GENERAL WETLAND SCIENCE

Habitat Characteristics Affecting Wading Bird Use of Geographically Isolated Wetlands in the U.S. Southeastern Coastal Plain

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Abstract

Geographically isolated wetlands (GIWs) have been increasingly recognized for their importance in providing ecosystem services, including support of regional biodiversity. These wetlands serve as valuable foraging and breeding habitat for wetland-dependent species, including wading birds. In certain regions of the U.S. Southeastern Coastal Plain approximately two-thirds of GIWs are impacted by adjacent human land use. We quantified wading bird density in agricultural and natural GIWs to determine the factors influencing their use of these habitats. Using monthly transect surveys, we found that wetland-specific variables, including prey abundance and size, wetland surface area, and dry-down rate, were better predictors of wading bird density than landscape level variables such as wetland density and distance to breeding colony. Bird density was highest in agricultural wetlands early in the hydroperiod, but as GIWs dried down, density dropped in agricultural wetlands and rose in natural wetlands. Collectively, these results suggest that wading birds in the Coastal Plain rely on a matrix of both agricultural and natural wetlands, and their use of wetlands varies temporally, peaking in late spring, to maximize prey availability. The seasonal process of receding water levels in GIWs and subsequent concentration of aquatic fauna provides important food resources for nesting wading birds.

Keywords Wading birds · Habitat selection · Isolated wetlands · Agriculture · Foraging

Introduction

Wading birds (orders Ciconiiformes and Pelecaniformes) are widespread and conspicuous apex predators in wetlands (Davis and Ogden 1994). To forage successfully, they require both suitable prey densities and shallow water (< 40 cm for most species; Powell 1987) that facilitates prey capture. These essential foraging conditions are often short-lived, causing birds to change foraging locations frequently and therefore

have large home ranges (Hafner et al. 1982; Erwin 1983). Due to their high position in aquatic food webs and considerable mobility, wading birds are important functional components in wetland ecosystems (Frederick and Ogden 2003). Because of their trophic status, they are also considered good indicators of wetland quality (Kushlan 1993; Frederick et al. 2009). Wetlands in much of the U.S. tend to be unevenly distributed across landscapes and can be unpredictable habitats due to seasonal changes in hydroperiod and land use change (Lane et al. 2012). Therefore, wading birds must rely on a combination of social and environmental cues to select the best wetland foraging habitat (Gawlik and Crozier 2007).

Among wetland types, geographically isolated wetlands (GIWs) are generally small, but abundant, and by definition they are completely surrounded by uplands (Haukos and Smith 1994; Euliss Jr et al. 1999; Tiner 2003; Zedler 2003). GIWs in the southeastern U.S. often fill and dry seasonally, thus fauna generally populate these sites in the winter and spring as wetlands fill (Snodgrass et al. 2000). In the summer, evapotranspiration increases and wetlands dry down, concentrating species within them prior to their migration to terrestrial habitats

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or perennial wetlands after wetlands dry completely (Snodgrass et al. 2000). Despite their small size and unpredictable hydroperiod, GIWs serve as sites of biodiversity concentration within U.S. Southeastern Coastal Plain ecosystems (Kirkman et al. 1999; Gibbons 2003; Means 2007; Sutter and Kral 1994).

Land use change has greatly altered the ecological functions of wetlands, and GIWs in particular. The main driver in wetland loss globally is the conversion or drainage of wetlands for agriculture (Millennium Ecosystem Assessment 2005). Southwestern Georgia is currently influenced by intensive agriculture in the form of commercial pine plantations and irrigated row crops; within this region approximately 68% of GIWs are impaired by adjacent human disturbance (Stuber et al. 2016). Agricultural irrigation directly affects wetland hydroperiods either through supplemental water inputs or water withdrawals for irrigation, and indirectly by lowering the groundwater table (Martin et al. 2013). Many wetlands within agricultural fields in southwestern Georgia have been structurally altered by the clearing of vegetation and creation of ditches and berms, which allow for the center pivot irrigation system to pass through the wetland. The small size and seasonal dry-down pattern of GIWs, coupled with their lack of legal protection make them particularly vulnerable to continued land use impacts (U.S. Environmental Protection Agency and U.S. Army Corps of Engineers 2015; Stuber et al. 2016). Loss and degradation of GIWs affects wetland-dependent species and results in a marked reduction in regional biodiversity (Gibbs 2000). Wading birds are one wetland-dependent taxa of particular conservation interest due to their high position in aquatic food webs and their significant population declines throughout portions of southeastern U.S. over the past several decades (Fleury and Sherry 1995; Kushlan 1997).

The conversion of wetlands for human development and agriculture can have detrimental effects on bird populations; however, some human-modified wetlands still provide valuable waterbird habitat (Fidorra et al. 2015). Human-modified wetlands often receive nutrient input from agricultural or lawn runoff resulting in high secondary productivity and increased prey base and foraging opportunities for birds (Gibbons et al. 2006; Fidorra et al. 2015). Many human-modified wetlands have open water and shorelines clear of dense vegetation that may impede foraging (Lantz et al. 2011). Also, wetlands located on agricultural land may have a more stable hydroperiod than natural wetlands, allowing them to support prey throughout the dry season (Fidorra et al. 2015).

