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Distribution and Habitat Associations of California Black Rail (*Laterallus jamaicensis coturniculus*) in the Sacramento–San Joaquin Delta

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ABSTRACT

Past studies documenting the distribution and status of state "Threatened" California black rail (*Laterallus jamaicensis coturniculus*; hereafter black rail) have largely omitted the Sacramento–San Joaquin Delta (hereafter Delta). During March to May of 2009–2011, we conducted call–playback surveys to assess the status of the species within a wide range of wetland habitats of the central Delta region. We detected black rails at 21 of 107 discrete wetland sites, primarily on in-channel islands with dense cover. To better understand the habitat and land cover characteristics, we developed a model of habitat suitability from these occurrence data and a fine-scale vegetation and land use dataset using MaxEnt. We also evaluated differences in the size of wetlands at sites where black rails were detected versus where they were not. Through surveys and quantitative modeling, we found black rail presence differed from other regions within California and Arizona, in that it was positively associated with tall (1 to 5 m) emergent vegetation interspersed with riparian shrubs. Specific plants correlated with black rail presence included emergent wetland (*Bolboschoenus acutus*, *B. californicus*, *B. acutus*, *Typha angustifolia*, *T. latifolia*, *Phragmites australis*) and riparian (*Salix exigua*, *S. lasiolepis*, *Rosa californica*, *Rubus discolor*, *Cornus sericea*) species. Median patch size was significantly larger and perimeter-to-area ratios were significantly lower at wetland sites where black rails were found. These results provide a preliminary characterization of black rail habitat in the Delta region and highlight the need for better understanding of this listed species' population size and habitat use in the region, in light of anticipated climate change effects and proposed large-scale restoration in the Delta.

KEY WORDS

California black rail, *Laterallus jamaicensis coturniculus*, Sacramento-San Joaquin Delta

INTRODUCTION

The California black rail (*Laterallus jamaicensis coturniculus*; hereafter black rail) resides in a variety of wetland habitats across its range in California and Arizona (Eddleman et al. 1994). The most geographically extensive occupied habitats exist in the San Francisco Estuary, specifically along the Petaluma and Napa rivers, San Pablo Bay, Suisun Bay, and Suisun Marsh, which supports a large proportion of the subspecies (Evens et al. 1991; Spautz et al. 2005). Black rails also inhabit the Sacramento–San Joaquin Delta (hereafter Delta), small coastal wetland sites (e.g., Tomales Bay and Morro Bay), the Sierra Nevada foothills, and along the Colorado River (Manolis 1978; Aigner et al. 1995; Evens et al. 1991; Richmond et al. 2008). The California Fish and Game Commission listed this species as "Threatened" in 1971 because of population declines attributed in large part to loss of greater than 90% (1.8 million hectares) of historic wetland habitat statewide (Dahl 1990; CDFW 2015; Eddleman et al. 1988; Tiner 1984).

Black rails are secretive and difficult to detect, complicating the study of their natural history. The species has long been known to occur in the Delta (Belding 1878); but its distribution and habitat associations within this region are not well described in the published literature. The earliest recorded specimens in the Delta were documented near Stockton (San Joaquin County) in 1879 and 1960 (Belding 1878; Arnold 1960). Surveys conducted in the 1970s found black rails at Big Break Regional Shoreline (Contra Costa County), and Tule Island and White Slough Wildlife Area (San Joaquin County; Winter and Manolis 1978; Manolis 1977; Manolis 1978; Laymon and Shuford 1979). A recent study confirmed the continued presence of the species at White Slough Wildlife Area (Richmond et al. 2008). Two individuals were detected on Bacon Island (San Joaquin County) in a 1986–1988 study that documented a low abundance (0.25 birds per survey station) within the Delta; however, this study only covered the western extent of the Delta (Evens et al. 1991). Black rails were detected in 1992–1993 at several sites within the central Delta during surveys conducted by California Department of Fish and Game (now California Department of Fish and Wildlife, hereafter CDFW; Gifford and Karlton 2003), but the findings of that study were not described in the published literature.

The Delta is a distributary network of channels located at the confluence of the Sacramento and San Joaquin rivers, which flow into the San Francisco estuary. Historically, the Delta comprised more than 500,000 acres of tidal marsh with sinuous channels formed by seasonal freshwater river inflow and daily tidal fluctuations; however, only 5% to 10% of that habitat remains today (Nichols et al. 1986; Lund et al. 2010; Whipple et al. 2012). The Delta has been substantially modified by humans since the 1800s, resulting in a network of islands disconnected from tidal action and the riverine system (Whipple et al. 2012). Remaining tidal marsh habitat now exists primarily in narrow linear corridors along channel margins and drainage canals, on discrete in-channel islands ("bench islands—elongated, planar, and elevated marshlands located mid-river" in Evens et al. 1991), and within a few relatively small restored parcels with muted tidal or nontidal managed wetland habitat.

Large-scale planning efforts are currently underway in the Delta which aim to restore tidal marsh habitat to benefit native species, including the black rail (Delta Conservancy 2012); however, little information is available to restoration practitioners and land managers about the habitat requirements or distribution of the Delta population of black rails. Given this data gap, surrogate information on habitat characteristics derived from studies in the San Francisco Bay are often used to describe black rail habitat within the Delta. Black rails within the San Francisco Bay have been found to be positively associated with pickleweed (*Sarcocornia pacifica*), gumplant (*Grindelia stricta*), bulrush (*Bolboschoenus maritimus*), rush (*Juncus* spp.), and cattail (*Typha* spp.; Manolis 1978; Evens et al. 1991; Spautz et al. 2005). These vegetation stands grow on upper marsh plains and do not exceed 1 to 1.5 m in height. Black rails also respond to landscape features including distance to channels and marsh size (Spautz et al. 2005).

Within the Delta, existing wetland habitats on in-channel island, channel margin, and non-tidal managed habitats differ in both structure and species composition from those in other regions where black rails are found (e.g., San Francisco estuarine and coastal wetlands, the Sierra Nevada Foothills, the Colorado River basin). Delta in-channel island and channel margin wetlands are at elevations within the tidal range; non-tidal wetlands are often found on subsided islands up to 8 m below sea level (Ingebritsen et al. 2000). Emergent wetlands in the Delta are primarily composed of tall (1 to 5 m), dense stands of bulrush species (*Bolboschoenus americanus*, *B. californicus*, *B. acutus*), cattail species (*Typha latifolia*, *T. angustifolia*), and non-native phragmites (*Phragmites australis*). Additionally, Delta wetlands contain woody riparian species including sandbar willow (*Salix exigua*), red osier dogwood (*Cornus sericea*), and non-native Himalayan blackberry (*Rubus discolor*). These wetland types were noted in the few records of black rail within the Delta region (Manolis 1978; Winter and Manolis 1978; Evens et al. 1991; Richmond et al. 2008).

Black rails are difficult to study given their localized distributions and the limited access to the wetland habitats in which they reside. Additionally, the secretive nature of all rail species leads to low and imperfect detection rates which require the use of call playback survey techniques and high levels of survey replication in order to estimate the metrics needed to model distributions and habitat associations (Spear et al. 1999; Legare et al. 1999; Conway et al. 2004). Data which are collected using less intensive methods are still useful but should be considered to represent presence–only rather than abundance or presence–absence (Conaway et al. 2004). For example, occurrence (presence–only) can be used to model distribution and habitat suitability (Elith et al. 2006, 2010).

