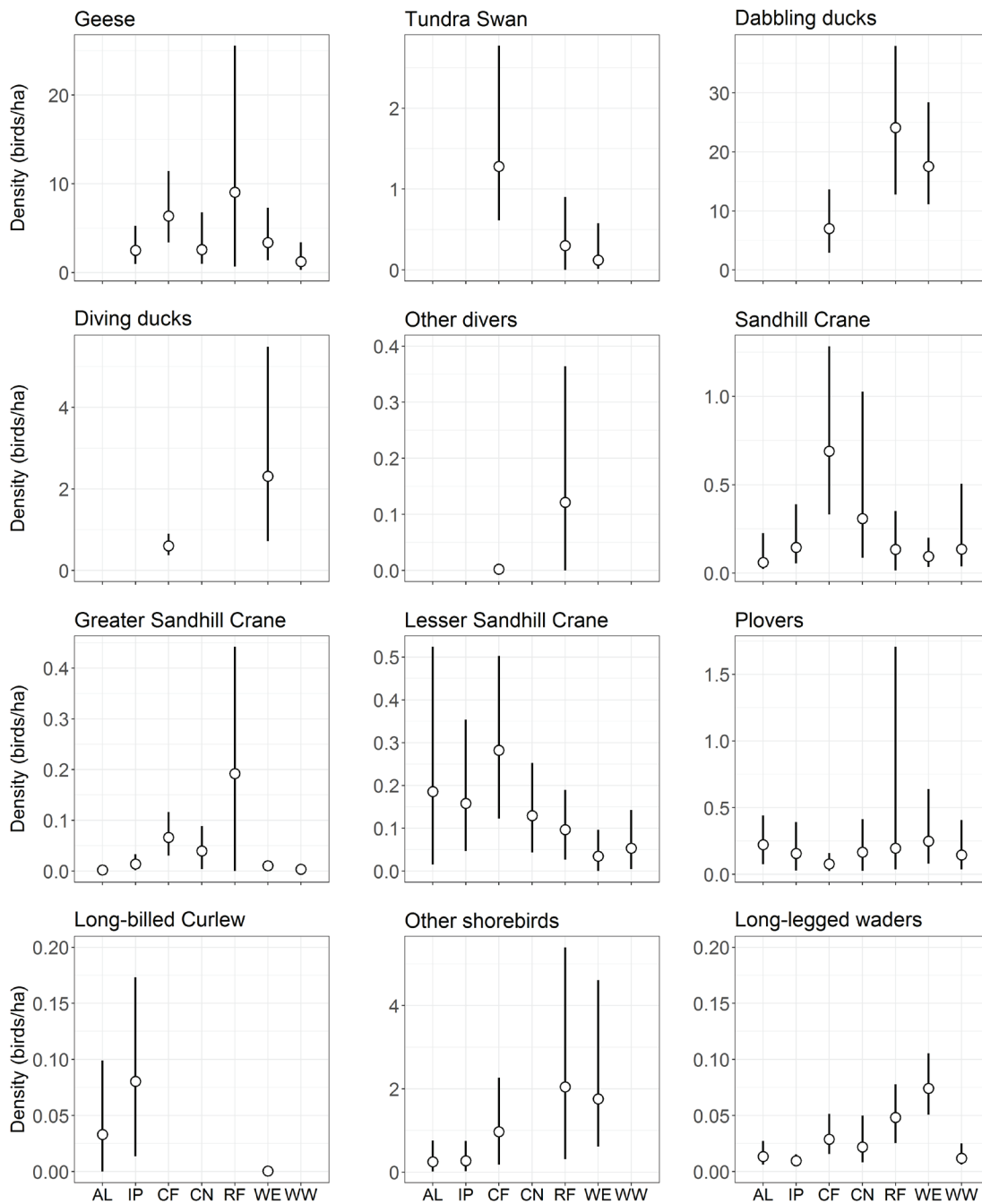


Figure 7 Mean density (birds ha⁻¹) and 95% CI for 10 waterbird groups (and two component subspecies of the Sandhill Crane) in areas surveyed in the Delta in winter (November 17 – March 5), 2013–14 and 2014–15. Cover types: AL = alfalfa, IP = irrigated pasture, CF = corn flooded, CNF = corn non-flooded, RF = rice flooded, WE = wetland, WW = winter wheat (growing). Simple bootstrapping was used for other divers, Long-billed Curlew, and Greater and Lesser Sandhill Cranes.

