

Waterfowl use of wetland habitats informs wetland restoration designs for multi-species benefits

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Abstract

1. Extensive global estuarine wetland losses have prompted intensive focus on restoration of these habitats. In California, substantial tracts of freshwater, brackish and tidal wetlands have been lost. Given the anthropogenic footprint of development and urbanization in this region, wetland restoration must rely on conversion of existing habitat types rather than adding new wetlands. These restorations can cause conflicts among stakeholders and species that win or lose depending on identified restoration priorities.
2. Suisun Marsh on the San Francisco Bay Estuary is the largest brackish marsh on the US Pacific coast. To understand how conversion of brackish managed wetlands to tidal marsh would impact waterfowl populations and whether future tidal marsh restorations could provide suitable habitat for dabbling ducks, we examined waterfowl wetland use with a robust GPS-GSM tracking dataset (442,017 locations) from six dabbling duck species ($N = 315$).
3. Managed wetlands, which comprise 47% of Suisun Marsh, were consistently and strongly selected by waterfowl over tidal marshes, with use ~98% across seasons and species.
4. However, while use of tidal marsh (only 14% of Suisun Marsh) was generally <2%, almost half our ducks (~44%) spent some time in this habitat and exhibited strong utilization of pond-like features. Ponds only comprise ~10% of this habitat but attracted 44% use (~4.5 times greater than availability).
5. *Synthesis and applications.* Managed wetlands were vital to dabbling ducks, but losses from conversion of these habitats may be partially mitigated by incorporating pond features that are more attractive to waterfowl, and likely to offer multi-species benefits, into tidal marsh restoration designs. While waterfowl are presently a common taxon, previously seen calamitous population declines can be avoided through informed ecosystem-based management that promotes species richness, biodiversity and helps 'keep common species common'.

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KEYWORDS

GPS tracking, habitat loss, restoration design, San Francisco Bay Estuary, Suisun Marsh, tidal marsh, wetland restoration

1 | INTRODUCTION

Globally, 30%–90% of all wetlands are threatened, destroyed or heavily modified through land reclamation, pollution and hydrological changes (Abramovitz, 1996; Moser et al., 1996). The resulting losses of habitat heterogeneity, biodiversity and ecosystem services have widespread effects, contributing to invasions of exotic species and losses of native or endemic species (Batzer & Sharitz, 2014; Moser et al., 1996; Ramsar, 2013).

Given the amount of wetland loss, wetland restoration is an increasingly common environmental management practice (Langman et al., 2012; Palmer et al., 1997). For example, substantial historic wetland losses in the largest wetlands on the Pacific Coast of the United States (90%–95%; Brophy et al., 2019; Moser et al., 1996), in and around the San Francisco Bay Estuary (SFBE), mandated prioritization of increasing habitats, protecting species, improving water quality, protecting against flooding and providing recreational opportunities (Central Valley Joint Venture, 2006; Goals Project, 1999). However, decades of development have highly urbanized the SFBE (Nichols et al. 1986), creating a novel ecosystem which prevents a return to its original state (Goals Project, 1999; Moyle et al., 2014). Consequently, managers look to other areas such as Suisun Marsh on the eastern edge of the SFBE to fulfil restoration targets with the aim of providing habitat for tidal marsh obligates, endemic or listed taxa such as California Ridgway's rail *Rallus obsoletus obsoletus* and salt marsh harvest mouse *Reithrodontomys raviventris* and restore ecological values (Moyle et al., 2014; U.S. Department of the Interior, 2013).

However, management strategies that focus on restoring particular species or habitat types can cause conflict among stakeholders with diverging priorities and demands. In Suisun, the heavy emphasis on restoring large tracts of tidal marsh to increase habitat for some threatened species, such as salt marsh harvest mouse (Moyle et al., 2014; U.S. Department of the Interior, 2013), will come at the expense of habitat that accommodates large populations of waterfowl. There is little evidence that dabbling ducks take advantage of tidal marshes in Suisun, and restoration will convert >10% (2,000–3,000 ha) of seasonally managed wetlands upon which waterfowl rely, into tidal marsh (Goals Project, 2015; U.S. Department of the Interior, 2013). Consequently, waterfowl could be excluded from restored tidal marsh habitat if unsuitable to their needs.