From 2009–2011, we conducted surveys to inform water resource and restoration planning throughout the Delta, including call–playback surveys for black rails. We used these data, as well as a remotely sensed land cover dataset (Hickson and Keeler–Wolf 2007) and the species distribution modeling tool MaxEnt, which is effective at estimating species distribution and habitat suitability from occurrence–only data (Phillips et al. 2006), to answer two major questions:

1. What habitat conditions are black rails associated with in the Delta?
2. What is the distribution of potentially suitable black rail habitat in the Delta?

Our study aims to improve the understanding of black rail distribution and habitat use within the Delta to inform future habitat management and restoration in the region.

MATERIALS AND METHODS

Study Area

We conducted black rail surveys within the central sub-region of the Delta in eastern Contra Costa County and western San Joaquin County, California (Figure 1). Surveys were conducted along Disappointment Slough, Old River, Connection Slough, Middle River, White Slough, Fourteenmile Slough, and San Joaquin River, as well as along managed wetland sites on the land side of levees at White Slough Wildlife Area, Mandeville Island, Twitchell Island, Stone Lakes National Wildlife Refuge, and Prospect Island; on tidal wetlands at Big Break Regional Shoreline; and in irrigated pasture south of Dutch Slough.

Survey Methods

We conducted call–playback surveys by boat or on foot from March through May 2009–2011 as part of a Delta-wide avian survey effort, following methods adapted from those used by Evens et al. (1991). Combined survey transect length was approximately 75 km. Survey station selection was non-random; observers surveyed as many stations as could fit, spaced at least 100 m apart, within sites containing wetland vegetation on in-channel islands, channel margin benches exposed to tidal cycles, and non-tidal managed wetland patches located on Delta islands bounded by levees. Some survey stations were visited two times during a survey year; not all stations were surveyed each year. Surveys took place between sun-

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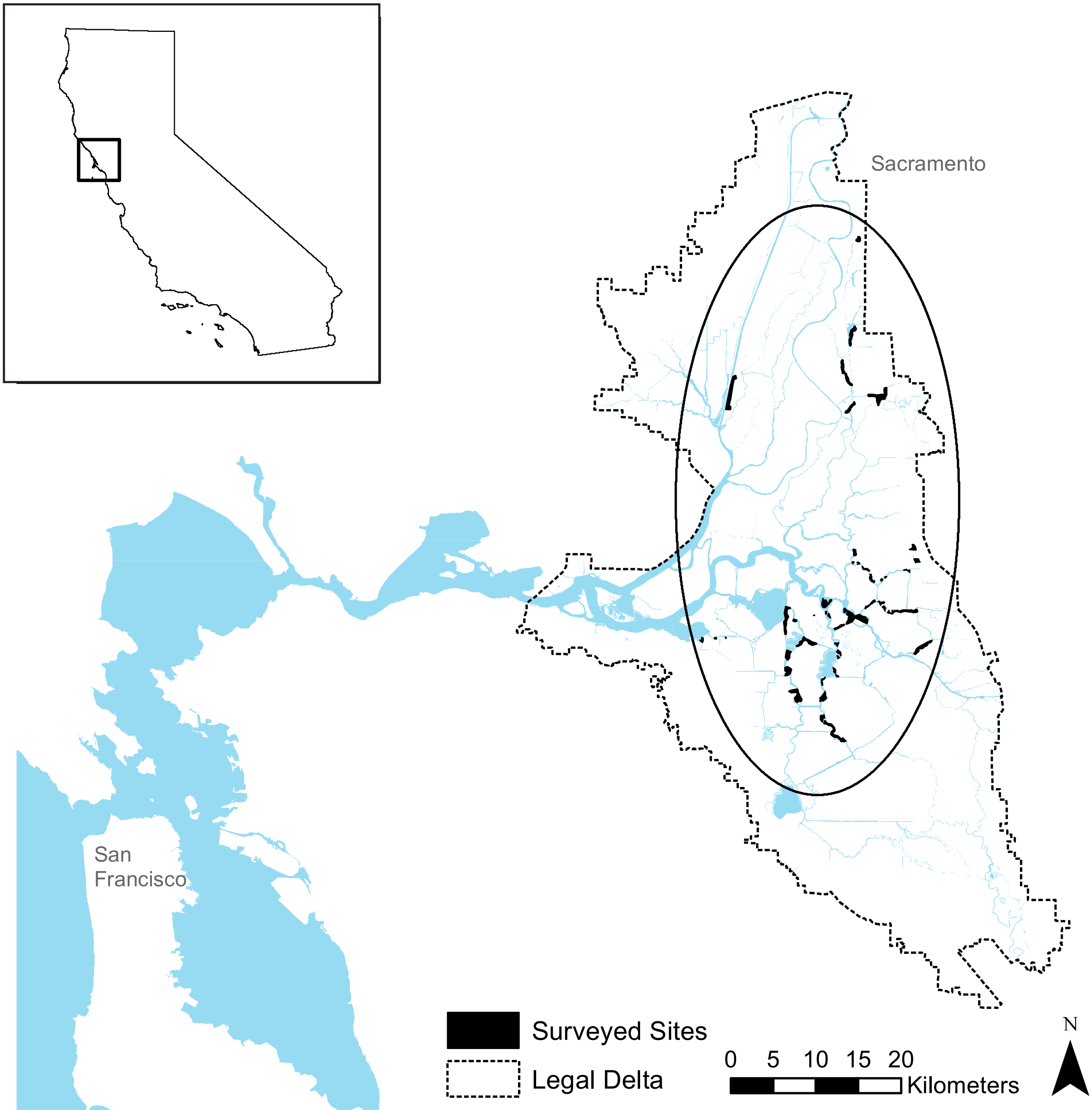

Figure 1 Study area map showing the location of California black rail surveys conducted in the Sacramento–San Joaquin Delta in 2009–2011. The Legal Delta (black dashed-line polygon), survey area (black oval), and survey sites (black polygons) are displayed.

rise and 3 hours after sunrise and were not conducted in windy or rainy conditions. At each survey station, observers stood at a fixed position for 7 minutes and broadcast a recorded black rail call series. The call sequence consisted of one minute of passive listening time, followed by one minute of recorded calls (*ki–ki–do* and *grr*). Observers then listened for five minutes before moving to the next point count station. When a response was heard, we recorded estimated distance and direction to the birds; all survey station locations were recorded in a Trimble GeoXM GPS receiver (Trimble Navigation Limited, Sunnyvale, CA) installed with Arc Pad (ESRI, Redlands, CA). We also recorded spontaneously calling black rails heard at and between survey stations.

Model Building and Assessment

Because our sampling design focused on maximizing geographic coverage within a large study area by surveying at more sites rather than repeating surveys within season at each point, we did not attempt to estimate abundance. Rather, we treated detections as presence-only data to develop models for black rail distribution and habitat suitability. For sites where black rails were detected on both visits, we removed duplicate detections. We used MaxEnt (Version 3.3.3e; Phillips et al. 2006) to explore the relationship between black rail occurrences and remotely sensed land cover characteristics and tidal influence. We then extrapolated our analysis to the entire Delta, given the similarity of the landscape to the sub-region where surveys were carried out. MaxEnt performs consistently well on datasets with small sample sizes and presence–only information and has been used to explore distributions and habitat associations of multiple taxa including birds (Elith et al. 2006; Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008; Benito et al. 2009; Kumar and Stohlgren 2009; Kumar et al. 2006). The model calculates potential suitability of an environment, scoring map cells from 0 to 1, with 1 indicating the most suitable areas based on model training. The model uses a non-parametric approach, accounting for non-linearity by including interactions among predictor variables.