Table 5 Significant positive and negative associations of 10 waterbird groups (and two component subspecies of the Sandhill Crane) with various water and cover conditions from single-factor models fit to winter (November 17 – March 5) waterbird survey data in the Delta, 2013–14 and 2014–15. Magnitude of positive and negative parameter estimates, respectively: “+,” <5; “++,” 5–10; “+++,” >10 and “-,” > -5; “--,” -5–10; “---,” < -10. Blank cells indicate no significant association (see Table A5 for full set of results).

Group	Water conditions			Cover conditions			
	Flooded	Moist	Dry	Open water	Vegetation	Crop residue	Bare ground
Geese	+		--	++	-		
Tundra Swan				++			
Dabbling ducks	++	--	---	++		--	---
Diving ducks	++	---	--	++	-	--	---
Other divers				+			
Sandhill Crane			-		-	+	
Greater Sandhill Crane						+	
Lesser Sandhill Crane		+				+	
Plovers	+			+			
Long-billed Curlew							
Other shorebirds	++		---	++	--		+++
Long-legged waders	+	-	-	+	-		-

The Sandhill Crane, and both of its two subspecies when considered separately, showed a significant positive association with crop residue. Conversely, dabbling and diving ducks had significant negative associations with crop residue. Similar to crop residue, moist ground and bare ground had mixed associations with waterbird groups. Dabbling ducks, diving ducks and long-legged waders were all negatively associated with moist and bare ground, whereas Lesser Sandhill Cranes and other shorebirds had significant positive associations with moist ground and bare ground, respectively. As in fall, the Long-billed Curlew did not show a significant association with any of the water or cover conditions assessed.

Landscape Factors. In winter, significant associations between individual landscape variables and waterbird groups were consistent in their direction, no matter the number of scales involved, and for geese, dabbling ducks, and the Sandhill Crane the patterns were significant at all three scales (Figure 8, Table A8). Associations with the total extent of grain were significantly positive at all three scales for geese, and for each of the two subspecies of the Sandhill Crane (Figure 8, Table A8), consistent with their high use of corn (flooded or non-flooded) or

flooded rice at the field level (Figure 7). Dabbling ducks were positively associated with the proportion of flooded grain at all three scales, as were other shorebirds at just the 2-km scale. All significant associations with the extent of hay/pasture were negative: at all three scales for geese, the Sandhill Crane, the Greater Sandhill Crane subspecies, and long-legged waders, and for two scales for the Lesser Sandhill Crane and other shorebirds. Conversely, all significant associations for the proportion of flooded wetlands were positive: at all three scales for dabbling ducks, at two scales for diving ducks, and for one scale each for other shorebirds and long-legged waders. Groups with positive associations with flooded grain or flooded wetlands and negative associations with hay/pasture generally had high use of flooded crops and wetlands and low use of alfalfa and irrigated pasture at the field level (Figure 7). Overall, the strongest associations were for geese and cranes (both negative) for hay/pasture at the 2-km scale, for dabbling ducks (positive) for both flooded wetlands and flooded grain at the 10-km scale, and

