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Article type : Feature article

Distribution, abundance, and vegetation associations of birds in Mississippi tidal marshes during the non-breeding season

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Received 19 January 2021; accepted 14 June 2021

ABSTRACT. Accurate estimation of populations of secretive marsh birds is difficult, especially during the non-breeding season when vocalizations are infrequent. Thus, dynamics of marsh bird populations remain relatively unknown, especially during the non-breeding season along the northern coast of the Gulf of Mexico. To address this lack of information about populations of marsh birds during the non-breeding season along the coast of Mississippi, we conducted 650 surveys along 130 line transects distributed across a spatially balanced sampling framework of tidal marshes from December to February, 2018 – 2020. Using hierarchical distance sampling models for unmarked populations, we estimated species-specific non-breeding population densities, abundances, and vegetation associations of eight species of marsh birds across a mosaic of tidal marsh communities, spanning oligohaline to polyhaline emergent and open marsh systems. We estimated that 127,000 Red-winged Blackbirds (*Agelaius phoeniceus*), 106,000 Marsh Wrens (*Cistothorus palustris*), 37,000 Seaside Sparrows (*Ammospiza maritima*), 17,000 Clapper Rails (*Rallus crepitans*), 15,000 Swamp Sparrows (*Melospiza georgiana*), 14,000 Nelson's Sparrows (*Ammospiza nelsoni*), 10,000 Sedge Wrens (*Cistothorus platensis*), and 2000 Common Yellowthroats (*Geothlypis trichas*) overwintered in the tidal marshes of Mississippi during our study. Further, we show that these species associate with different salinity ranges and vegetation communities within the broader estuarine marsh. Our population estimates and vegetation associations for vulnerable species provide important baselines from which assessments of future change can be compared.

RESUMEN. **Distribución, abundancia y asociaciones a vegetación de aves de pantanos de marismas durante la temporada no-reproductiva**

La estimación precisa de poblaciones de aves sigilosas de pantano es difícil, especialmente durante la temporada no-reproductiva cuando las vocalizaciones son infrecuentes. Por ello, las dinámicas de las poblaciones de aves de pantano siguen siendo relativamente desconocidas, especialmente durante la temporada no-reproductiva a lo largo de la costa norte del Golfo de México. Para atender esta falta de información acerca de poblaciones de aves de pantano durante la temporada no-reproductiva a lo largo de la costa de Mississippi, llevamos a cabo 650 reconocimientos a lo largo de 130 transectos lineales distribuidos a lo amplio de una estructura de muestreo espacialmente balanceada de pantanos de marismas de diciembre a febrero, 2018 – 2020. Usando modelos jerárquicos de muestreo a distancia para poblaciones no-marcadas, estimamos densidades no-reproductivas específicas a especies, abundancias y asociaciones a vegetación de ocho especies de aves de pantano a lo largo de un mosaico de comunidades de pantanos de marismas que varían de sistemas oligohalinos a polihalinos emergentes y en pantanos abiertos. Estimamos que 127,000 tordos *Agelaius phoeniceus*, 106,000 saltaparedes *Cistothorus palustris*, 37,000 gorriones *Ammospiza maritima*, 17,000 rascones *Rallus crepitans*, 15,000 gorriones *Melospiza georgiana*, 14,000 gorriones *Ammospiza nelsoni*, 10,000 saltaparedes *Cistothorus platensis* y 2000 mascaritas *Geothlypis trichas* invernan en los pantanos de Mississippi durante nuestro estudio. Además, mostramos que estas especies se asocian más ampliamente con diferentes rangos de salinidad y comunidades vegetales en el pantano estuarino. Nuestras estimaciones poblacionales y asociaciones a vegetación para especies vulnerables proveen una línea base que será importancia para comparaciones de futuros cambios.