For our analysis, we input 44 black rail occurrence locations within a processing extent defined by the Vegetation and Land Use Classification Map of the Sacramento–San Joaquin River Delta (Hickson and Keeler–Wolf 2007), which encompasses the Legal Delta, a legal geographic boundary defined in the Delta Protection Act of 1959 (California State Water Code Section 12220). We used two categorical predictor variables: vegetation type and tidal status. The vegetation type predictor consisted of a combination of 70 National Vegetation Classification System vegetation associations and 13 land cover types from Hickson and Keeler–Wolf (2007). For the tidal status predictor, we used a binary Geographic Information Systems (GIS) layer that indicated which lands were connected or disconnected from tidal influence.
For each of 100 replicate model runs, we randomly selected training (70%, $n=29$) and testing (30%, $n=12$) samples, and model predictions were averaged to produce a final map of the probability of presence of black rails within the Delta based on vegetation type, land use, and tidal influence.

We assessed our model using the "Area Under the Receiver Operating Characteristic Curve" (AUC), which is a threshold-independent measure of model accuracy that varies from 0 to 1 (Fielding and Bell 1997). An AUC value close to 1 indicates a model with high predictive ability, and values of 0.5 or less indicate models with no better than random discrimination. We used two functions within the MaxEnt tool to characterize the relative importance of vegetation and land cover variables: percent variable contributions and jackknife estimation (Phillips et al. 2006). We also examined individual response curves for each of the variables that provide information on the relationships between species associations within the predictor variables.

We used the mean MaxEnt suitability output to map habitat suitability for the entire Legal Delta based on vegetation type and tidal influence. The Minimum Training Presence Logistic was used as the threshold to define which habitat cells were suitable. This threshold uses the values of the black rail occurrence location with the lowest suitability in the training dataset, which results in inclusion of all habitat cells that are at least as suitable as those with the lowest

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suitability in the training dataset. "Suitable" habitat is defined as areas with values above this threshold, "Potentially Suitable" habitat is defined as areas with values less than the threshold and above 0.01, and "Not Suitable" habitat is defined as areas with values below 0.01.

Quantifying Patch Size

We calculated patch size (hectares) and perimeter-to-area (meters/hectares) ratios at each of 107 wetland sites using the "Calculate Geometry" function in ArcMap version 10.1 (ESRI, Redlands, CA). We used both National Agriculture Imagery Program (NAIP) aerial photographs (USDA 2010) and the *Vegetation and Land Use Classification Map of the Sacramento–San Joaquin River Delta* (Hickson and Keeler–Wolf 2007) to guide the vectorization work. We then conducted Mann–Whitney U tests to test the hypotheses that there are no differences in patch size and perimeter-to-area metrics at sites where black rails were detected, versus sites where they were not detected. Because of the low detection probability of black rails, non-detection does not indicate absence.

RESULTS

Survey Results

We detected black rails at 21 of 107 (19.6%) wetland sites within the central Delta, including the southern marsh plain of Big Break Regional Shoreline; irrigated pastures at Dutch Slough; on in-channel islands within Old River, Connection Slough, Middle River, San Joaquin River, Disappointment Slough, White Slough, and Fourteenmile Slough; and in managed marshes of Mandeville Island and White Slough Wildlife Management Area (Table 1, Figure 2). Forty-four individual detections (15%) were made during 287 call–playback surveys (Table 1). In-channel islands, where black rails were detected, supported tall (>2 m), dense stands of emergent vegetation (e.g., *Bolboschoenus* spp., *Typha* spp.) consisting of well integrated stands of woody riparian species (*S. exigua* and *S. lasiolepis*, *R. discolor*, and *C. sericea*). In managed marsh, we detected black rails at sites with dense stands of emergent vegetation; however, woody riparian vegetation was not necessarily an integrated component at these sites. At irrigated pastures south of Dutch Slough, black rails were detected in dense but low stands of *Juncus* spp. and bulrush, more similar in structure to habitats found in the estuarine marshes to the west of the study area.

MaxEnt Model

The MaxEnt analysis, using both predictor variables (Vegetation Type and Tidal Status), derived a highly predictive model with an average test AUC value of 0.928 (SE = 0.064). The model was most informed by contributions from the Vegetation Type (81.8%, SE = 0.34), and less informed by Tidal Status (18.2%, SE = 0.34). The jackknife test of variable importance also indicated that Vegetation Type had the most predictive power, with a mean training gain of 3.92 (SE = 0.01) and test AUC values of 0.94 (SE = 0.001), versus Tidal Status, which had mean training gain of 1.0782 (SE = 0.011) and mean test AUC values of 0.82 (SE = 0.01).

The response curve for Vegetation Type that described the relationships between the probability of black rail presence and the top predictors showed an increasing probability of black rail presence at sites with the presence of 11 of the vegetation associations including *S. exigua* and *S. lasiolepis*, *C. sericea*, *Bolboschoenus* spp. and *Typha* spp., and non-native *P. australis* (Figure 3). The response curve for Tidal Status showed the highest probability of presence (70.1%, SE 0.001) when the site was tidally influenced and non-tidal wetland sites showed a lower probability of presence (10.0%, SE 0.001). Table 2 summarizes the descriptions of species composition, percent cover, and height for each land cover type (Hickson and Keeler–Wolf 2007) identified in the model that increased the probability of black rail presence.

MaxEnt predicted suitable habitat for black rail throughout the Delta, including areas not surveyed (Figures 4–7). The Minimum Training Presence Logistic threshold value, used to define the thresholds for the habitat suitability map, was 0.063 (SE 0.004).

Table 1 Comparison of California black rail survey results conducted in the Sacramento–San Joaquin Delta in 1992–1993 (Gifford and Karlton 2003) and in 2009–2011 for this study

	Years	Wetlands surveyed	Wetlands with black rails	Proportion of wetlands occupied	Call playback stations	Call playback stations with rails	Proportion of call playback stations with rails
CDWR	2009–2011	107	21	0.20	287	43	0.15
CDFW	1992–1993	98	14	0.14	267	33	0.12