Tidal marsh is composed of marsh plains vegetated with emergent vegetation such as bulrushes *Schoenoplectus* spp. and pickleweed *Salicornia pacifica* in wetland areas, intertidal and subtidal channels, and occasionally, deeper more permanent ponds, and offers little in the way of foraging resources or ideal waterfowl habitat (Casazza et al., 2012; Coates et al., 2012; U.S. Department of the Interior, 2013). Managed wetlands, which also have suffered

heavy decadal losses (Frayer et al., 1989), provide flooded habitat using levees and water control structures (Gray et al., 2013). These habitats optimize food (e.g. swamp timothy *Crypsis schoenoides* and brass buttons *Cotula coronopifolia*) for waterfowl, particularly in the winter (Casazza et al., 2012; Central Valley Joint Venture, 2006; Coates et al., 2012), and are vegetated with many plants, for example, sea purslane *Sesuvium verrucosum*, pickleweed and bulrushes (U.S. Department of the Interior, 2013). Northern pintail *Anas acuta*, for example, are known to utilize these wetland areas almost exclusively. Therefore, losing optimal habitat through conversion to less suitable habitat could have deleterious impacts to these populations. Moreover, agricultural rice in California's Central Valley currently provides essential resources to waterfowl (Central Valley Joint Venture, 2006; Miller et al., 2010) which, if lost (e.g. through conversion to orchards or vineyards) due to economic pressures, would increase reliance upon the remaining managed wetlands. Conversion of managed wetlands to tidal marsh would reduce the carrying capacity of California waterfowl habitat, and potentially compromise waterfowl populations, even if those remaining managed wetlands are protected and enhanced as asserted in goals of the Suisun Management Plan (U.S. Department of the Interior, 2013).

The aim of this study was to understand waterfowl use of wetland habitats in Suisun Marsh and how proposed wetland restoration might impact these large populations. We leveraged an extensive waterfowl tracking dataset as a case study of Suisun Marsh, to examine waterfowl use of managed wetlands and tidal marsh in relation to their availability on the landscape in SFBE's Suisun Marsh. In addition, we assessed waterfowl use of micro-habitats within tidal marshes to determine whether specific features may be useful to ducks allowing tidal marsh restoration designs to be modified to incorporate a broader variety of habitat features compensating for the loss and supporting co-benefits for multiple taxa.

2 | MATERIALS AND METHODS**2.1 | Study site, species and capture locations**

Suisun Marsh, in the SFBE, is one of North America's largest and most ecologically significant estuaries (Ramsar, 2013). Hosting over 1,000 species of plants and animals, including 130 species of fish and the largest population of winter shorebirds south of Alaska (Moyle et al., 2014; Ramsar, 2013), the wetlands are the focus of extensive ongoing conservation and management planning efforts.

We captured six species of Pacific Flyway ducks: gadwall *Mareca strepera*, mallard *Anas platyrhynchos*, northern pintail (hereafter pintail), northern shoveler *Spatula clypeata* (hereafter shoveler), cinnamon teal *Spatula cyanoptera* (hereafter teal) and American

wigeon *Mareca americana* (hereafter wigeon) from January 2015 to October 2018, using baited funnel traps, rocket nets and handheld dip nets (Drewien & Clegg, 1992; Haramis et al., 1982; Schemnitz et al., 2009). Birds were captured at Grizzly Island State Wildlife Area (SWA; 38.138°, -121.978°), surrounding private properties within Suisun Marsh, and at Howard Slough SWA in the Sacramento Valley (39.467256°, -121.877411°) before and after the hunting season. Nesting gadwall and mallard females were found on Grizzly Island SWA using standard nest dragging techniques in the summer (McLanress et al., 1996). Teal were also captured at various locations within Oregon, Idaho, Colorado, Nevada, Washington and Utah. Individuals were aged as hatch-year (HY) or after-hatch-year (AHY) based on feather and moult plumage (Carney, 1992) and only AHY birds received GPS transmitters.

2.2 | Electronic tracking

We deployed high-resolution Ecotone[®] (Ecotone Telemetry) and Ornitela[®] (Ornitela) GPS-GSM electronic transmitters (~5 m location accuracy) on 338 adult ducks that were individually identified with numbered aluminium U.S. Geological Survey Bird Banding Lab leg bands. We assessed body size with morphometric measurements (wing chord, tarsus, culmen and mass) to ensure the transmitter weight was within the accepted 3%–5% body weight limit for birds (Barron et al., 2010; Kenward, 2001). Ecotone Saker L (58 × 27 × 18 mm; 17 g) and CREX-XS (36 × 25 × 19 mm; 14 g for the smaller teal) and Ornitela Ornitrack-15 (58 × 25 × 14 mm; 15 g) transmitters are remotely programmable and solar-powered. The ability of the solar panels to recharge the GPS batteries can be affected by inclement weather and duck behaviour (sheltering in vegetation). Location data intervals varied according to battery power levels from 30 min at highest battery to 6 hr at lowest. Location, date and time data were transmitted via cellular GSM text message when in network range. When out of range, data were stored on devices and backfilled when ducks returned within network range. Transmitters were fitted with a 3 mm foam base pad to reduce abrasion and lift the transmitter above the feathers and attached to back-mounted body harnesses constructed of 9.5 mm automotive elastic, adding 1–1.25 g to the deployment weight. Each duck was released at the location of capture after a handling time of 20–30 min.