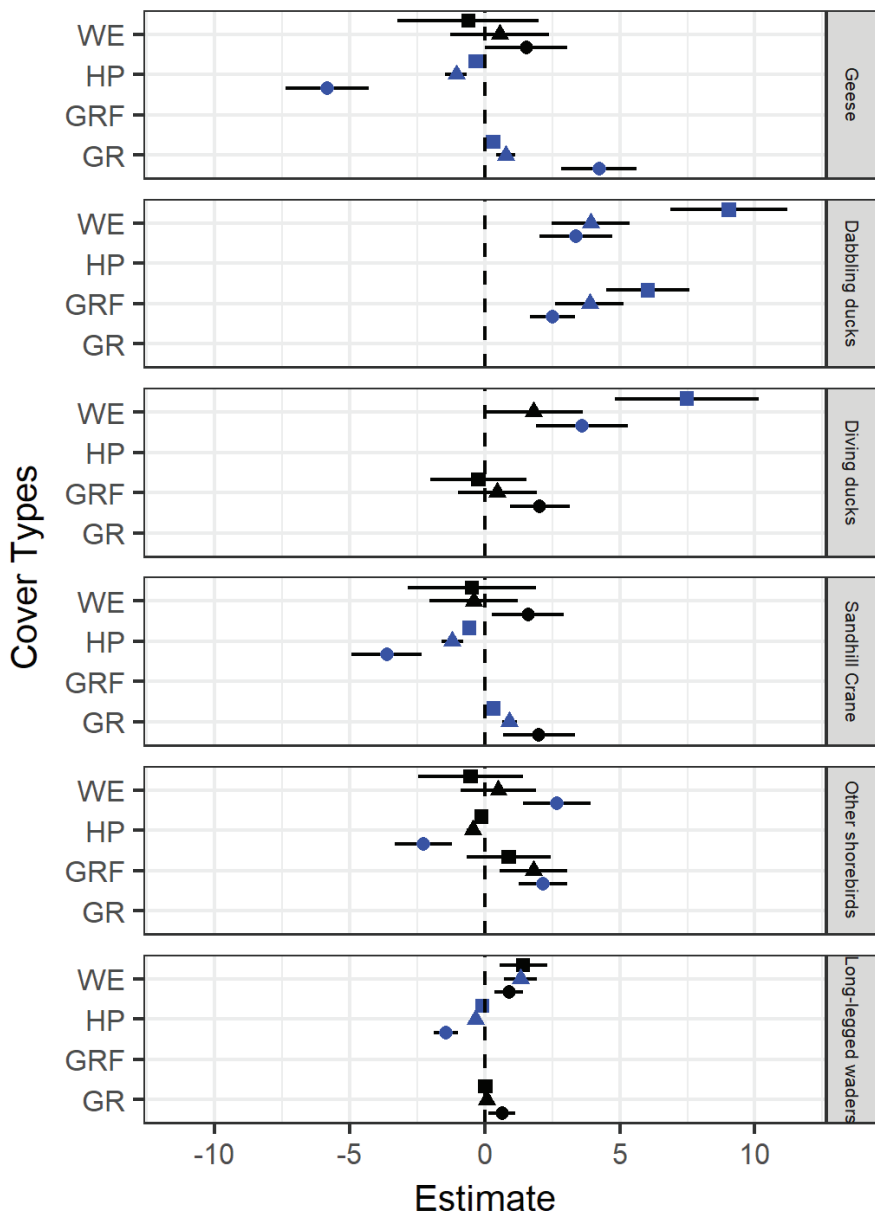


Figure 8 Summary of parameter estimates for landscape models fit to winter (November 17–March 5) waterbird survey data in the Delta, 2013–14 and 2014–15, quantifying the associations between the amount of specific cover types and bird abundance. Each cover type was evaluated for buffers at three scales (■ = 10 km, ▲ = 5 km, ● = 2 km). Blue symbols are significant ($P < 0.05$). Data presented only for those groups with at least one significant result (full set of results in Table A8). Cover types: WE = wetlands, HP = hay/pasture, GRF = flooded grain crops, GR = all grain crops (flooded or dry).

for diving ducks (positive) for flooded wetlands at the 10-km scale (Figure 8, Table A8). Four groups (Tundra Swan, other divers, plovers, and Long-billed Curlew) had no significant associations for any of the landscape variables evaluated.

DISCUSSION

Patterns and Variability of Waterbird Use

Our study demonstrates that waterbirds' use of focal cover types (crops, managed wetlands) in the Delta varies substantially among groups and by

season. Likewise, the factors that appear to influence waterbird abundance and distribution do vary among groups, species, and even subspecies (Sandhill Crane). These patterns should be expected for the diverse waterbird assemblage that currently inhabits the Delta.

The concentration of waterbirds early in the fall in only four focal cover types (alfalfa, irrigated pasture, growing rice, and wetlands), and the higher densities of many groups in wetlands than in crops, emphasize the importance of fully flooded or periodically flood-irrigated cover types

for waterbirds during this time. This was further highlighted by the significant positive associations that seven of 10 waterbird groups evaluated had with the amount of flooding or open water. For groups such as shorebirds that migrate through the Delta starting in late June to early July, this time of year is a bottleneck because open flooded habitats are at their annual nadir in the region (Dybala et al. 2017). Still, some waterbirds—such as geese, White-faced Ibis, and Long-billed Curlews—take advantage of irrigated pasture and flooded alfalfa in fall. Although waterbird densities generally are not as high in these crops as in flooded managed wetlands, some of these crops are more widely available than wetlands in the Delta, particularly before the annual flood-up of managed wetlands, mainly from mid-September through October. During early fall, habitat could be enhanced by flooding more post-harvest winter wheat and potato fields (Shuford et al. 2013b), and by planting early-maturing varieties of corn, which would allow for post-harvest fields to be flooded earlier in fall, as has been done on Staten Island (2016 email correspondence among L. Shaskey, D. Shuford, and others, unreferenced, see “Notes”).