Although previous studies have documented wading bird presence in GIWs within Coastal Plain ecosystems (Smith et al. 2006; Means 2007), no studies that quantify bird density and identify drivers of habitat use in these wetlands currently exist. Similarly, no studies have examined the importance of disturbed GIWs for wading bird foraging habitat compared to

their undisturbed counterparts in longleaf pine (*Pinus palustris*) forests. Therefore, the objectives of this study were to (1) quantify wading bird (herons, egrets, ibis, and storks) use of GIWs and examine how habitat characteristics affecting bird use change over time and among types of GIWs (2) determine the relative importance of habitat characteristics affecting wading bird use of GIWs in southwestern Georgia at two spatial scales (landscape and individual wetland-scale, hereafter referred to as site), and (3) to test for differences in wading bird use of wetlands between agriculturally-altered sites and minimally-disturbed natural sites.

Methods

Study Site

Our study took place in GIWs within the Dougherty Plain Physiographic District of Georgia in the U.S. The Dougherty Plain is a flat karst landscape in the southwestern portion of the state, covering approximately 6690 km^2 and characterized by a high density of GIWs (1.7 GIWs per km^2 on average; Martin et al. 2012). Today, much of the Dougherty Plain is dominated by irrigated row crop agriculture (e.g. peanuts, cotton) and intensive silviculture, with few small, fragmented longleaf pine forests remaining. Even with the majority of uplands converted for agricultural practices, it has been estimated that 11,620 isolated wetlands spanning 42,431 ha within the Dougherty Plain currently exist (Martin et al. 2013). More than 80% of these GIWs are small, at ≤4 ha in total area (Martin et al. 2012).

Study wetlands were within or near Ichauway (UTM Zone 16 N, 740187 m E, 3456706 m N), a private reserve with one of the most extensive and contiguous tracts of second-growth longleaf pine and wiregrass (*Aristida stricta*) in Georgia which has been managed with frequent prescribed fire since the 1930s (Kirkman et al. 2000). There are over 90 GIWs located on Ichauway, and most are relatively undisturbed by agricultural practices, recent timber harvest, or altered hydrology. Land immediately surrounding Ichauway is primarily in agricultural use, with pine plantations and irrigated-row crop agriculture dominating the region (Martin et al. 2013).

Individual study sites were a combination of natural and altered wetlands. The two types of natural wetlands, cypress-gum swamps and herbaceous marshes (Kirkman et al. 2000), were in relatively undisturbed condition, located within the Ichauway property boundary. Natural study wetlands were selected from a pool of 21 wetlands that had staff gauges to monitor water levels and were concurrently being sampled for aquatic prey as part of another study (Joseph W. Jones Ecological Research Center, unpublished data). We used existing GIS data to locate and select five wetlands of each type that were spatially diverse, as well as a variety of sizes (between 0.3 and 12.5 ha at peak fill, Joseph W. Jones Ecological Research Center, unpublished data)

(Fig. 1). Altered wetlands had been cleared of surrounding vegetation and ditched for irrigation, and all were located in privately-owned agricultural fields within 3 km of Ichauway. We sampled five altered wetlands where landowners granted permission for access. Thus, we sampled five cypress-gum swamps, five marsh, and five agriculturally altered wetlands for a total of 15 study sites.

Wading Bird Surveys

Wading bird use was measured from systematic ground surveys of each wetland. We utilized the general avian protocol from the U.S. Environmental Protection Agency's "Methods for Evaluating Wetland Condition" (2002) to best suit the detection of egrets, herons, storks, and ibis, as this protocol was developed specifically for wetland species identification. Because wading birds vocalize infrequently, this protocol was modified for an emphasis on visual searches. We sampled a straight line fixed transect at each wetland study site weekly from February through July in 2016 and February through June in 2017. July was not included in 2017 surveys as more than half of the wetland study sites were either nearly dry (< 0.1 ha surface area inundated) or completely dry. For both years, this time period reflected the migration of many species to South Georgia (eBird 2016) and continued through the duration of the nesting season.