2.3 | Habitat use

We excluded all GPS locations outside the boundaries of Suisun Marsh leaving a total of 450,215 locations. Much of Suisun Marsh is composed of privately owned land, primarily duck hunting clubs that actively manage water levels for waterfowl food production and seasonal hunting opportunities. The land boundaries of these seasonally managed wetlands within Suisun Marsh are mapped by the Suisun Resource Conservation District (SRCD) and have an average size of 282 ha (range: 0.37–405 ha). Habitat within the parcels

was classified based on visual assessment using very high-resolution (sub-meter) NAIP from 2014 (USDA Farm Service Agency, 2014, sub-meter) Worldview from 2016, LIDAR in ArcGIS 10.7 for Desktop (Esri). Combining this parcel map with Bay Area Aquatic Resource Inventory (BAARI) v2.1 Baylands and BAARI v2.1 Wetlands data, produced by the San Francisco Estuary Institute (SFEI, 2019), we produced a polygon map of Suisun Marsh with all habitat classified as (seasonal) managed wetlands, tidal marsh, permanent water and other. The BAARI wetlands data have a 50 m² minimum mapping unit in tidal areas and 100 m² unit for non-tidal areas. Permanent water areas that offer little forage are not typically used by dabbling ducks (Casazza et al., 2012; Coates et al., 2012). The habitat classed as 'other' encompassed all non-wetland areas. We attributed all duck GPS locations with the corresponding habitat class and retained only locations within tidal and managed wetland habitats for our habitat use analyses (Figure 1), in R statistical software (R Core Team, 2019). Data utilized in the analyses are available from the US Geological Survey (Overton et al. 2021).

To analyse bird use of specific habitats, it was necessary to eliminate GPS locations of birds in flight. In the absence of accelerometer data to differentiate flight from on-ground movements, we adopted a conservative method of identifying and excluding GPS locations likely to represent flight. We calculated minimum movement rates between all successive GPS locations for each individual and excluded all GPS locations with movement rates >5 km/hr from the previous location. This method removed a small fraction of the total GPS locations (4,383 locations removed: 1% of the original dataset).

For each individual, we calculated the proportion of observations that were recorded in each habitat class for every day where the individual was observed in Suisun Marsh (Table 1). These daily proportions were then aggregated to calculate median daily use of managed wetlands and tidal marshes for each individual in each season and for each season for every species. We used median daily use instead of mean daily use because mean daily use was influenced by a few outlier individuals making the distributions of habitat use heavily skewed and non-normal. To examine seasonal differences, we placed data into bins by season according to varying water levels across the landscape as well as how duck movements vary seasonally (McDuie et al., 2019), defining these as fall (September 1st–October 14th), winter (hunting season; October 15th–January 31st), spring (February 1st–April 30th) and summer (May 1st–August 31st), on the basis of hydrology, waterfowl life history and hunting pressure on the landscape (Casazza et al., 2012; Central Valley Joint Venture, 2006; Fleskes & Yee, 2007; McDuie et al., 2019). Any species × season combination with too small a sample size (<5 total individuals, and any individual that had fewer than 25 total observations in a season) in Suisun Marsh, were omitted prior to analysis.

2.4 | Tidal feature use

We classified the tidal habitat into three tidal features, (channel, pond and vegetation; Table 2). Channels were classified using the