Key words: line transect, overwintering, population estimate, Rallidae, salt marsh

As one of the first terrestrial ecosystems to be inundated with oil from the Deepwater Horizon Oil Spill, tidal marshes and the organisms living in them suffered a number of negative ecological consequences (Silliman et al. 2012, Bergeon Burns et al. 2014, Rabalais and Turner 2016). Marsh birds in particular were documented to have increased contaminant levels (Bonisoli-Alquati et al. 2016, Perez-Umphrey et al. 2018), exposures that may have resulted in a subsequent reduction in reproductive success (Bergeon Burns et al. 2014, Bonisoli-Alquati et al. 2016). The number of total bird mortalities as a direct result from this oil spill was estimated to exceed 50,000 birds (Deepwater Horizon Natural Resource Damage Assessment Trustees 2017). However, given the lack of ecological baseline data, quantitative assessments of population-level impacts on most bird species were not possible (Henkel et al. 2012).

Along the tidal marshes of Mississippi, previous local-scale studies of marsh birds have provided information about densities in small marsh complexes (Rush 2009, Leggett 2014, M. Woodrey, pers. comm.), but no large-scale, coast-wide surveys or population estimates are available. Only recently have scientists begun to better understand the distribution, abundance, habitat associations, and ecology of marsh birds with the introduction of a national monitoring protocol (Conway 2011), and an inter-state, inter-agency research group in the northeastern United States dedicated to studying the ecology of tidal marsh birds (SHARP 2020). Complementing this effort have been several studies conducted along the northern coast of the Gulf of Mexico (GoM) focusing on the ecology of marsh birds in Mississippi (Rush et al. 2009a, b, 2010a, b, Leggett 2014, Lehmicke 2014). However, all of these studies focused on the breeding season.

Although investigators have examined the distribution and site fidelity of marsh birds during the non-breeding season along the Atlantic coast of the United States (Greenlaw and Woolfenden 2007, Michaelis 2009, Winder et al. 2012, Watts and Smith 2015), little is known about how vegetation associations and landscape-scale characteristics influence their use by birds in GoM tidal marsh ecosystems during this period. This is problematic because many bird species along the northern GoM rely on tidal wetlands as wintering habitat (Woodrey et al. 2012), including some only present during the winter that may require different habitats than breeding marsh birds (Woodrey et al. 2019). Our objectives, therefore, were to: (1) conduct the first systematic and rigorously designed sampling framework for non-breeding tidal marsh birds on the Mississippi Coast, (2) generate species-specific densities at the marsh complex scale and population estimates for the entire Mississippi Coast, and (3) determine vegetation associations for non-breeding tidal marsh birds along the Mississippi Coast.

METHODS

We conducted surveys in estuarine, emergent, and scrub-shrub tidal marshes across all three coastal counties of Mississippi (Hancock, Harrison, and Jackson) during the winters

(December – February) of 2018 – 2019 and 2019 – 2020 (Fig. 1). Selection of our sites was based on a broad-scale, probabilistic random sampling framework outlined by Johnson et al. (2009) and successfully implemented in the northeastern United States by Wiest et al. (2016). The Johnson et al. (2009) framework is a two-stage probabilistic Generalized Random Tessellation Stratified (GRTS) study design that uses the Environmental Protection Agency North American continental hexagonal grid (40-km^2 hexagons; Johnson et al. 2009). Hexagons were overlaid along the entire coast of the northern GoM (hereafter, region) from Texas to Florida (i.e., sampling universe). Then, using land-cover data from the 2010 Coastal Change Analysis Program (C-CAP; National Oceanic and Atmospheric Administration 2010), we identified all hexagons containing at least one contiguous marsh patch of either estuarine emergent wetland (C-CAP class 18) or estuarine scrub-shrub wetland (C-CAP class 17) larger than 10 ha (i.e., sampling frame).

Estuarine marsh systems along the Gulf Coast differ in scope and configuration from those in other parts of the United States so we deviated from stratification recommended in Conway and Droege (2006) and instead used the nexus of ecoregions identified by the Gulf Coast Vulnerability Assessment (Watson et al. 2015) and state borders. We made this modification because subregions for the GoM proposed by Conway and Droege (2006) did not align with relevant physiographic province boundaries or ecological mapping schemes for the region. We chose state boundaries because that is the scale at which bird monitoring, management, and restoration is likely to be conducted due to the availability of long-term (20+ years) funding made available to states as a result of the 2010 Deepwater Horizon oil spill settlement (Wilson et al. 2019).