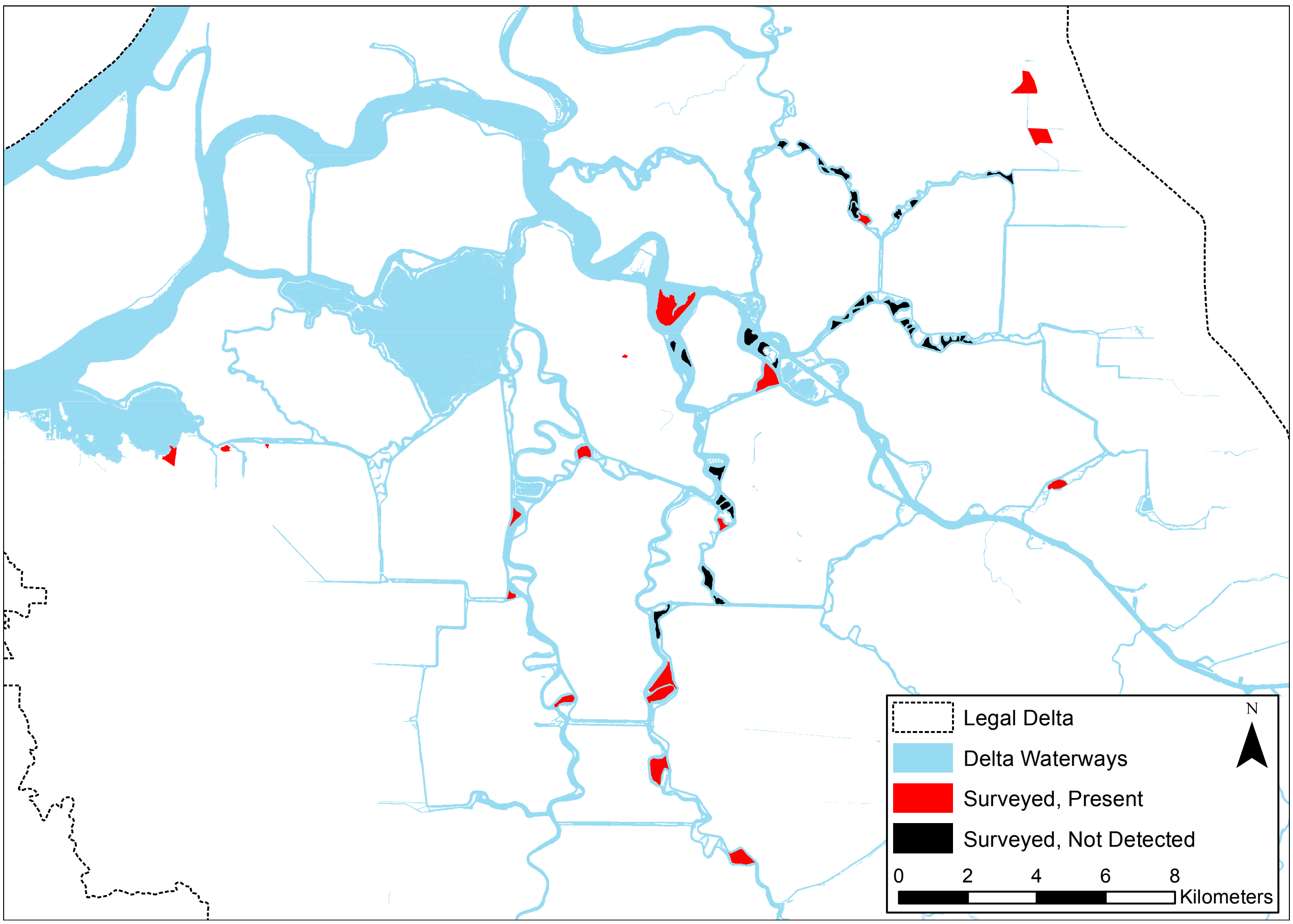

Figure 2 Map indicating California black rail survey results in the Sacramento–San Joaquin Delta, California in 2009–2011. Surveyed sites with black rails present (red) and not detected (black) are displayed; surveyed sites to the north and south with no detections are not displayed.

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Table 2 Probability of presence (± SE) of California black rail for the top vegetation type predictors in the MaxEnt model. Descriptions include density, percent cover, and height of each vegetation type derived from the Vegetation and Landuse Classification Map of the Sacramento–San Joaquin River Delta (Hickson and Keeler–Wolf 2007).

Habitat type	Vegetation type	Probability of presence	Standard error	Vegetation descriptions
Freshwater emergent wetland	*Bolboschoenus acutus*	0.210	0.010	Provisional association: herbaceous layer that is intermittent to dense (60%–100%, mean 85% cover) at 1–5 m tall; *Bolboschoenus acutus* dominates the herb layer, with *Typha latifolia* sometimes present (<5% cover); sampled in Central West Delta, East Delta, North Delta.
	Bolboschoenus acutus — Phragmites australis	0.600	0.005	Association: intermittent to dense herbaceous layer (52%–83%, mean 66%cover) at 1–2 m tall; *Bolboschoenus acutus* dominates the tall herb layer, with *Phragmites australis* constant at 1%–15% cover; *Bolboschoenus californicus*, *Eichhornia crassipes*, *Hydrocotyle ranunculoides*, and *Calystegia sepium* are usually present.
	Bolboschoenus acutus — Typha latifolia	0.200	0.009	Provisional association: dense herbaceous layer (75%–80%, mean 78% cover) at 105 m tall; *Bolboschoenus acutus* dominates the tall herb layer, with *Typha latifolia* and *Bolboschoenus californicus* (10%–15%); more sheltered inner marsh settings; sampled in North Delta.
	Bolboschoenus americanus	0.870	0.004	Alliance: dominated by *Bolboschoenus americanus* (55% cover) at 1–2m tall; interdigitate with stands of *Typha angustifolia* (1% cover); additionally low percent cover of *Distichlis spicata*, and *Sarcocornia pacifica*; associated with saline soils; sampled in Central West Delta.
	Bolboschoenus californicus — Bolboschoenus acutus	0.180	0.012	Provisional association: intermittent to dense (50%–99%, mean 73% cover) at 1–5 m tall; *Bolboschoenus californicus* and *Bolboschoenus acutus* are codominant in tall herb layer with *Eichhornia crassipes* and *Pluchea odorata* often in herb layer; sampled in Central West Delta, East Delta, North Delta, and South Delta.
	Phragmites australis	0.900	0.003	Alliance: dense herbaceous layer (84%–90%, mean 87%) at 1–5 m tall; may include emergent shrubs *Baccharis pilularis*, *Cephalanthus occidentalis*, *Salix exigua*, and *Salix lasiolepis*; codominant with *Bolboschoenus californicus*; sample in Central West Delta.
	Typha angustifolia	0.470	0.028	Association: intermittent to dense (45%–85%, mean 65%) herbaceous layer at 1–2 m tall; no emergent shrub or tree layer; *Distichils spicata* is constant with 5-78% cover; sampled in Central West Delta.
	Typha latifolia	0.800	0.008	Provisional association: pure *Typha latifolia* dense herbaceous layer (75%–97%, mean 82%) at 0.5–5 m tall; *Bolboschoenus acutus* and *Cyperus eragrostis* sometimes (3%–10% and <1%–3% respectively) occur in stands; sampled in Central West Delta, East Delta, North Delta.

Table 2 Probability of presence (± SE) of California black rail for the top vegetation type predictors in the MaxEnt model. Descriptions include density, percent cover, and height of each vegetation type derived from the Vegetation and Landuse Classification Map of the Sacramento–San Joaquin River Delta (Hickson and Keeler–Wolf 2007). *(Cont.)*

Habitat type	Vegetation type	Probability of presence	Standard error	Vegetation descriptions
Riparian shrub–scrub	*Cornus sericea—Salix exigua*	0.830	0.002	Provisional association: dense shrub layer (75%–95%, mean 83% cover) at 2–5 m and tall shrubs/understory trees 5–10 m tall; herbaceous layer contains *Juncus* spp. or *Bolboschoenus acutus*; sampled in North Delta.
	Cornus sericea—Salix lasiolepis	0.790	0.003	Association: open to dense shrub layer (27%–99%, mean 72% cover) at 1-5 m tall and tall shrubs/understory trees at 2–10 m tall; *Cornus sericea* codominates with *Salix lasiolepis*, and herb layer often supports *Phragmites australis* and *Bolboschoenus acutus*, or both species; sampled in Central West Delta, North Delta.
	Salix lasiolepis—Rosa californica—Rubus discolor	0.120	0.009	Association: open to dense shrub layer (30 %–90%, mean 82%) at 0.5–5 m tall and tall shrubs/understory trees at 2–5 m tall; herbaceous layer is open (< 1 %–30%, mean 4%) at 0–2 m tall; *Salix exigua* may codominate with *Salix lasiolepis*; high cover of non-native *Rubus discolor*, but occasionally *Rosa californica*; sampled in Central West Delta, East Delta, North Delta, South Delta.