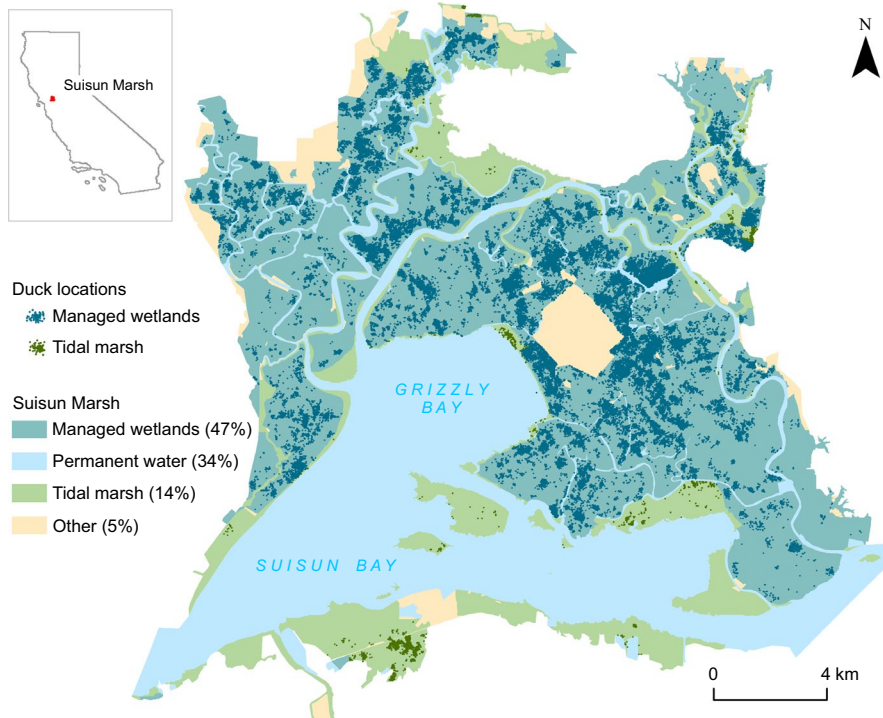


FIGURE 1 Habitat map of Suisun Marsh, CA, USA (SFEI, 2019), showing classified habitat types with associated duck GPS locations. Percentages represent the proportion of Suisun Marsh that the habitat constitutes. Duck locations are classified and coloured according to the habitat in which they occur—managed wetlands (blues) and tidal marsh (greens). All locations in upland and permanent water areas were excluded for the analyses

Habitat class	Area (ha)	Proportion of the Marsh	Proportion of individuals with any use	Median individual proportion of use
Managed wetland	18,128	0.47	0.99	0.98
Permanent water	12,986	0.34	0.57	0
Tidal marsh	5,442	0.14	0.44	0
Other	1,967	0.05	0.54	0

TABLE 1 Total area and proportion of Suisun Marsh, CA that each of our four habitat classes comprise

TABLE 2 Total area and proportion of features within tidal marshes of Suisun Marsh, CA

Tidal feature	Area (ha)	Proportion of tidal marshes	Median individual proportion of use
Vegetation	4,473	0.82	0.51
Pond	550	0.10	0.44
Channel	419	0.08	0.02
Total	5,442		

BAARI v2.1 Baylands and BAARI v2.1 Wetlands data produced by the San Francisco Estuary Institute (SFEI, 2019). Ponds and vegetation were identified and digitized using expert visual classification of high-resolution, multi-temporal, multispectral satellite imagery (Planet Team, 2018). The imagery from December 2017 (winter) and July 2018 (summer) was displayed in false colour (near-infrared, red, green) to differentiate vegetated and flooded areas. Areas that were flooded for at least one of the time periods were classified as ponds. The remaining areas were classified as vegetation. As with habitat use, we overlaid individual GPS locations on the tidal marsh feature map and coded each datapoint

with a tidal marsh feature (channel, pond or vegetation) in ArcGIS (Esri; Figure 2).

As with the previous habitat analysis, locations with minimum movement rates >5 km/hr from the previous location were removed. For every day an individual was in tidal marsh, we calculated the proportion of locations that were recorded in each tidal feature (Table 2). Daily proportions were then aggregated to calculate median individual daily use of vegetation, ponds and channels for each individual in each season (Table 2). To summarize by species, we calculated the median daily use of tidal marsh features for each season for every species. Median daily use was again used due to non-normal distributions, and for consistency with habitat use calculations. Any species \times season combination with too small a sample size (<5 total individuals, and any individual that had fewer than 25 total observations in tidal marshes) were removed prior to analyses.

2.5 | Statistics

We present median daily use calculated from the individual-level data and used a bootstrapping approach to generate confidence

intervals around those medians. Confidence intervals for each species × habitat or species × tidal feature combination were generated using the boot() function in R (R Core Team, 2019). We present 95%

confidence intervals around the median throughout, based on 1,000 bootstrap replicates. We also quantified use:availability ratios by dividing use of habitat or feature by each individual, by the proportion of that habitat or feature available (Tables 1 and 2) similar to Manly et al. (2002), as presented in Tables 3 and 4. Use:availability ratios were then summarized by species × habitat class and species × tidal feature. All ratios are standardized to zero by subtracting 1 so that positive ratios indicate selection for a habitat or tidal feature, and negative ratios indicate selection against a habitat or tidal feature. To test if ratios were significantly different than zero (null hypothesis: no selection), we bootstrapped confidence intervals of the median ratio for each species × habitat or species × feature combination, using the same methods as for bootstrapped median daily use. Confidence intervals that did not overlap zero indicated either selection (>0) or avoidance (<0).