Following Johnson et al. (2009), we then used the GRTS sampling approach to select hexagons in each subregion strata from the sampling frame. These hexagons, or Primary Sampling Units (PSUs), formed the backbone of the sampling effort allocation. In each selected hexagon, or PSU, we then selected an equal probability sample of survey points that were distributed randomly, or Secondary Sample Unit (SSUs), within the boundaries of the estuarine emergent and scrub-shrub marsh. Points within 400 m of another point were iteratively removed based on the sequence in which they were selected by the GRTS design to maintain independence of bird observations between sample points. This method allowed us to distribute points used for point-count surveys conducted during the breeding season in conjunction with the non-breeding season paired line transects that were the focus of this study.

We established line transects from these sample points where suitable to survey for marsh birds. However, except for Deer Island, most barrier islands were not sampled due to logistical constraints. We acknowledge this limitation in our sampling design, but believe, based on the area of conditions suitable to support marsh birds, the impact of not including these islands in our population estimates of each species in Mississippi is negligible.

Due to the difficulty of detecting marsh birds during the non-breeding period when they seldom vocalize, we opted for line transects that generally result in more detections in open vegetative structure than point count surveys (Bibby et al. 1992). Line transects ranged in length from 200 to 500 m, depending on our ability to walk in a straight-line up to 500 m without encountering a physical barrier such as a tidal creek too deep or wide to cross. We systematically oriented line transects perpendicular to shorelines starting at the water-marsh interface and going toward or through the associated sample points (Fig. 1). When marsh topography prevented walkable line transects perpendicular to the shoreline, we adjusted transects to be near perpendicular. We marked line transects every 100 m with PVC poles (1.27 cm x 3.05 m) to ensure repeatability and aid in distance estimation. Line transects could not be placed at every sample point due to impassable water bodies to access the point, inability to fit a transect >200 m of walkable marsh, inaccessibility via boat during low tide, time efficiency considerations, and/or safety concerns. These constraints restricted our winter sampling effort to 130 line transects out of 268 sampling points surveyed during the breeding season.

Bird surveys. We used a distance-sampling approach to collect data along survey transects. We walked at an average pace of 1 km/hr (Bibby et al. 1992) while recording all birds seen or heard, including birds flying over. We conducted 2 – 3 repeat surveys along each transect during each field season (December – February) to increase the number of detections for each species, increase the statistical power and precision of our estimates, and sample throughout the winter season (Buckland et al. 2001, Kéry and Royle 2016). For each bird or flock detected, we recorded the species, estimated perpendicular distance from the transect to where the bird or flock was first detected, how it was detected (e.g., aural or visual), and the number of individuals. For each transect, we also recorded the observer, date, start and end times, temperature (°C), visually estimated the percent cloud cover (0 – 100%), wind speed (km/hr), and ranked the background noise level on a categorical scale from zero to four (SHARP 2020) because these factors can affect detectability (Rush et al. 2009a, b, Conway 2011, Leggett 2014).

Vegetation surveys. We used the line-intercept method to quantify vegetation composition because it allowed us to efficiently characterize the vegetation on and around our transects (Mueller-Dombois and Ellenberg 1974). We recorded the linear distances of vegetation ecotones (i.e., a change in vegetation species) along each transect, yielding the amount of vegetation as a percentage of the total transect length. For example, if black needlerush (*Juncus roemerianus*) was the dominant vegetation type from 50 to 150 m along a 200-m transect, it comprised ~50 % of the available vegetation on that transect. We recorded these vegetation data concurrently with the first survey along each transect of each sampling season.