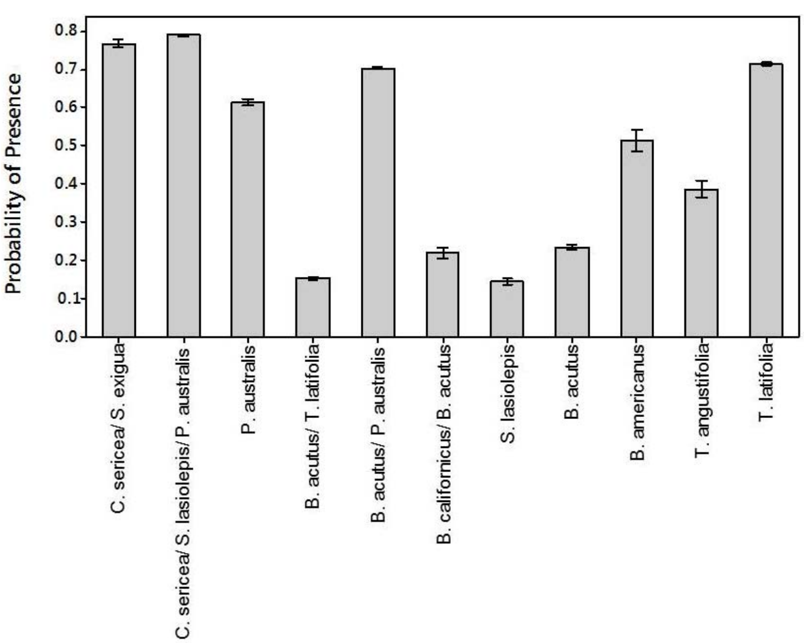

Figure 3 Relationship between the top predictors and probability of presence of California black rail in the Sacramento–San Joaquin Delta. Eleven vegetation types including riparian (*Salix exigua*, *Salix lasiolepus*, *Cornus sericea) and wetland* (*Bolboschoenus* spp., *Typha* spp., *Phragmites australis*) increased the probability of presence.

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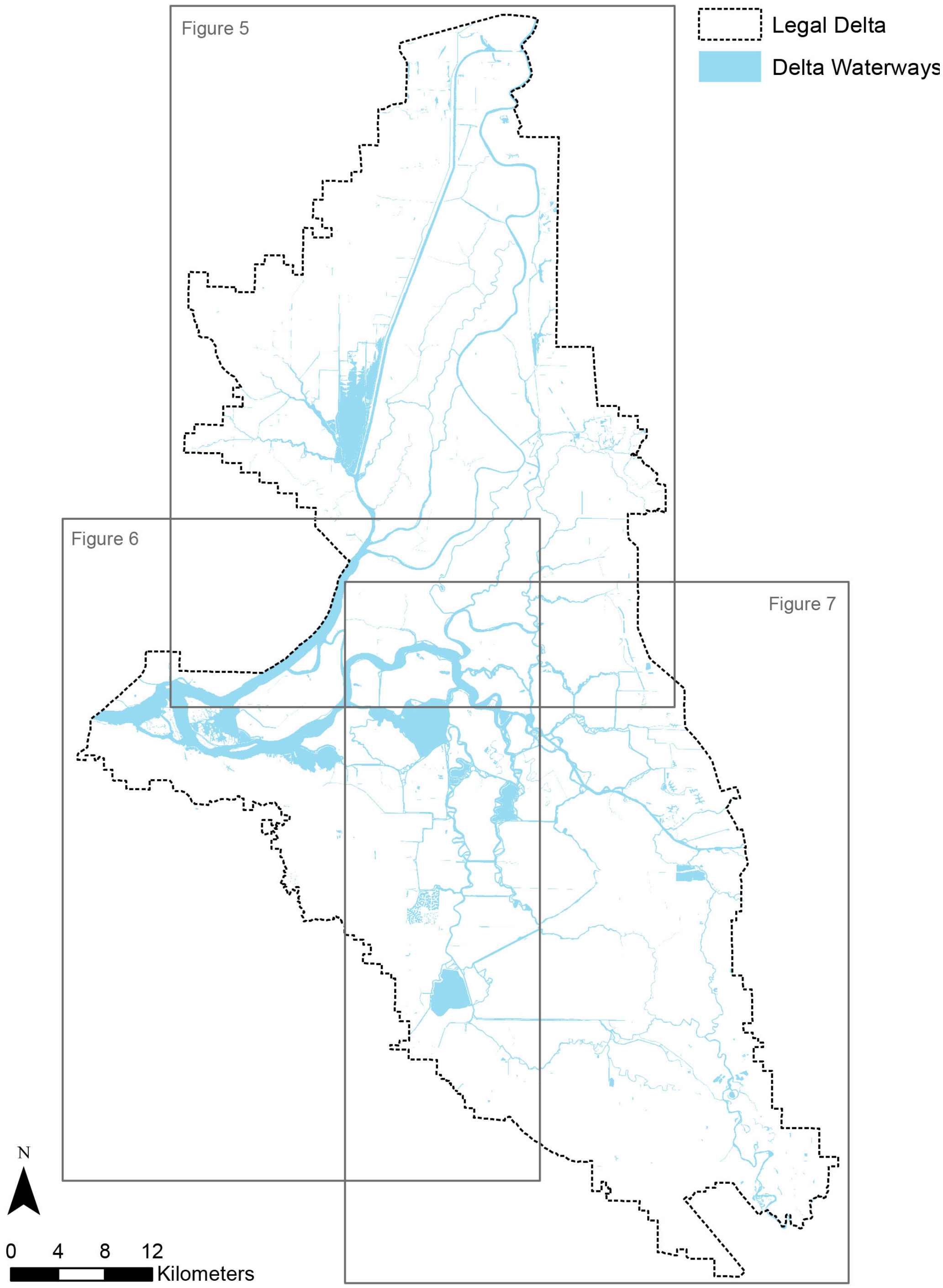

Figure 4 Map of the Legal Delta indicating the areas detailed in Figures 5–7.