Transects routes were chosen to optimize visibility. In cypress swamps and herbaceous marshes, transects ran through open water in the middle of the wetland. In agricultural wetlands, which were generally very open, transects ran along the
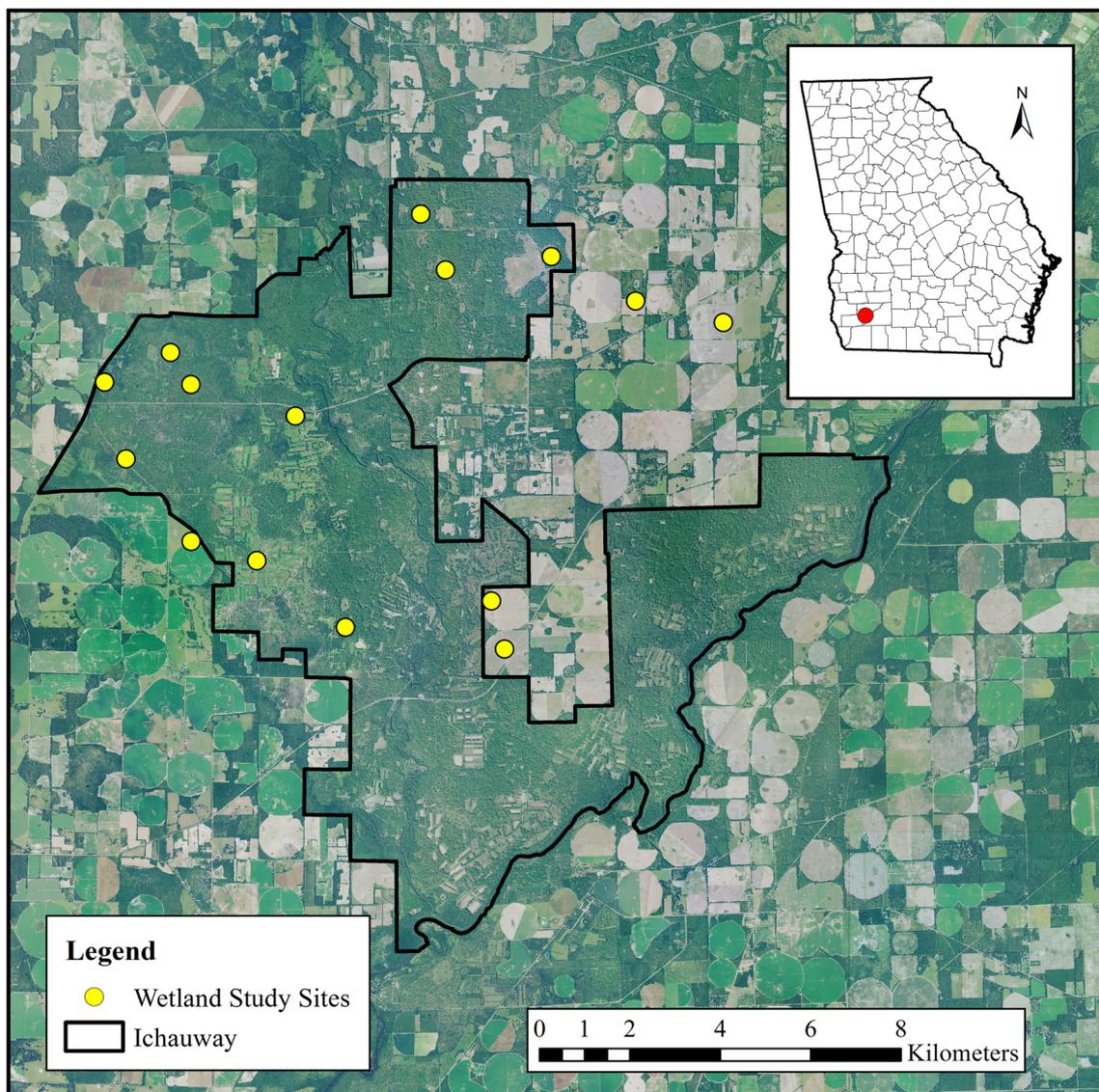
Fig. 1 Aerial photograph of the landscape surrounding study wetlands within and around the Joseph W. Jones Ecological Research Center at Ichauway, in Baker County, Georgia, USA, in the Dougherty Plain Physiographic District. Yellow dots indicate the locations of the 15 study wetlands

shore, perpendicular to the direction of any berms, so berms could not obscure any birds behind them. Transects were established using a compass and hip chain (Forestry Suppliers Inc., Jackson, MS) to measure distance and were permanently marked with flagging tape in 25-m increments at each site. Transect length varied among wetlands (25–150 m in length) based on wetland size, shape, and presence of berms (see Online Resource 1). While transect length generally increased with wetland size, one small wetland, which was located in an agricultural setting had been modified to contain three parallel ditches with tall berms, so three 50-m transects totaling 150 m were used to allow visibility of the wetland basin.

To estimate wetland searchable area, plastic yard flamingos (Southern Patio, Camp Hill, PA) spray painted white or navy blue were used as wading bird replicas. An independent observer placed 5 to 15 replicas in one wetland of each vegetation type (marsh, cypress-gum swamp, and agricultural); replica locations were then mapped with a GPS unit. With no knowledge of replica locations, a second researcher then walked the transect and recorded the approximate distance and angle from the transect to all replicas detected. This approach allowed for the locations of detected replicas to be mapped relative to the transect so the "maximum searchable area" could be estimated by wetland type (Calle 2014).

Wading bird surveys took place each week between the hours of 07:00 and 10:00 EDT, using binoculars (Nikon Monarch 5, 8 × 42, Nikon Corporation, Tokyo, Japan). During the weekly survey period, one observer approached each wetland on foot, and recorded all wading birds that flushed within the maximum searchable area during this approach. The transect was then walked, and any birds sighted were identified to species and recorded. Subsequently, wading bird abundance at each site was calculated as birds observed per unit area (density), based on searchable area estimated with the replica study described above. We calculated mean density by month for each study wetland so that comparisons could be made across wetlands and across the sampling season. We conducted four surveys per month in the 15 study wetlands, for a total of 360 surveys in 2016 and 300 surveys in 2017.

Landscape-Scale Variables

Landscape-scale characteristics potentially influencing habitat use in wading birds included wetland density and distance of wetlands from wading bird breeding colonies (Trocki and Paton 2006). These variables were determined in ArcGIS v.10.2 (ESRI, Redlands, CA) from existing land cover data for Ichauway and the surrounding landscape (Joseph W. Jones Ecological Research Center, unpublished data). National Wetlands Inventory data (U.S. Fish and Wildlife Service 2017) were used to identify all palustrine wetlands within a

1-km buffer around each study wetland and to determine the surface area of study wetlands (in hectares). Wetland density was defined as the proportion of total wetland area within the buffer. We selected a 1-km buffer because a larger scale would have created a high degree of overlap among wetlands. Distance to nearest breeding colony was calculated in ArcGIS using the Euclidean distance from each study site to the nearest known colony. The locations of colonies were determined from aerial survey data collected by the Georgia Department of Natural Resources in 1996 (Tim Keyes, Georgia Department of Natural Resources, personal communication), and then verified through a 2016 aerial survey of previously identified colony locations within a 30-km radius of the Ichauway property boundary. We limited the search area because wading birds forage within relatively close proximity to their nesting sites to minimize energy costs associated with feeding chicks (Smith 1995).