Although managed wetlands remain important to many groups of waterbirds in winter, their importance relative to other cover types wanes. By late fall to early winter, several other cover types also become widely available, particularly post-harvest corn, both flooded and non-flooded (Dybala et al. 2017). Although managed wetlands can support high densities of some waterbird groups, they are patchily distributed in the Delta, and their overall extent on the landscape is not as great as that of some crop types important to waterbirds, particularly corn. Even if densities of some groups may not be as high in corn as in wetlands, corn and some other crops because of their greater overall extent across the Delta may hold higher numbers of certain waterbirds.

Drivers of Use

Local Factors. The site characteristics that help explain waterbird use patterns are frequently correlated with particular cover types. In fall, many groups showed a positive association with the amount of open water and/or flooded ground, and had relatively high densities in managed wetlands,

which was the primary flooded cover type in this season. Such groups often had a negative association with dry ground or vegetation, which are either not prevalent in flooded wetlands or are not used extensively by most waterbirds. In winter, most groups had a positive association with the amount of open water and/or flooded ground, with the Sandhill Crane and Long-billed Curlew being the only ones lacking an association with one or both of these factors.

In both fall and winter, the abundance of Sandhill Cranes had a significant negative association with increasing distance from known nighttime roost sites, though the strength of the association was weaker in winter, suggesting cranes were not as strongly tied to roosts in winter as in fall. Perhaps later in the winter a reduction in food resources forces cranes to increase the length of their foraging flights, or perhaps more roost sites become available later in the season over a broader area as more fields are intentionally flooded, leading to more distant flights by cranes. Ivey et al. (2015) reported that most foraging flights of Greater and Lesser Sandhill Cranes were within 5 km and 10 km of nighttime roosts, respectively, but they recorded very little change in foraging flight distance with date in the season.

The Delta-wide patterns of associations with site characteristics we found in winter were similar to those in a prior study on Staten Island in the central sub-region of the Delta (Shuford et al. 2016b). For example, both studies found dabbling ducks associated positively with the amount of the survey area flooded, and negatively with crop residue (also negatively with moist soil, dry soil, and bare ground Delta-wide). Likewise, across the Delta and at Staten Island, diving ducks were positively associated with flooding, and negatively with crop residue and moist soil (also negatively with dry soil, bare ground, and vegetation Delta-wide). In both studies, long-legged waders were positively associated with flooding, and cranes positively with crop residue, which is prevalent in dry, harvested corn fields. Both groups of ducks have particular depth preferences and generally avoid very shallow water (Strum et al. 2013; Shuford et al. 2016b), which is often positively correlated with the amount of crop residue. This finding, while consistent with previous studies,

should be interpreted carefully, given the lack of water depth data in our study.

To ensure effective conservation actions, further research on individual species may be needed to refine our understanding of patterns of bird use related to cover types and field conditions in the Delta. Our study provided data only on overall daytime habitat use patterns but may have obscured consistent diel variation in use patterns for birds such as cranes, which may use different cover types for morning and afternoon foraging periods than for midday loafing (Ivey 2015), and for waterfowl and shorebirds, which may vary by species, daily environmental conditions, and season in the degree to which they forage in the day or night (Miller et al. 1985; McNeil et al. 1992; Austin et al. 2016). Similarly, our data do not account for any differences in habitat use by ducks between day and night in response to disturbance from hunting (Casazza et al. 2012; Coates et al. 2012). Also, the probability of detection for some birds in tall or dense cover types (e.g., rice in growing season) may be less than 1, possibly resulting in lower estimated densities.