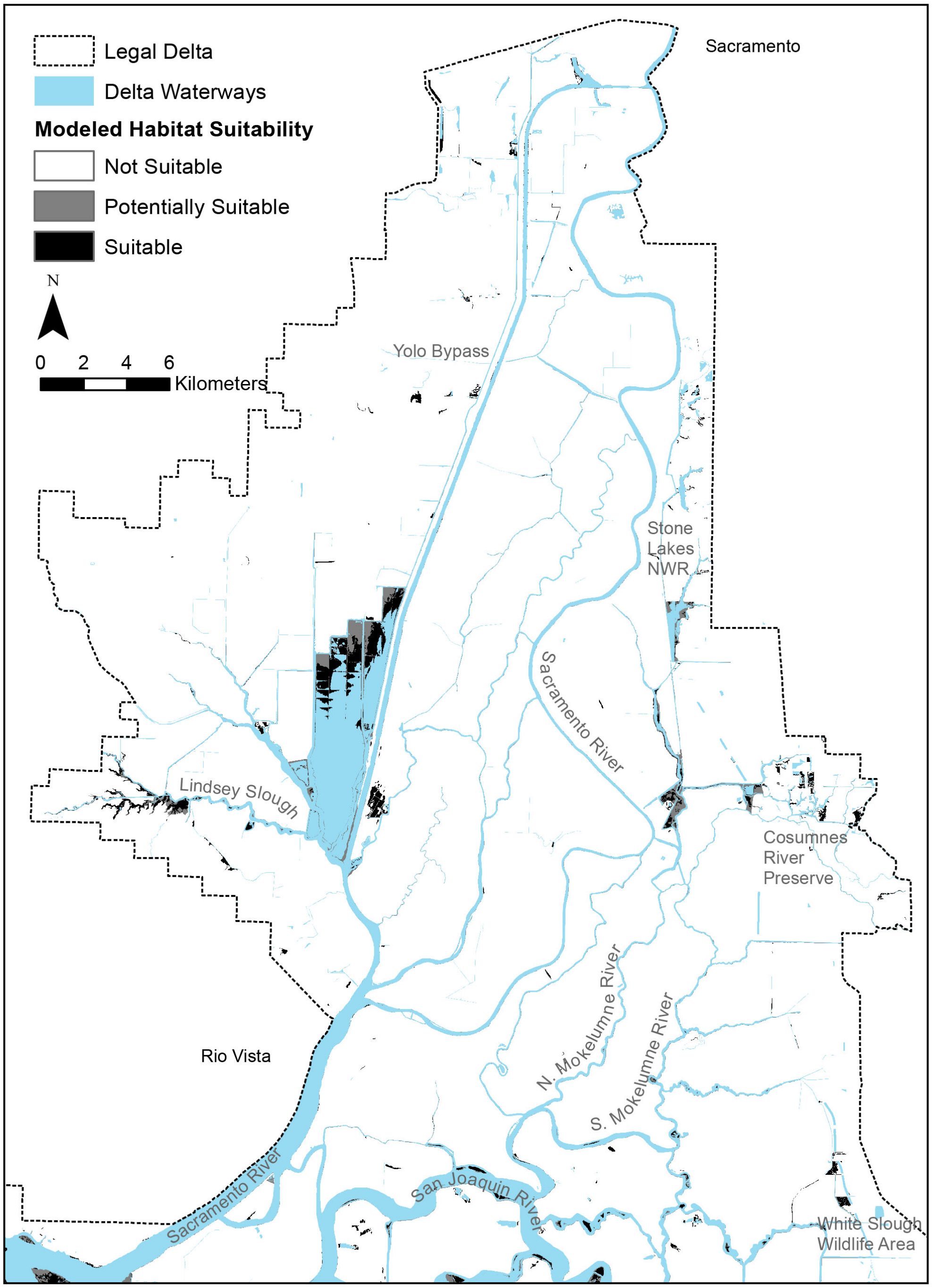

Figure 5 Predicted probability of presence of California black rail in the Sacramento–San Joaquin Delta, California (average test AUC = 0.928; SE = 0.064) for the north Delta subregion. Predictions are averages over 100 replicate runs. "Suitable" habitat is defined as areas with suitability above the Minimum Training Percentage Logistic threshold (0.063 ± 0.004). "Potentially Suitable" habitat is defined as those values less than the Minimum Training Percentage Logistic threshold and above 0.01; "Not Suitable" is defined as values below 0.01.

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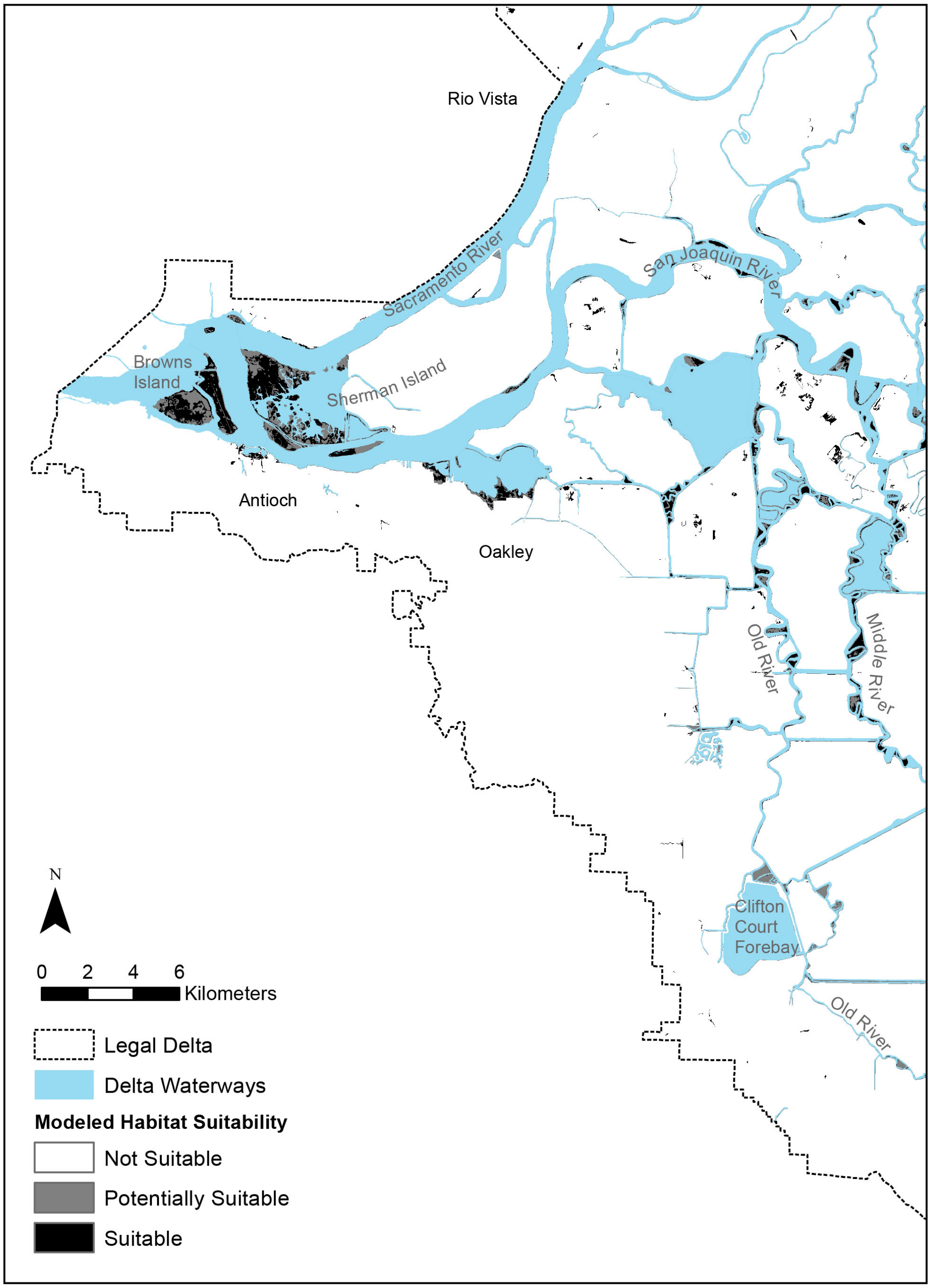

Figure 6 Predicted probability of presence of California black rail in the Sacramento–San Joaquin Delta, California (average test AUC = 0.928; SE 0.064) for the west Delta subregion. Predictions are averages over 100 replicate runs. "Suitable" habitat is defined as areas with suitability above the Minimum Training Percentage Logistic threshold (0.063 ± 0.004). "Potentially Suitable" habitat is defined as those values less than the Minimum Training Percentage Logistic threshold and above 0.01; "Not Suitable" is defined as values below 0.01.