Site-Specific Variables

Site-specific variables included wetland type, wetland dry-down rate, surface area, prey relative abundance, and prey size. Wetland study site types were herbaceous marsh ($n = 5$), cypress-gum swamp ($n = 5$), and agricultural ($n = 5$), based on dominant vegetation and land use. Staff-gauges at each site were used biweekly to measure water levels to the nearest 0.01 m, which were then averaged across the month. These values were used to determine wetland dry-down rate, expressed as the difference in the monthly average staff-gauge reading between consecutive months. They were also combined with wetland basin contour data (delineated at 0.25-m intervals) to calculate the average surface area of study sites each month (Joseph W. Jones Ecological Research Center, unpublished data). Wetland area was selected as a variable of interest because it influences prey density and available foraging area that could affect bird use (Gawlik 2002; Gawlik and Crozier 2007), and it is efficient to monitor at a landscape extent.

Prey relative abundance was estimated using standardized dipnetting, following the methods outlined by Farmer et al. (2009). Each study site was dipnetted once monthly in 2017 (150 approximately 1-m sweeps) using a metal D-frame dip net with 3-mm mesh size (Memphis Net and Twine, Memphis, TN) from February through June, which coincided with the wading bird survey period. Wading birds select for prey items ≥2 cm in length (Klassen et al. 2016); therefore, all potential prey including amphibians, macroinvertebrates, and fish captured that met or exceeded this size were counted and recorded to the lowest possible taxonomic level. All sampled prey were released back to the wetland following identification and enumeration. Prey abundance was expressed as catch-per-unit-effort (average number of prey items per dipnet sweep). The average lengths of prey items ≥2 cm in each taxonomic group were also recorded to the nearest centimeter.

We used previously published length/weight regression equations for amphibian larvae, fish, and aquatic macroinvertebrates (Benke et al. 1999; Esmaeili and Ebrahimi 2006; McLeay 2017) to determine the average monthly dry mass of individual prey items by wetland.

Analyses

As a preliminary step in the analysis, variables were screened for colinearity using a correlation analysis among all variables to determine if $|r| > 0.7$ for any pair of parameters. No two variables met this correlation threshold, therefore all variables were retained. To determine if prey abundance, prey size, and wetland surface area varied by month or wetland type, we ran analysis of variance tests (ANOVAs) in the Program R "car" package with wetland study site as a random effect (Fox and Weisberg 2011; R Core Development Team 2017).

An information-theoretic approach and Akaike's Information Criterion corrected for small sample size (AICc) were used to determine the variables that most influenced habitat use in wading birds (Burnham and Anderson 2002). We developed a candidate set of biologically relevant a priori models based on hypothesized relationships between measured variables and the response variable (e.g. Burnham and Anderson 2002; Table 1). Candidate models were initially analyzed without interaction terms, but upon closer evaluation of the data, it was clear that bird use of wetland types varied by month. Therefore, the interaction term wetland*month was added post hoc.

We used the 'lme4' package in Program R to construct generalized linear mixed-models (Bates et al. 2015), with average monthly wading bird density for each study site as the response variable and wetland study site as a random factor. Only the field data collected in 2017 were input into models because this field season contained complete datasets for all explanatory variables of interest. Among the models with lowest AICc values, parameter estimates from competing models (ΔAICc <2) were model averaged using the "model.avg" function in the 'MuMIn' package (Barton 2016). To examine relative importance of predictor variables in the candidate set, we summed Akaike weights for each model containing the variable and calculated model-averaged parameter estimates. We calculated adjusted standard error and 95% confidence intervals of the parameter estimates to assess uncertainty. We tested residuals for homogeneity of variance and deviations from normality for each variable, and log-transformed variables when necessary.

Results

Wetland Searchable Area

In wetlands with only emergent vegetation (i.e. herbaceous marshes and agricultural wetlands) we detected all white and dark colored replicas in five trials of each wetland type. In cypress-gum swamps, replicas less than 48 m from the transect were detected, but there was a decrease in detection at further distances. Therefore, searchable area in cypress-gum swamps was truncated at 48 m from any point on the survey transect. To estimate bird density in cypress-gum swamps searchable area was calculated as a 48-m buffer around each transect, and in herbaceous marshes and agricultural wetlands the entire surface area of the wetland was considered searchable area.

Wading Bird Surveys

Over the course of two survey seasons, we recorded a total of 641 wading bird sightings. Three hundred and ninety-two of these sightings occurred in 2016, and 249 sightings occurred in 2017. Six species were encountered each year (Fig. 2); of these, the Little Blue Heron (*Egretta caerulea*) made up the majority of sightings, accounting for approximately 36% of total sightings in 2016 and 30% of total sightings in 2017. Other species included Great Egret (*Ardea alba*), Great Blue Heron (*Ardea herodias*), Green Heron (*Butorides virescens*), White Ibis (*Eudocimus albus*), and Wood Stork (*Mycteria americana*).