Landscape Factors. In both seasons, many significant associations with landscape factors were consistent in their direction (positive or negative) across spatial scales. These patterns of associations for particular waterbird groups were generally consistent with their patterns of cover type use at the field level. Only one group—other shorebirds—exhibited a consistency pattern of association with a single spatial scale. The significant influence at the 2-km scale for shorebirds is consistent with patterns found in other studies (Taft and Haig 2006; Elphick 2008; Reiter et al. 2015b). Reiter et al. (2015b), however, found that while shorebirds in wetlands in the winter were significantly associated with the amount of water in the surrounding landscape at the 2-km scale, they were most strongly associated with the amount of water at the 10-km scale. In addition to the 2-km scale, Elphick (2008) also found a marginally significant association of shorebirds with flooded rice at the 10-km scale. The lack of a specific scale of influence for dabbling ducks in our study contrasts with Elphick's (2008) finding that dabbling ducks had a significant association at the 5-km scale. Because these other studies were conducted in the Sacramento Valley with a focus on bird use just in

wetlands (Reiter et al. 2015b) and rice (Elphick 2008), they may not be comparable to our evaluations of multiple cover types in the Delta. Understanding the spatial scale at which birds respond to the landscape can help to identify where—relative to existing habitat—new habitat should be created.

In fall, the associations of bird groups with cover-type classes at various landscape scales appeared to reflect the habitat preferences of groups and how those habitats were distributed within the study area. For example, in fall, the Long-billed Curlew was recorded almost entirely in alfalfa and irrigated pasture, and correspondingly was positively associated with hay/pasture at the 2-, 5-, and 10-km scales. Curlews were consistently abundant primarily in the western portion of the northern Delta (west of the Yolo Bypass), where irrigated pasture and alfalfa are by far the dominant crops (Figure 3). Prior local and broad-scale surveys, as well as satellite tracking in the Central Valley, have previously documented large concentrations of Long-billed Curlews in the northwestern portion of the Delta in fall using these same cover types (Shuford et al. 2009, 2013a; Sesser 2013). Because irrigated pasture and alfalfa are irrigated for just short concentrated periods, it seems likely that curlews require large amounts of these two crop types so when some fields are dry between irrigations other fields are being flood-irrigated. This need to move among flooded fields may preclude curlews occurring in abundance in areas with limited amounts of hay/pasture, even though individual fields may be (periodically) suitable for foraging.

Conversely, groups like the Sandhill Crane and other shorebirds have negative associations with the extent of hay/pasture at all three scales in fall. This may reflect cranes' dependence (particularly the Greater subspecies, which does not forage much in alfalfa) on grain crops, which are in short supply when hay/pasture dominates the landscape, and the limited availability of shallow-water areas that cranes use for nighttime roosting. For other shorebirds, this may reflect the lack of much standing water in periodically flooded hay/pasture fields—when irrigated post-harvest vegetation is short—as well as their being precluded from foraging when alfalfa and hay crops become denser and taller later in the crop cycle.

That long-legged waders had the only positive association with the extent of flooded rice in fall at all three scales may reflect that these large birds are the only ones that can effectively forage in rice fields when the crop is tall and dense before harvest. The associations of certain bird groups with the extent of flooded wetlands on the landscape in fall are difficult to explain. It seems anomalous that dabbling ducks, diving ducks, and other divers had no significant positive associations with the extent of flooded wetlands on the landscape in fall, but this may, in part, reflect the general lack of this important habitat early in this season, and that densities in wetlands may decrease as there are more wetlands on the landscape. Other shorebirds and long-legged waders had positive associations with the extent of flooded wetlands—the former at just the 2-km scale, the latter at both the 2- and 5-km scales.

In winter, at the three landscape scales evaluated, geese and cranes had significant positive associations with the total extent of grain. This was consistent with cranes in the Delta focusing most of their foraging on grain crops (Ivey 2015), and the concentration of our observations of cranes and geese in the central portion of the Delta (Point Blue Conservation Science 2015, unpublished data, see “Notes”) where corn and rice are concentrated (Figure 3). Dabbling ducks had significant positive associations with the total extent of both flooded grain and flooded wetlands at all three landscape scales, consistent with their use of shallowly flooded habitats in general. Diving ducks also had a significant positive association with the total extent of wetlands, but at just the 2- and 10-km scales. The only crop class with which various groups (geese, cranes, long-legged waders, other shorebirds) were negatively associated in winter was the total extent of hay/pasture. Similar to the case in fall, this appears to reflect the dependence of geese and cranes on grain crops, which are in short supply (as are the birds) when the landscape is dominated by hay/pasture. The negative association of long-legged waders and other shorebirds with hay/pasture may reflect the limited standing water in crops that are not irrigated during this season—water which was not augmented much by rainfall, given the drought during our study—and by the lack of other shallow-water habitats (wetlands, flooded corn) west of the

Yolo Bypass, where irrigated pasture and, to a lesser extent, alfalfa are concentrated (Figure 3).