Statistical analyses. We estimated species-specific densities and determined vegetation associations for eight marsh bird species with sufficient numbers of detections, excluding flyover detections, on our surveys ($N > 60$ observations per species to adequately fit a detection function, Buckland et al. 2001). We used the function gdistsamp in package unmarked (Fiske and Chandler 2011) in program R (R Core Team 2018) to generate hierarchical models for unmarked populations. Before modeling, we truncated the farthest 5% of detections for each species to improve model fit (Buckland et al. 2001). However, for Swamp Sparrows (*Melospiza georgiana*), Clapper Rails (*Rallus crepitans*), and Red-winged Blackbirds (*Agelaius phoeniceus*), data revealed evidence of observer distance-estimate rounding at greater distances from transects (beyond 50, 70, and 150 m) so we truncated a higher percentage (13, 20, and 30%, respectively) of these data. We also binned exact distance estimates into distance bins and scaled all continuous covariates to a mean of zero to allow for better model fit (Buckland et al. 2001, Kéry and Royle 2016). We also computed a Pearson's correlation matrix for all vegetation variables to identify correlated variables ($r \geq 0.7$) and removed them from further analyses. Then, in a model selection framework, we generated *a priori* models using these covariates on λ (density), φ (availability), and p (detection).

Following the model building and selection process of Kéry and Royle (2016), we first fitted our null models with three different key functions (half-normal, hazard-rate, and uniform). We then compared these models using their associated Akaike's information criterion (AIC; Akaike 1974, Burnham and Anderson 2002) scores and selected the model(s) with ΔAIC < 2 from the best model to then fit covariates on availability (Kéry and Royle 2016). We added the survey visit (categorical; 1 – 3) as a covariate on availability to allow for bird movement and thus fluctuating population sizes available for detection between each survey along a transect during each winter season. We then computed AIC values with and without this visit covariate and selected the model(s) with a ΔAIC < 2 from the best model to fit covariates on density (Kéry and Royle 2016).

While conducting our initial surveys, we found considerable variation in the number of individuals of a given species detected between major marsh complexes. Therefore, to estimate species densities in a more biologically meaningful way, we divided the Mississippi coast into 12 major marsh complexes (Fig. 1). We then created *a priori* candidate models for the density parameter using a combination of this 'complex' variable, study year, and vegetation types that made up at least 5% of the vegetation detected on all surveys. After comparing these models via AIC, we used the top models to fit covariates of observer, wind speed, ordinal date, and vegetation types on detection (Kéry and Royle 2016). After performing a last model selection based on AIC < 2, we modeled all top models using a negative binomial distribution to account for overdispersion in the data (Kéry and Royle 2016). All models contained study year (year one or year two) as a covariate on density to account for population closure assumptions within a season.

Finally, we model-averaged parameter estimates from the best competing models to obtain final model parameter estimates. The global model structure was: Density(year + complex + [vegetation types ≥ 5 % of total]), Availability(visit), Detection(observer + wind speed + ordinal date + [vegetation types ≥ 5 % of total]). Because Red-winged Blackbirds were often detected in flocks, we followed the recommendation of Buckland et al. (2001) for clustered populations to estimate density by estimating the distance to flock centers rather than individual birds, modeling the estimated density of flocks rather than individuals, and then multiplying the estimated flock density by the average number of individuals in each flock. Once we had species-specific density estimates by marsh complex, we calculated the estimated species population abundance across the Mississippi Coast by summing the density estimates multiplied by the amount of estuarine emergent marsh for each marsh complex. We report population estimates accompanied by either a 95% confidence interval (CI) or standard error (SE) and rounded to the nearest thousand because we believe that to be the precision at which these estimates should be interpreted.

RESULTS

We established 130 line transects across the three coastal Mississippi counties. We surveyed each transect twice ($N = 260$ surveys) in January-February 2019, and three times ($N = 390$ surveys) from December 2019 through February 2020, totaling 650 bird surveys and 230 vegetation surveys. The most frequently detected species were Marsh Wrens (*Cistothorus palustris*, $N = 1593$; Table S1), Red-winged Blackbirds ($N = 1456$), Seaside Sparrows (*Ammospiza maritima*; $N = 410$), Clapper Rails ($N = 606$), Nelson's Sparrows (*Ammospiza nelsoni*; $N = 109$), Swamp Sparrows ($N = 286$), Sedge Wrens (*Cistothorus platensis*; $N = 99$), and Common Yellowthroats (*Geothlypis trichas*; $N = 82$). All eight species had a sufficient number of detections to fit a detection function (Tables 1 and S1). Dominant plant species included black needlerush, comprising 53% of the vegetation coverage along the transects, followed by smooth cordgrass (*Spartina alterniflora*, 12%), saw-grass (*Cladium mariscus*, 7%), saltmeadow cordgrass (*Spartina patens*, 5%), and big cordgrass (*Spartina cynosuroides*, 5%).