In both years, wading bird density (birds/ha) was higher in agricultural wetlands than other types early in the sampling period but was higher in natural wetlands later in the season (Fig. 3). In 2016 density was highest in agricultural wetlands from March–June (Mean of Mar.-Jun. = 8.12 sightings/ha, Range = 0–26), and highest in marsh wetlands in July (Mean = 17.89, Range = 12.10–26). In 2017, density was highest in agricultural wetlands from March–May (Mean = 11.83, Range = 0–31.68) and highest in marsh wetlands in June (Mean = 10.69, Range = 5.74–25.49). Density was relatively low in cypress-gum swamps throughout the season for both years. The highest density in cypress-gum swamps occurred in June and July of 2016 (Mean = 8.56, Range = 0–28) and May and June of 2017 (Mean = 4.41, Range = 0–12.33).

Prey Sampling

Prey relative abundance (catch-per-unit-effort, CPUE) varied significantly over time (Fig. 4, ANOVA (Month), $F_{4,66}$ = 10.02, $P < 0.001$) but not significantly across wetland types. Mean CPUE was 0.59 individuals/sweep, with a range of 0.01 to 2.30 individuals/sweep. Prey abundance peaked in March (Mean = 0.96, SE = 0.14), and was on average higher in marsh wetlands than cypress-gum swamps (Mean = 0.45, SE = 0.08) and agricultural sites (Mean = 0.55, SE = 0.11).

Estimated prey dry mass varied significantly across wetland type but not significantly over time (Fig. 5, ANOVA (Type): $F_{2,66}$ = 4.39, $P = 0.04$). Mean dry mass was 0.48 g per individual and ranged between 0.03 and 2.79 g. Prey mass was significantly smaller in marsh wetlands (Mean = 0.21 g,

Table 1 List of *a priori* models from Akaike's Information Criterion model selection for factors affecting wading bird use of geographically isolated wetlands. All models incorporate wetland site as a random effect. Y, wading bird density; CPUE, prey catch-per-unit-effort; MASS, prey dry mass; SA, wetland surface area; DRYRATE, wetland dry-down rate; TYPE, wetland type; MONTH, sampling month; COLDIST, distance to nearest wading bird nesting colony; WETDENS, density of wetlands; SITE, wetland study site. *Post hoc* models, which include an interaction term, are indicated in italics.

Hypothesis	Parameters	References
Prey Abundance	Y ~ CPUE + SA + TYPE + MONTH *Y ~ CPUE + SA + TYPE * MONTH*	Kushlan 1976, Gawlik 2002
Prey Size	Y ~ MASS + TYPE + MONTH *Y ~ MASS + TYPE * MONTH*	Trexler et al. 1994, Klassen et al. 2016
Hydrological	Y ~ SA + DRYRATE + TYPE + MONTH *Y ~ SA + DRYRATE + TYPE * MONTH*	Bancroft et al. 2002, Gawlik & Crozier 2007
Wetland Type	Y ~ TYPE *Y ~ TYPE * MONTH*	Fidorra et al. 2015
Site-Specific	Y ~ SA + DRYRATE + MASS + CPUE + TYPE + MONTH *Y ~ SA + DRYRATE + MASS + CPUE + TYPE * MONTH*	Trocki and Paton 2006
Landscape-Scale	Y ~ COLDIST + WETDENS	Fasola 1986, Gibbs 1991, Haig et al. 1998
Global	Y ~ SA + DRYRATE + CPUE + MASS + TYPE + MONTH + COLDIST + WETDENS *Y ~ SA + DRYRATE + CPUE + MASS + TYPE * MONTH + COLDIST + WETDENS*	
Null	Y ~ SITE	

All models incorporate wetland site as a random effect. Y, wading bird density; CPUE, prey catch-per-unit-effort; MASS, prey dry mass; SA, wetland surface area; DRYRATE, wetland dry-down rate; TYPE, wetland type; MONTH, sampling month; COLDIST, distance to nearest wading bird nesting colony; WETDENS, density of wetlands; SITE, wetland study site. Post hoc models, which include an interaction term, are indicated in italics

SE = 0.05) than cypress-gum swamps and agricultural sites (Mean = 0.43 g, SE = 0.06 and Mean = 0.82 g, SE = 0.19, respectively). Agricultural sites had significantly larger prey items compared to the two types of natural sites combined (Welch's T-test, $T(37.29) = -2.37$, $P = 0.023$).

Wetland Hydrology

Wetland maximum depth across the sampling period ranged between 0 and 1.56 m. The mean dry-down rate of all sites was 0.08 m per month and ranged between 0.01 and 0.29 m per month. Surface area of wetlands (ha) varied significantly over time (Fig. 6, ANOVA (Month): $F_{4,66} = 17.79$, $P < 0.001$) and across wetland types (ANOVA (Type): $F_{2,66} = 9.83$, $P = 0.003$). Surface area was significantly greater in cypress-gum swamps (Mean = 5.061 ha, SE = 0.72) than marshes and agricultural wetlands (Mean = 1.81 ha, SE = 0.34 and Mean = 0.84 ha, SE = 0.16, respectively). On average, wetland surface area was greatest in February (Mean = 3.95 ha, SE = 0.79) and decreased over time.