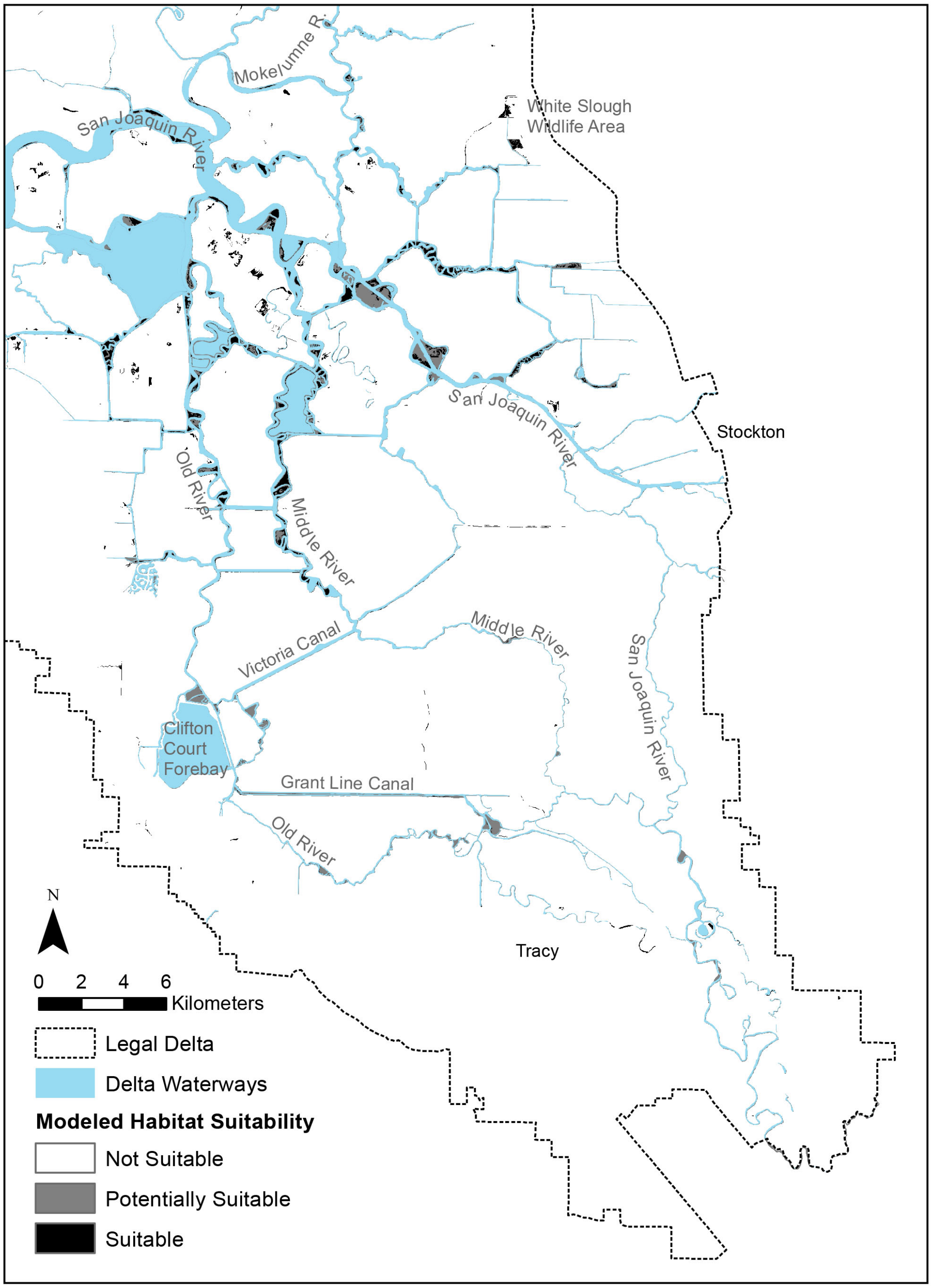

Figure 7 Predicted probability of presence of California black rail in the Sacramento–San Joaquin Delta, California (average test AUC = 0.928; SE 0.064) for the east and south Delta subregion. Predictions are averages over 100 replicate runs. "Suitable" habitat is defined as areas with suitability above the Minimum Training Percentage Logistic threshold (0.063 ± 0.004). "Potentially Suitable" habitat is defined as those values less than the Minimum Training Percentage Logistic threshold and above 0.01; "Not Suitable" is defined as values below 0.01.

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Wetland Size and Perimeter to Area

The mean and median size of wetland sites surveyed was 9.22 ha (SE 1.52) and 4.82 ha, respectively. The smallest site surveyed was 0.13 ha, and the largest was 115.23 ha. Black rails were detected at sites as small as 0.99 ha, and the mean and median size where detections were made was 22.74 ha (SE 6.62) and 10.19 ha, respectively. Sites where black rails were detected were significantly larger than those with no detections ($W = 1550.0$, $p < 0.001$), with a difference of 5.90 ha (95% CI = 2.19, 15.65 ha) between sites with and without detections. The mean and median perimeter-to-area ratio of wetland sites surveyed were 395.20 (SE 25.0) and 363.50, respectively, with a minimum perimeter-to-area ratio (least edge) of 105.0 and a maximum (most edge) of 1930.9. The site with the highest ratio (most edge) where black rails were detected was 726.3, and the median value at sites with black rail detections was 241.6. We found that sites where black rails were detected had significantly lower perimeter-to-area ratios [$W = 5037$, $p = 0.002$; difference = 118 (95% CI = 40.4, 197.7)].

DISCUSSION

Distribution within the Delta

The tidal wetland habitats and landscape features within the Delta have been described as too limited in geographic extent and quality to support populations of sensitive species such as black rail (Herbold and Moyle 1989; Manolis 1977; Evens et al. 1991). Previous studies have indicated that black rails are largely absent from the Central Valley, but the Delta may provide a stopover linkage between San Francisco Bay and Sierra Nevada foothills populations (Richmond et al. 2008; Girard et al. 2010).

We detected black rails inhabiting remnant in-channel islands and managed wetlands throughout the study area (Figure 2). These findings are consistent with the unpublished results of surveys conducted by CDFW in 1992–1993, showing a similar distribution (Gifford and Karlton 2003; Table 1). The continued occupancy of sites during the nesting season within the study area between studies conducted nearly 20 years apart, in addition to historic black rail records from as early as 1879 (Belding 1878; Grinnell and Miller 1944; Arnold 1960; Winter and Manolis 1978; Manolis 1977; Manolis 1978; Laymon and Shuford 1979), indicate that Delta habitats do support a breeding population of black rails. Recent observations in the north Delta at Barker Slough and Lindsey Slough (Solano County) in fall 2014 through summer 2015, and Stone Lakes National Wildlife Refuge and Cosumnes River Preserve (Sacramento County) in summer 2015 suggest that the population likely inhabits a broader distribution within the Delta than previously understood (2015 email from *S. Estrella*, CDFW, to D. Tsao, unreferenced, see "Notes"; 2015 email from M. Sawyer to D. Tsao, unreferenced, see "Notes"; CV Birds 2015).