Top-ranked models indicated influences of survey visit on bird availability, and marsh complex, year, and vegetation on bird density (Table 1). Detection covariates varied, but wind speed, observer, and the ordinal date of surveys were most influential (Table 1). The negative-binomial distribution and hazard-rate key function were used in most top models, with the half-normal key function in the other two models (Table 1).

Density and subsequent population estimates varied among species and marsh complexes (Table 2). In general, the most frequently detected species had the largest estimated populations (Table 2). Vegetation associations among species also differed, but matched expectations based on known life history and associations with water salinity and consequent changes in vegetation coverage (Fig. 2). Tidal marsh obligate overwintering species (Marsh Wrens, Seaside Sparrows, Clapper Rails, and Nelson's Sparrows) were positively associated with percent cover of *S. alterniflora*, the vegetation type most diagnostic of salt marsh, whereas lesser obligate marsh birds (Swamp Sparrows, Sedge Wrens, and Common Yellowthroats) had contrasting associations. Only Marsh Wrens, Seaside Sparrows, and Clapper Rails were positively associated with *J. roemerianus*, the most dominant vegetation type in Mississippi tidal marshes. Swamp Sparrows, Sedge Wrens, and Common Yellowthroats showed negative associations with increasing cover of *J. roemerianus*. For *C. mariscus*, the fresh to intermediate water associated dominant vegetation species, Marsh Wrens, Red-winged Blackbirds, Swamp Sparrows, and

Common Yellowthroats showed positive associations. Marsh Wrens, Nelson’s Sparrows, and Clapper Rails exhibited a positive association with an increasing number of vegetation ecotones along transects.

DISCUSSION

The results from our hierarchical distance sampling models for unmarked populations are consistent with previous research detailing factors that influence distance estimation, detection probabilities, and density estimates of tidal marsh birds (Rush et al. 2009a, b, Conway 2011). Although the effect of year on density was strong in the top models, we report the density and population estimates averaged over the two years to account for demographic and environmental stochasticity over a relatively short time period. Consistent with anecdotal observations during the surveys, marsh complex being included in all top models was not unexpected because salinity, vegetation communities, and area of suitable habitat all of which can affect marsh bird distributions, varied among the different complexes. The effects of observer, wind speed, date, and vegetation species as covariates on detection in the top models highlight the importance and care that must be taken into account for differing detection probabilities when making inferences about relative population densities among sites. The inclusion of survey visit number on availability in the top models for most species suggests the importance of accounting for inter-seasonal movements of birds among transects when estimating density parameters even within a season when these birds are believed to be non-migratory.

Our baseline abundance estimates support the conservation and informed management of obligate tidal marsh birds by providing quantitative estimates based on a standardized sampling framework that will allow measurement of population status and trends, data necessary to track these populations across the GoM region (Woodrey et al. 2019). These data will also allow critical evaluation of potential impacts of natural (e.g., hurricanes and sea level rise) or anthropogenic (e.g., oil spills, chemical releases, and freshwater diversions) events on marsh bird populations during the non-breeding season complemented by a monitoring template for neighboring Gulf States. Species-specific density estimates also provide quantitative targets to evaluate the effectiveness of tidal marsh management actions such as prescribed fire, and marsh restoration and management such as current and future RESTORE Act-funded projects across the northern GoM (Deepwater Horizon Natural Resource Damage Assessment Trustees 2017, National Academies of Sciences, Engineering, and Medicine 2017).