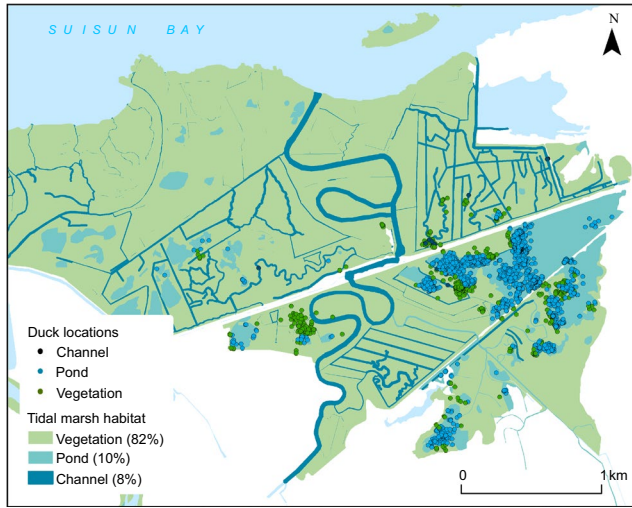


FIGURE 2 An example of tidal marsh habitat in Suisun Marsh, CA, USA (SFEI, 2019), coloured by habitat types—vegetation, permanent water (channels) and ponds. The outer light blue areas are Suisun Bay open permanent water. Percentages represent the proportion of tidal habitat each feature represents. Duck locations are classified and coloured according to the tidal feature they occur in

3 | RESULTS

Overall, 439,758 GPS locations from 315 individuals of six dabbling duck species during four seasons were analysed for habitat use (Table 3) and 10,147 GPS locations from 21 individuals of two dabbling duck species (mallard and gadwall) during two seasons (summer, *n* = 8,490: gadwall = 726; mallard = 7,764, and fall, mallard = 1657) were analysed for tidal feature use (Table 4). Most use

TABLE 3 Median habitat use (% daily use) and standardized use:availability ratios of managed wetlands (managed) and tidal marshes (tidal) for six dabbling duck species across four seasons in Suisun Marsh, California, USA

Species	Season	# indiv.	Total # obs.	Managed % daily use	Managed use:avail.	Tidal % daily use	Tidal use:avail
Overall	Overall	315	439,758	98.0	1.1	0.0	-1.0
American wigeon	Fall	30	2,047	96.1	1.0	0.0	-1.0
	Winter	22	4,158	99.0	1.1	0.0	-1.0
	Spring	5	1,853	92.3	1.0	0.0	-1.0
Cinnamon teal	Winter	5	2,607	98.3	1.1	0.2	-1.0
	Spring	5	7,954	96.3	1.0	0.0	-1.0
	Summer	19	14,988	95.5	1.0	0.0	-1.0
Gadwall	Fall	5	1,860	98.8	1.1	0.0	-1.0
	Winter	8	3,941	99.7	1.1	0.0	-1.0
	Spring	6	4,307	94.3	1.0	0.3	-1.0
	Summer	59	93,214	88.3	0.9	0.0	-1.0
Mallard	Fall	28	22,438	98.6	1.1	0.0	-1.0
	Winter	28	17,084	97.3	1.1	0.0	-1.0
	Spring	34	17,443	89.2	0.9	0.0	-1.0
	Summer	98	159,206	93.8	1.0	0.0	-1.0
Northern pintail	Fall	85	53,089	100.0	1.1	0.0	-1.0
	Winter	46	25,418	99.6	1.1	0.0	-1.0
	Spring	7	2,743	97.9	1.1	0.0	-1.0
Northern shoveler	Fall	14	2,348	100.0	1.1	0.0	-1.0
	Winter	10	3,060	99.4	1.1	0.0	-1.0

occurred in managed wetlands and less than half the tracked birds used tidal marsh habitat (Table 1), regardless of season or species (Figure 3; Table 3). The individuals that spent substantial time in tidal habitat keyed in on permanent pond features within those habitats (Figure 4; Tables 2 and 4).

3.1 | Habitat availability and use

In all cases, median daily use was >88% in managed wetlands, compared to median use of essentially zero in tidal marshes (Table 3; Figure 3). There was little variation in use between individuals,

TABLE 4 Median tidal marsh use (% daily use) and standardized use:availability ratios of channel, vegetation and pond features for two dabbling duck species across two seasons in Suisun Marsh, California, USA

Species	Season	# indiv.	Total # obs.	Channel % daily use	Channel use:avail	Vegetation % daily use	Vegetation use:avail	Pond % daily use	Pond use:avail
Overall	Overall	21	10,147	1.5	-0.8	51.2	-0.4	44.1	3.4
Gadwall	Summer	6	726	3.9	-0.5	56.1	-0.3	35.5	2.5
Mallard	Fall	7	1,657	0.0	-1.0	51.2	-0.4	49.0	3.4
	Summer	10	7,764	4.6	-0.4	46.3	-0.4	44.1	3.9