Environmental Variability

Because our surveys were conducted in a period of extreme drought in the Central Valley, including the Delta, the patterns of waterbird use we recorded may not be typical of those under average climatic conditions. Although Reiter et al. (2015a) suggested that, overall, the total amount of surface water in the Delta (2000–2011) was relatively resilient to drought, recent analyses suggest that waterbird habitats common in the Delta—specifically flooded corn and wetlands—substantially declined during the extreme drought of 2013–2015 (Reiter et al. 2018). In wetter years, more winter rain may pool in fields, and many fields may be flooded entirely during periods of extended rainfall and runoff. Drought conditions prevailed throughout California and large parts of the West during our 2-year study (<http://droughtmonitor.unl.edu/Maps.aspx>), possibly affecting the abundance or movements of migratory waterbirds over large spatial scales, which could have influenced patterns we observed in the Delta. The patterns we observed, however, may be increasingly likely in the future when droughts (and floods) are projected to be more frequent and severe (Dettinger and Cayan 2014; Dettinger et al. 2016). In any case, model uncertainty in the present study might be improved by conducting surveys over additional years to capture a greater range of climatic conditions.

CONCLUSIONS

Our study demonstrates that a wide variety of waterbirds in the Delta use both wetlands and croplands, which vary in their importance seasonally. Wetlands are particularly important to waterbirds in fall, when there is little persistently flooded agricultural land, but intermittently flood-irrigated alfalfa and pasture are also key habitats for some species at that time. In winter, agricultural fields, particularly of flooded and non-flooded corn, become increasingly important after harvest, when food resources become more available. Knowledge of the broad habitat preferences of various bird groups and species and their use of particular ranges of water

and cover-type conditions will enable management to benefit these birds.

For the Delta to retain its importance to waterbirds, it will be necessary to maintain a mosaic of wetlands and wildlife-friendly crops. A restoration or conservation program that focused on wetland habitat and allowed agriculture to respond solely to market forces – without providing incentives for crops suitable for waterbirds – would likely result in reduced habitat quality for many migratory birds, as exemplified by the continuing replacement of waterbird-friendly crops with orchards and vineyards. Specifically, managers will need to prioritize maintaining corn, alfalfa, irrigated pasture, and rice, and ensure that a substantial portion of corn and rice is flooded in winter.

Additionally, our results illustrate that a mosaic of agriculture and wetlands will be most effective if it accounts for the importance of the landscape. In winter, dabbling ducks, diving ducks, shorebirds, and long-legged waders were more abundant when there were more wetlands or flooded grain fields in the surrounding landscape. Geese and cranes, however, were more numerous when there were more surrounding grain fields of any kind (flooded and non-flooded). In fall, the Long-billed Curlew was more abundant when there was more surrounding irrigated pasture and alfalfa.

Another issue is the potential loss of extensive waterbird habitat from restoration of islands back to tidal marsh or their inundation after levee failure. Our results suggest that the greatest concern would be the loss of managed wetlands with relatively shallow water that provide important habitat in both fall and winter. Changes to the agricultural matrix could also be important, particularly if islands were inundated in the central sub-region of the Delta, where the probability of inundation is high (Mount and Twiss 2005) and where most corn is grown.

Given the great uncertainty in the future extent and pace of habitat loss and degradation in the Delta – but with rapid or catastrophic change certainly possible – prioritizing the conservation actions needed to maintain robust waterbird populations in this region is urgent. Data from the current study, including further landscape influences and predictions of bird occurrence not reported here

(Shuford et al. 2016a), are well suited for immediate use in the prioritization of landscapes in the Delta for waterbird conservation using established methods (e.g., Moilanen et al. 2005). This would provide more refined and integrated guidance for land managers, planners, and conservation practitioners to support biodiversity and working landscapes in the Delta. Reconciling human uses with ecological recovery in the Delta will require a creative approach to designing and adaptively managing these emergent landscapes (Milligan and Kraus-Polk 2017).

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