Overwintering Marsh Wrens along the northern GoM include both resident (*C. p. marianae*) and migratory inland subspecies (*C. p. iliacus* and *C. p. dissaeptus*) only present during the winter (Kroodsma and Verner 2020). Remsen et al. (2019) suggested that the resident subspecies, restricted to the northern GoM, may occur at lower densities than those in other geographic regions. However, because these inland subspecies migrate south to overwinter and mix with the resident subspecies in the coastal wetlands of the northern GoM, we were unable to assess density relationships for these subspecies. Our non-breeding population estimate with the mixing of subspecies was much higher (106,000) than the estimated abundance of the resident subspecies (2500; Remsen et al. 2019b), suggesting that the number of migrants outnumbers the number of residents during the non-breeding period in Mississippi. Previous observations in Georgia and Florida have revealed that Marsh Wrens inhabit a wide variety of wetland types from freshwater to salt marshes during the non-breeding period (Kale 1965, Stevenson and Anderson 1994, Kroodsma and Verner 2020). Similarly, we documented this species in freshwater/intermediate marsh (e.g., *C. mariscus*-dominated marshes; Eleuterius 1972) as well as more saline/brackish marsh (e.g., *S. alterniflora* and *J. roemerianus*; Eleuterius 1972), demonstrating that this species is ubiquitous and a habitat generalist in Mississippi tidal marshes during the winter.

Red-winged Blackbirds are among the most abundant and widespread birds in North America (Yasukawa and Searcy 2020), with the coastal marshes along the northern GoM identified as a major population center for this species during winter (Meanley 1965). Although widespread across different wetland types (Yasukawa and Searcy 2020), Red-winged Blackbirds were most often associated with the transition zone from saline to intermediate marsh types, tracking the salinity range in these marshes (Eleuterius 1972).

Seaside Sparrows are year-round residents along the northern GoM (Woodrey et al. 2012, Post and Greenlaw 2020). Our winter density estimate of Seaside Sparrows (1.58 ± 0.41 birds/ha) is greater than those reported along the Mississippi Coast during the breeding season (0.73 [95% CI = 0.62 – 0.86] birds/ha; Leggett 2014), but similar to those reported for the isolated subspecies (*A. m. senetti*) along the lower Texas coast during the non-breeding season (1.9 [CV = 21.92] birds/ha; Ferrato et al. 2017). This higher density during the non-breeding season suggests that the Mississippi Coast acts as a valuable respite for non-resident Seaside Sparrows, attracting birds from a wide area including the east coast of North America. Current and concomitant breeding season marsh bird surveys along the Mississippi Coast, in parallel with genetic testing of birds wintering in these coastal marshes, will help elucidate the conservation benefit to Seaside Sparrows during the non-breeding season. Such an assessment could be performed employing methods similar to Roeder et al. (2021), but conducted with a focus on Seaside Sparrows in winter along the northern coast of the Gulf of Mexico. Seaside Sparrows maintained their associations with salt marsh consistent with previous reports for this species during winter (Post and Greenlaw 2020).

Clapper Rails are specialized towards life in tidal salt marsh (Meanley 1985, Rush et al. 2020), and have been used as indicators of estuarine ecosystem health (Novak et al. 2006, Cumbee et al. 2008), which is why accurate population estimates are important. Our population estimate (17,000 [10,000 – 32,000]) is similar to the only other estimate based on breeding season data of the number of Clapper Rails in Mississippi (25,000 [11,000 – 39,000]; Remsen et al. 2019b). Our mean density estimate (0.74 ± 0.23 birds/ha) is also comparable to previous breeding season estimates in Mississippi's tidal marshes (Rush 2009: 0.22 – 1.44 birds/ha, Leggett 2014: 0.57 – 1.77 birds/ha). Because Clapper Rails are thought to be permanent residents in GoM marshes, this result is consistent with our *a priori* expectation of similar density estimates across seasons. The positive relationship of non-breeding rail density with *J. roemerianus* and *S. alterniflora* is also consistent with previous findings from the breeding and non-breeding periods (Adams and Quay 1958, Rush et al. 2009b, Leggett 2014), again likely a reflection of the resident status of Clapper Rails in Mississippi. Their year-round use of low (*S. alterniflora*) and mid-marsh (*J. roemerianus*) habitats across the coast make them vulnerable to the predicted impacts of sea level rise in coastal Mississippi and across the Gulf of Mexico region (Watson et al. 2015).