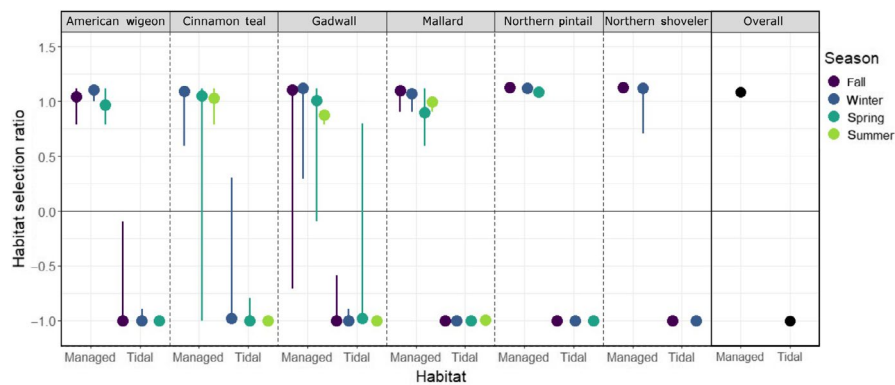


FIGURE 3 Suisun Marsh, California, USA, habitat use:availability ratios in managed wetland and tidal marsh by six species of dabbling duck (315 individuals; see Table 3) across four seasons. Points are median daily use; error bars are 95% confidence intervals around the median, from 1,000 bootstrap replicates. Ratios above 0 (horizontal line) indicate selection for, and ratios below 0 indicate selection against. The final panel is the overall result of all species and seasons combined (note that confidence intervals are smaller than daily use points in some instances)

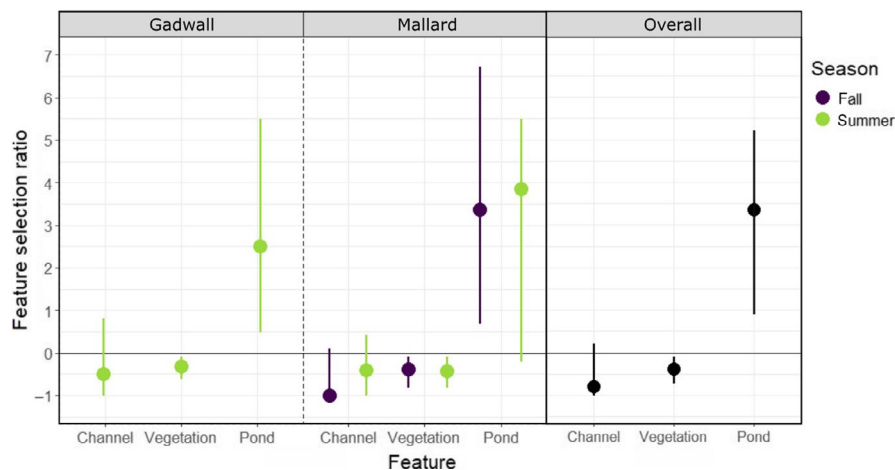


FIGURE 4 Suisun Marsh, California, USA, habitat use:availability ratios in tidal marsh habitat features. Data were limited to gadwall and mallard across two seasons due to too small sample sizes for other species \times season combinations. Points are median daily use; error bars are 95% confidence intervals around the median, from 1,000 bootstrap replicates. Ratios above 0 (horizontal line) indicate selection for, and ratios below 0 indicate selection against. The final panel is the overall result of both species and seasons combined

species or within species across seasons, and individuals consistently selected for managed wetlands and against tidal marsh (Figure 3). A few species \times season combinations had fewer than 10 total individuals: the bootstrapped confidence intervals for these combinations were occasionally very broad due to variability from low sampling intensity (cinnamon teal winter, spring; gadwall fall, winter, spring; Figure 3).

3.2 | Tidal feature availability and use

Only gadwall in summer ($n = 6$) and mallard in summer ($n = 10$) and fall ($n = 7$) had enough individuals using tidal habitat to analyse use of tidal marsh features (Table 4). Individuals demonstrated very low use of channels but used ponds and vegetation in similar proportions (Table 4; Figures 2 and 4). However, despite nearly equal use, since vegetation dominated the tidal marsh habitat (82%) and pond-like features were much rarer (10%), individuals demonstrated strong selection for pond-like features ('overall' panel in Figure 4), selection against vegetation features and did not select for or against channels.