Linear Mixed Effects Models

Landscape-scale characteristics (colony distance and wetland density) were not important for predicting

Fig. 2 Wading bird total numbers of sightings and species composition, collected over two field seasons of weekly surveys in isolated wetlands in southwestern Georgia. Species are listed with standard four-letter alpha code, in accordance with the 58th annual American Ornithologists' Union Supplement (Chesser et al. 2018)
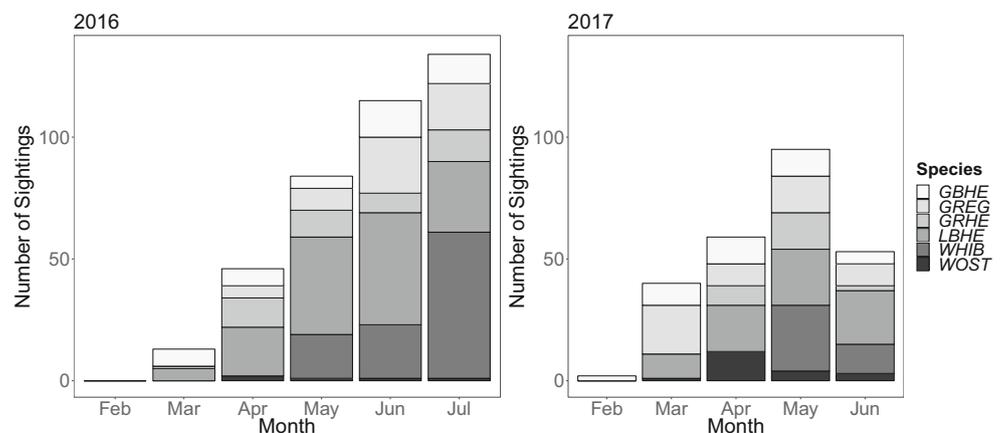
Fig. 3 Wading bird average density (with standard error bars) across two field seasons and separated by study wetland type. Average monthly bird density for each of 15 study sites was calculated from conducting weekly bird surveys.
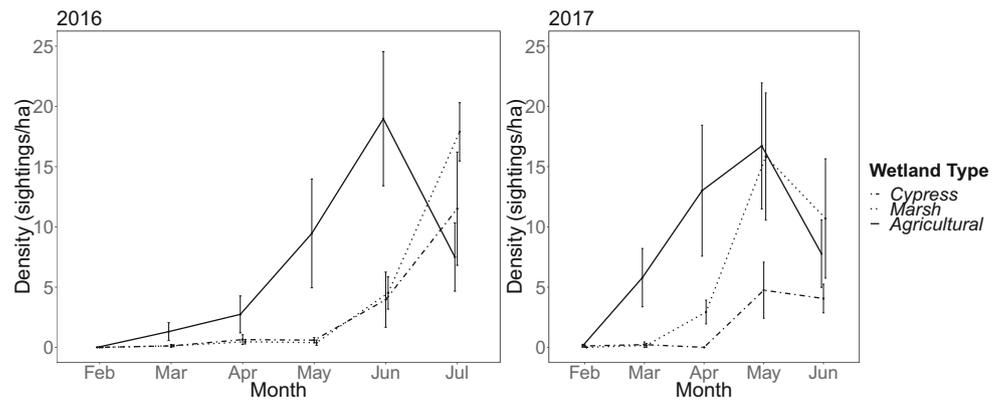
wading bird use of wetlands. However, top models included all site-specific variables (Table 2). Model-averaged prey size and prey abundance both had positive parameter estimates with 95% confidence intervals that did not overlap zero, indicating a significant positive relationship with wading bird density (Table 3). Wetland surface area had a negative parameter estimate with 95% confidence intervals that did not cross zero, indicating a significant negative relationship with wading bird density. Although the 95% confidence intervals slightly overlapped zero, wetland dry-down rate had a positive relationship with wading bird density. The interaction of wetland type and month had a significant positive effect on bird density in marshes and agricultural wetlands during April and May, and no significant effect in cypress-gum swamps during any of the sampling months (Table 3). Wetland type and month interaction and prey size had the highest relative importance values (1 and 0.91, respectively) of the variables considered. Wetland surface area, dry-down rate, and prey abundance had lower relative importance values of 0.66, 0.63, and 0.60 respectively.

Discussion

Our study highlights the importance of wetland-specific characteristics in wading bird use of GIWs. Wading bird density was positively related to both prey size and abundance; however, prey size was more influential than prey abundance, likely because wading birds select for larger prey to minimize foraging energy expenditure (Moser 1986, Trexler et al. 1994, Klassen et al. 2016). Wading bird use of GIWs also varied with wetland hydrology. Inundated surface area was an important predictor of bird use, and bird density increased with decreasing surface area, indicating that birds were selecting for smaller wetlands. Decreasing surface area results in an increase in prey density, and shallower water makes prey more accessible to birds (Gawlik 2002, Bancroft et al. 2002, Gawlik and Crozier 2007).