Habitat Associations

We recognize that this model does not capture the potential influence of other important environmental factors such as elevation, more quantitative measures of vegetation structure, or effects of adjacent land use; however, our results indicate that black rail presence is associated with both tall (> 1 to 5 m) emergent wetland vegetation (*Bolboschoenus* spp., *Typha* spp., *Phragmites australis*) and woody riparian shrub species (*Cornus sericea*, *Salix lasiolepis*, and *S. exigua*).

California black rail habitat associations vary regionally across their range, both in vegetation species composition and structure (Flores and Eddleman 1995; Spautz et al. 2005; Richmond et al. 2008, 2010). Our findings describe an additional plant assemblage and vegetation physiognomy which the species occupies within the Delta; the very tall height of emergent vegetation and the presence of woody riparian species is unique when compared to other regions. Across its range in California and Arizona, black rails prefer emergent wetland habitats. Though we did not directly measure elevation, the presence of riparian species, which grow at higher elevation than emergent wetland species, may indicate areas of high elevation refugia within in-stream islands, many of which were former natural levees. Tall, dense woody cover from these riparian species may also provide refuge from high tides in the absence of an extended marsh plain with elevation gradient connected to upland habitat, as is preferred by black rails in San Francisco Bay (Spautz et al. 2005). In this respect, our findings are consistent with those of previous black rail habitat studies, indicating that, though preferred vegetation composition varies widely because of regional climate and other landscape factors, the species across their range is most commonly found among structural features that provide refuge from high tides and cover from predators (Flores and Eddleman 1995; Legare and Eddleman 2001; Spautz et al. 2005; Tsao et al. 2009; Richmond et al. 2008).

The MaxEnt analysis yielded a highly predictive model that indicates suitable habitat within the Delta based on vegetation type and tidal status, including areas outside of the study area where we trained the model using available land cover data (Figures 4–7). In the northern portion of the Delta, the model identified suitable habitat in wetlands that were surveyed with no black rails detected, and also in wetlands that were not surveyed during our study (Figure 5). Similar to our survey results (Figure 2), the model identified the greatest amount of suitable habitat within western and central portions of the Delta (Figures 6 and 7). The southern portion of the Delta contains little modeled suitable habitat (Figure 7); this result is expected because of the lack of wetland habitat in the south. We acknowledge the implications of sampling bias and the potential for over-fitting in the absence of a spatially and temporally independent testing dataset when using MaxEnt (Merow et al. 2013; Radosavljevic and Anderson 2014), and thus, we caution that results of this model related to specific locations and habitat suitability values should be considered preliminary.

The model is supported by recent observations in 2014–2015 of black rails in the north Delta at Lindsey Slough (Solano County) and Cosumnes River Preserve (Sacramento County)—areas not surveyed during our study but identified in the model as having potential habitat (Figure 5; 2015 email from *S. Estrella*, CDFW, to D. Tsao, unreferenced, see "Notes"; CV Birds 2015). Considering the caveats discussed above, the model could be used to develop hypotheses to be evaluated through further study or to identify areas with potentially suitable habitat, but should be verified with standardized surveys.

We detected black rails at larger sites (median 10.19 ha), despite having sampled a greater proportion of small sites, which is consistent with previous studies showing that the species prefers large wetland patches (Spautz et al. 2005). Though black rails have very small home ranges (< 1 ha) in San Francisco Bay, larger sites likely provide tidal and storm surge refuge and adequate food resources (Tsao et al. 2009). The smallest wetland site where a black rail was detected was on a 0.99 ha in-channel island, which is consistent with the use of small wetland sites within the Sierra Nevada foothills region (Richmond et al. 2008). This highlights the value of wetland patches of all sizes, especially in regions such as the Delta with limited availability of large, intact wetlands. These sites may be used by black rails as part of a larger matrix of wetland patches in close proximity to an individual's home range. Isolated small patches may not provide the necessary cover and food resources to support black rails.

Abundance Considerations

We detected fewer black rails per survey station than have been found by previous surveys in the San Francisco Bay Estuary and Sierra Nevada Foothill regions (Richmond et al. 2008; Spautz et al. 2005). Though this could indicate lower densities within the Delta, we suspect that detection rates were influenced by the timing of surveys, the logistical challenges associated with surveying Delta habitats (i.e., call–playback surveys from medium-sized watercraft), low detection probability, and a lack of survey replication within season (Spear et al. 1999; Legare et al. 1999; Conway et al. 2004). Our results do not represent a comprehensive survey of the Delta and should not be interpreted as an indication of population size or density in the region; focused surveys which incorporate occupancy sampling would better inform density and population size estimation.

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Climate Change

Predicted sea level rise and increased intensity of storm events from climate change may be problematic for black rail populations in the Delta. Sea level is projected to rise up to 90 cm by 2100 (IPCC 2001). Although sea level rise will be attenuated in the Delta, much of the suitable habitat for black rails found on in-channel islands is within the tidal range, and will be inundated more frequently or completely submerged. Because the in-channel island habitats are surrounded by open water, there is currently no connectivity to higher-elevation areas to replace this habitat as it becomes inundated by sea level rise. Non-tidal wetland habitats on subsided agricultural islands used by black rails may be at risk from flooding if increased pressure on levees or earthquakes degrade levees and cause breaches.

Perhaps of greater concern in the near-term is the threat of increased frequency and intensity of storm events, which would increase inundation and reduce the suitability of available habitat (Cayan et al. 2005, 2008). A severe winter storm event could increase water levels within San Francisco Bay by 25 to 30 cm (Ryan et al. 2000), and levels may be even higher within the Delta's constricted waterways. Studies have documented that black rails are particularly vulnerable to predation and habitat inundation during the breeding season (Evens and Page 1986; Erwin et al. 2006). Altered timing and increased intensity of high-water events in the spring could affect adult survival and the nesting success of populations within the Delta region (Takekawa et al., unpublished manuscript, see "Notes").

CONCLUSIONS

Through field surveys, review of unpublished data, and analyses of habitat suitability, we contribute to the understanding of the distribution and habitat needs of black rails within the Delta. The current configuration of the Delta supports a substantially reduced (>95%) and fragmented wetland land cover relative to historic levels, yet our findings indicate that black rails inhabit a variety of wetland types and are more widely distributed throughout the Delta than previously thought. Delta wetlands support a breeding black rail population that may provide a linkage between populations in San Francisco Bay and the Sierra Nevada foothills, rather than just temporarily used migratory stopover habitat.

The Delta black rail population, as well as populations of other listed species dependent on Delta wetlands, are at risk of loss of remaining suitable habitat from climate change and land use conversion as agricultural practices and water use shift. Wetland restoration efforts can mitigate this risk by increasing the availability of tidal and managed marsh habitat, and by providing connectivity of wetland habitats to upland features that provide high-water refuge, however, understanding of these species' habitat needs is limited. To predict the effects of climate change and land and water use changes in the region and inform restoration and management efforts to protect this threatened species, future investigations—including estimating occupancy, population size, and habitat models that incorporate fine-scale habitat measurements—are necessary to improve our understanding of Delta black rails.

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