4 | DISCUSSION

Dabbling ducks in Suisun Marsh, California overwhelmingly selected for managed wetlands over other habitats, which corresponds with past research showing that dabbling ducks, geese and other waterfowl prefer this habitat over tidal marshes (Ackerman et al., 2014; Casazza et al., 2012; Casazza & Miller, 2000; Coates et al., 2012). Managed wetlands across California (approximately 47% of Suisun Marsh) are optimized to provide habitat and dedicated food production for millions of waterfowl primarily in the winter months (Casazza, 1995; Casazza et al., 2012; Central Valley Joint Venture, 2006; Coates et al., 2012; U.S. Department of the Interior, 2013). However, should Central Valley cropping patterns shift away from the agricultural rice that provides critical de facto, supplementary food (Central Valley Joint Venture, 2006; U.S. Department of the Interior, 2013), waterfowl carrying capacity would be substantially reduced and managed wetlands would need to support greater bird density to maintain current wintering population levels (Central Valley Joint Venture, 2006; Coates et al., 2012; Fleskes et al., 2005; Miller et al., 2010). Currently, waterfowl carrying capacity across California is estimated in the 'SWAMP' and 'TRUOMET' bioenergetics models, which roughly calculate energy availability in managed wetlands and croplands, and the energy needed to support the 'average duck' over the winter (Central Valley Joint Venture, 2006; Miller et al., 2014). However, given wetland restoration plans that are scheduled to increase tidal marsh by 34% simultaneously reducing managed wetland habitats by 10%–15% (U.S. Department of the Interior, 2013), it is essential that models are based on, and provide, accurate information. Therefore, future research that develops a greater understanding

of carrying capacity is needed to inform conservation and restoration efforts.

After the over-wintering, migratory populations have departed (Fleskes & Yee, 2007), managed wetland water levels are decreased causing wetlands to dry, leaving little remaining flooded habitat for the resident breeding species including mallard, gadwall and teal (Casazza & Miller, 2000; Moyle et al., 2014; U.S. Department of the Interior, 2013). When ideal habitat is lacking, resident ducks may augment habitat needs by utilizing suboptimal habitat, as reflected by ~44% of individuals using tidal marshes at least some of the time in our study. When using tidal marshes ducks selected pond-like features which were physically similar to managed wetlands—shallow, more permanent features with submersed and emergent vegetation (Isola et al., 2000; Moyle et al., 2014). These types of shallow, open water pond features in tidal marshes are known to be important to waterfowl on the Atlantic coast of North America (Adamowicz & Roman, 2005; Erwin et al., 1994), where some species forage in these more saline habitats (Osborn et al., 2017). While tidal marsh habitats offer limited foraging opportunities for many waterfowl (Casazza et al., 2012; Coates et al., 2012; Johnson & Rohwer, 2000), they may be of some benefit to more flexible species that can take advantage of brackish habitats (Johnson & Rohwer, 2000; Sánchez-Zapata et al., 2005), when managed wetlands across the landscape are reduced.

Suisun tidal marshes containing permanent ponds could be an important habitat feature for resident mallard and gadwall that require cover during the post-breeding, catastrophic flightless moult (Fleskes et al., 2010; Kohl, 2019). Suisun currently lacks favourable moult habitat, forcing many individuals to migrate hundreds of miles north to moult in the Klamath Basin of southern Oregon, north-eastern California (Fleskes et al., 2010; Kohl, 2019). In addition to increasing energy expenditure (Schmidt-Nielsen, 1972; Tucker, 1970, 1971), migration elevates predation risk and deleterious disease outbreaks are more common where bird density is higher at migration stopover or end points (Fleskes et al., 2010). Therefore, creating suitable moult habitat is one of the objectives of the Management Plan for Suisun Marsh (U.S. Department of the Interior, 2013). Designing restored tidal marshes that incorporate duck-friendly habitat features may contribute to fulfilling these requirements and help compensate for waterfowl habitat lost during restoration—an important consideration given the planned reductions of managed wetlands (U.S. Department of the Interior, 2013). Ideal areas for tidal marsh restoration would be those with higher salinity or more limited access to regular fresh-water input, which makes them suboptimal for waterfowl (Central Valley Joint Venture, 2006). However, integrating variability in bottom topography that would create a range of water depths and permanent vegetated ponds could increase species diversity and provide some habitat for waterfowl as well as other species such as shorebirds (Isola et al., 2000).