Numerous studies globally have documented wading bird use of agricultural wetlands (Czech and Parsons 2002), but our results are unique because we observed temporal variation of habitat use in a landscape matrix of natural and agricultural wetlands. During both years of surveys, wading bird density was highest in agricultural wetlands early in the season as wetlands filled, but as these sites began to dry down, there

Fig. 4 Catch-per-unit-effort (average number of individuals per dipnet sweep with standard error bars) of wading bird prey in each wetland type category, sampled during February through June of 2017. Samples were collected once monthly with 150 dipnet sweeps from each of the 15 study sites
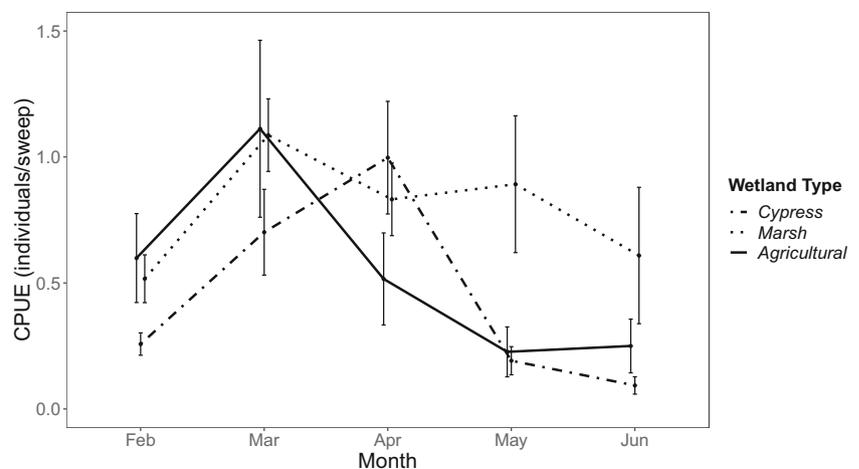
Fig. 5 The average dry mass of individual wading bird prey items in each wetland type category sampled during February through June of 2017. Mass was estimated by measuring standard length of prey items and using previously published regression equations (Benke et al. 1999; Esmaeili and Ebrahimi 2006; McLeay 2017). Samples were collected once monthly with 150 dipnet sweeps from each of the 15 study sites
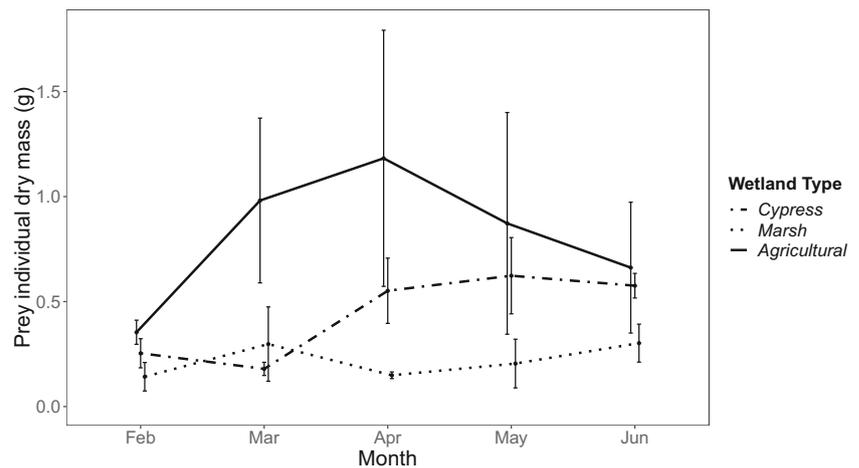
was in a shift in use towards natural wetlands, especially herbaceous marshes. Agricultural wetlands in our study region receive irrigation water in spring and this, along with the deep ditches excavated to create berms for center-pivot systems, cause these wetlands to fill earlier than natural wetlands (Martin et al. 2013). With extended hydroperiods, these wetlands support more large slow-developing anuran larvae which are important wading bird food resources, than natural wetlands in the same landscape (Denton and Richter 2013; Wellborn et al. 1996). Agricultural wetlands in the region are also often cleared of emergent vegetation (Stuber et al. 2016), making prey more accessible to foraging birds. The larger prey in agricultural sites coupled with the lack of vegetation may reduce foraging energy expenditure, making these sites more energetically profitable in the early to mid-hydrological season, until natural wetlands fill. Conversely, late in the hydrological season, the only standing water is in steep-sided ditches where prey items are often less accessible than in shallow, natural wetland basins (Clarke et al. 1984). Although agricultural wetlands were heavily used for a portion of the sampling season, foraging in modified wetlands carries risks for birds, from exposure to structural hazards, toxins, parasites, and disease. The degree to which these factors could impact wading

bird populations is unknown but could be the focus of further study (Frederick et al. 1996; Parsons et al. 2010).

Landscape-scale variables such as wetland density and the distance to nesting colonies were not as influential in bird use as were wetland-scale variables in our study. We suspect that small colonies of dark-colored birds such as Little Blue Herons were under-represented in the aerial surveys of colony sites. Likewise, the influence of landscape variables on habitat use by wading birds can vary with scale (Bancroft et al. 2002; Trocki and Paton 2006; Elphick 2008); thus, wetland density may be more informative on a larger scale than examined in our study. Also, NWI data tend to underestimate density of small isolated wetlands (Tiner 2003; Martin et al. 2012). Regardless, our finding that birds were using different wetland types across the season suggests that they were making decisions on resource use at a landscape scale, as has been reported in other studies (Fasola 1986; Gibbs 1991; Haig et al. 1998).

Globally, over 20% of bird species dependent on inland wetlands are classified as threatened. (Millennium Ecosystem Assessment 2005). Wading birds are becoming increasingly influenced by land use development and wetland loss (Fidorra et al. 2015). Wetland loss may be particularly consequential for

Fig. 6 The average surface area of geographically isolated wetlands in each wetland type category, sampled during February through June of 2017. Surface area values for each month were calculated using the average value of weekly depth readings combined with wetland basin contour data
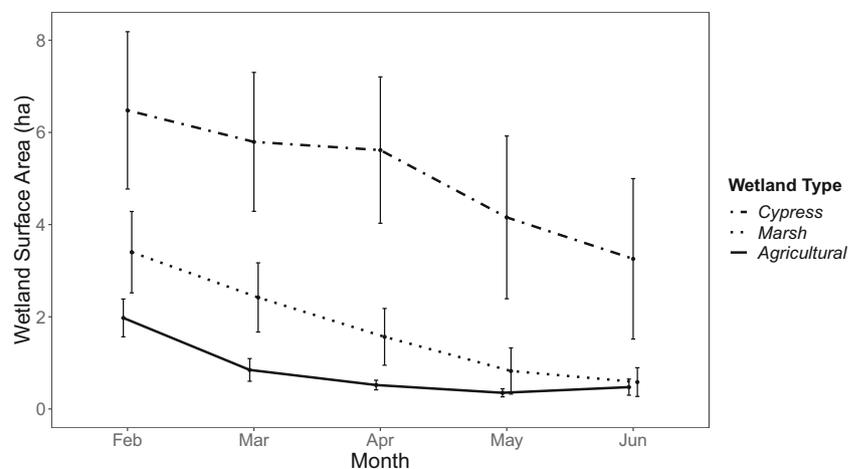
Table 2 List of top models (ΔAICc >7) as well as global and null models from Akaike's Information Criterion model selection for factors affecting wading bird use of geographically isolated wetlands

Model	K	AICc	ΔAICc	Log-Lik.	w_i
SA + DRYRATE + MASS + CPUE + TYPE * MONTH	13	230.27	0	−85.08	0.57
CPUE + TYPE * MONTH	10	231.31	1.04	−91.32	0.33
SA + DRYRATE + TYPE * MONTH	11	234.92	4.65	−91.29	0.06
CPUE + SA + TYPE * MONTH	11	235.86	5.59	−91.76	0.02
TYPE * MONTH	9	236.52	6.26	−95.70	0.02
Global	15	243.73	18.77	−105.31	0
Null	3	287.93	57.67	−140.79	0

All models incorporate wetland site as a random effect. CPUE, prey catch-per-unit-effort; MASS, prey dry mass; SA, wetland surface area; DRYRATE, wetland dry-down rate; TYPE, wetland type; MONTH, sampling month; COLDIST, distance to nearest wading bird nesting colony; WETDENS, density of wetlands

waterbirds, as multiple small wetlands can maintain the same or even greater waterbird diversity than one large wetland with equivalent area (Brown and Dinsmore 1986; Craig and Beal 1992; Scheffer et al. 2006). The maintenance of multiple, complementary wetlands within a mosaic can better provide temporally diverse foraging resources required by wading birds (Ma et al. 2010).

Our study demonstrated that open wetlands, such as marshes and agriculturally altered sites, served as important foraging habitat for wading birds. Cypress-gum swamps were not as heavily utilized for foraging as other wetland types, possibly because they are deeper (Kirkman et al. 2000) and prey abundance was found to be lower on average throughout much of the sampling season; however, they likely provide valuable roosting and nesting habitat for wading birds (Jones et al. 2010). The yearly dry-down process and subsequent concentration of aquatic fauna in GIWs provides an important food resource for birds in this region. Both peak amphibian breeding period and the wading bird nesting season occur while wetland water levels are receding and concentrating

aquatic prey (Jensen et al. 2008). Ultimately, these factors combined indicate that the seasonality of hydrological and biological processes in isolated wetlands may provide crucial resources for wading birds during the nesting season when energetic demands are greatest (Drent and Daan 1980).

The protection of natural wetlands offers the best chance of conserving waterbirds (Ma et al. 2004), but the value of agricultural wetlands should not be overlooked. The adaptability of these species to agricultural modification is beneficial in a region such as the Dougherty Plain, where approximately two-thirds of all isolated wetlands are impacted by human land use (Stuber et al. 2016). Tradeoffs still exist when assessing the value of modified wetlands within the landscape. Although we found comparable wading bird prey abundance in natural and altered sites, diversity of other taxa (plants and amphibians) in GIWs in this region was found to be lower in many of those altered sites (McElroy 2016; Stuber et al. 2016). Although it is not necessarily feasible to restore most wetlands in an agricultural setting back to their natural state, minimizing structural modifications when possible will likely benefit a wide variety of species and provide the greatest ecological value to Coastal Plain ecosystems.

Table 3 Model-averaged parameter estimates, adjusted standard error, 95% confidence intervals, and Z-values for parameters of interest in top competing models (ΔAICc <2)

	Estimate	Adj.SE	LCL	UCL	Z-value
Intercept	1.654	0.959	−0.225	3.533	1.725
Prey abundance	1.171	0.507	0.175	2.165	2.307
Prey size	1.011	0.314	0.394	1.627	3.215
Surface area	−0.361	0.152	−0.659	−0.062	2.369
Dry-down rate	0.641	0.373	−0.089	1.373	1.719
Marsh:April	1.793	0.781	0.263	3.323	2.297
Agricultural:April	3.669	0.977	1.755	5.584	3.757
Marsh:May	1.998	0.876	0.281	3.715	2.281
Agricultural:May	3.079	0.956	1.205	4.953	3.221

Categorical parameters with parameter estimates of 0 or confidence intervals overlapping 0 are not shown

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