Nevertheless, even the most well-designed restoration strategies can be subject to extrinsic factors which reduce their longevity and ability to achieve long-term objectives. Wetland habitats in the SFBE are threatened by sea-level rise (SLR) which is projected

to cause the loss of at least 90% of tidal marsh in the SFBE by 2,100 (Rosencranz et al., 2019; Takekawa et al., 2006; Thorne et al., 2013, 2015) and would render restoration plans ineffective. The only habitats with a chance of surviving are those with adjacent higher ground that they can migrate to, or sediment input that would allow accretion rates to keep up with SLR, but the managed wetland areas currently scheduled for restoration to tidal marsh in Suisun Marsh have low topographic gradients and are particularly at risk (Rosencranz et al., 2019; Takekawa et al., 2006; Thorne et al., 2015). Restored tidal marshes can take up to 50 years to be fully recovered, but SLR would eliminate habitat or reduce suitability for focal species (Rosencranz et al., 2019; Takekawa et al., 2006; Thorne et al., 2015) and threatens the very system managers and planners had focused on restoring. By contrast, the managed wetlands that are scheduled for conversion do already support some tidal marsh species, and their controlled water levels with dikes and levees (Smith & Kelt, 2019; Sommer et al., 2001, 2003) may make them more resistant to SLR.

California wetland losses have been extensive, even managed wetlands are reduced to 10% of their historic extents (Frayer et al., 1989), and these losses coincided with declines in Pacific Flyway waterfowl populations (Gilmer et al., 1982; Moyle et al., 2014; U.S. Department of the Interior, 2013). More recently, wetland management in this area of California has benefited waterfowl populations through dedicated and targeted management plans such as the North American Waterfowl Management Plan (NAWMP; US Department of the Interior, Environment Canada and Environment and Natural Resources Mexico, 2018). This North American plan was developed to respond to historic declines, and has successfully partnered with local joint ventures such as the Central Valley Joint Venture for the Pacific Flyway (Central Valley Joint Venture, 2006) to manage habitat for waterfowl. Since plan implementation almost 35 years ago, a period during which many other common bird families and species suffered calamitous population declines across North America, waterfowl have not been affected by these trends (Rosenberg et al., 2019). Both rare and common species contribute to biodiversity and ecosystem function, and precautionary principles for ecosystem-based management approaches encourage 'keeping common species common' to ensure ecological health of ecosystems (Chapman et al., 2018; Gaston, 2010). However, converting large tracts of effective waterfowl habitat to tidal marsh would elevate the risk of population declines in common waterfowl species while the long-term preservation of rarer target species in the face of SLR is uncertain.

Management objectives that aim to conserve rare species in favour of common ones or favour one goal over another can create conflict among species or between habitat restoration and species conservation. These conflicts reduce the ability to prevent the continued loss of biodiversity or achieve broadscale habitat and ecosystem goals. For example, past conservation plans aimed at protecting shorebird foraging habitat caused declines in the endangered California Ridgway's rail populations (Casazza et al., 2016) due to habitat restoration that removed non-native tidal marsh grasses. Another species of concern, the salt marsh harvest mouse,

previously thought to be a tidal marsh obligate, was recently found to be equally successful in managed wetlands (Smith & Kelt, 2019). Research has also shown that managed floodplains can provide valuable habitat for Sacramento splittail *Pogonichthys macrolepidotus* and juvenile chinook salmon *Onchorhynchus tshawytscha*, both federally listed fish species (Sommer et al., 2001, 2003). Combined, these studies demonstrate how evidence-based research can inform management and conservation strategies, as has been successfully achieved in marine environments (e.g. Malone & Knap, 2018; Marzloff et al., 2016; McDuie & Congdon, 2016).

5 | CONCLUSIONS

In the Suisun Marsh case study, we developed a thorough understanding of how ducks use wetland landscapes and provided a template for how restoration plans could be reconceptualized to incorporate features beneficial to multiple taxa. Simultaneously, protecting focal species of conservation concern in California wetlands while mitigating the loss of essential waterfowl habitat could increase stakeholders value and involvement (McKinstry & Anderson, 2002) and provide economic, social, cultural and environmental benefits by enhancing ecosystem services and biodiversity (De Groot et al., 2013; Mitsch et al., 2015; Moreno-Mateos et al., 2015). Multi-species conservation approaches should be underpinned by evidence from robust scientific studies to maintain or improve ecological health, integrity and species richness (Palmer et al., 1997, 2005; Rosencranz et al., 2019). Finally, by considering the potential impacts of extrinsic forces such as SLR and climate change, managers can improve habitat resilience and achieve effective, lasting adaptive ecosystem-based management.

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AUTHORS' CONTRIBUTIONS

M.L.C., J.T.A., K.M.T. and C.L.F. conceived the original idea, design and experiment; M.L.C. and F.M. authored the manuscript and all authors read and approved the final manuscript; C.T.O. provided and processed the dataset; analyses were conducted by S.J., A.A.L. and J.Y.

DATA AVAILABILITY STATEMENT

Data are available in the US Department of the Interior and U.S. Geological Survey's ScienceBase <https://doi.org/10.5066/P94B0WUV> (Overton et al., 2021).

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