An estimated 75% of the Nelson's Sparrow population is thought to breed in Canada (Partners in Flight 2019, Shriver et al. 2020), but marshes of the northern GoM are believed to harbor a large proportion of their population during the non-breeding period (Remsen et al. 2019a). Winter densities of Nelson's Sparrows in our study were positively associated with *S. alterniflora*, which is consistent with the results of studies along the Atlantic coast (Shriver et al. 2010). The positive association of Nelson's Sparrow density with increasing numbers of vegetation ecotone changes along transects suggests that they use more heterogeneous areas of *S. alterniflora* and avoid large homogenous patches of *J. roemerianus* and *C. mariscus*. In their wintering areas, Nelson's Sparrows shift their diet to mostly seeds, including cordgrass (*Spartina* spp.), wildrice (*Zizania* spp.), and panicgrass (*Panicum* spp.) among others (Shriver et al. 2020). Along the Mississippi Gulf Coast, Nelson's Sparrows feed extensively in patches of *S. alterniflora* where they consume ripened cordgrass seeds (M. Woodrey, pers. comm.).

Most Swamp Sparrows in our study were detected in areas of shrubby edges (predominantly eastern baccharis, *Baccharis halimifolia*) and where the marsh transitioned from emergent vegetation to scrub-shrub estuarine marsh. Beadell et al. (2003) reported similar vegetation associations for this species in coastal marshes along the Atlantic Coast. Swamp Sparrows use a variety of vegetation types from freshwater, intermediate, and high marsh to inland wet pine savannah along the Gulf of Mexico during winter (Herbert et al. 2020). Because the extent of wet pine savannah continues to decrease along the northern Gulf of Mexico (Morris et al. 2020), Swamp Sparrows overwintering in this region may be forced to be more reliant on freshwater marsh systems. With sea level rise, changes in land use patterns, and hydrology, these freshwater marsh systems and the emergent marsh they support may change in distribution likely, as elsewhere (Rush et al. 2018), influencing the distribution of Swamp Sparrows and other species that occupy these habitats.

Sedge Wrens are present along the northern coast of the GoM only during winter (Woodrey et al. 2012, Herkert et al. 2020). Sedge Wren densities were generally low throughout the emergent tidal marsh, but highly localized (42% of all detections) on two transects in areas of higher, drier marsh with dense vegetation cover. Therefore, our reported population abundance and density estimates should be viewed from this perspective. This and their generally low numbers suggest that tidal salt marsh is not preferred by this species. Based on our observations and the results of previous studies, Sedge Wrens appear to prefer drier, fresh to brackish water marshes with scattered scrub and wet pine/longleaf savanna habitats (Hamel 1992, Zenzal et al. 2019, Herkert et al. 2020).

Our estimate of mean Common Yellowthroat density (0.10 birds/ha) was lower than that reported in freshwater wetlands in Florida during the non-breeding season (2.0 birds/ha; Breininger 1992). Common Yellowthroats are not salt marsh specialists, especially during the non-breeding season, as indicated by their strong association with freshwater and intermediate marsh-type vegetation (e.g., *C. mariscus*) in our study. Hamel (1992) noted that Common Yellowthroats prefer "…damp places, such as brushy tangles, marsh edges, and damp thickets;

inhabit fresh and brackish marshes, usually near shrubs." We rarely found Common Yellowthroats in areas of dense *J. roemerianus* stands typical of tidal marshes in Mississippi (Eleuterius 1972), but did detect several in narrow vegetation zones where *S. cynosuroides* and common reed (*Phragmites australis*) formed thickets around large stands of *J. roemerianus*.

Our results suggest that line transect surveys in conjunction with a distance sampling approach are effective for assessing the distribution, abundance, and vegetation associations of birds in tidal marsh during the non-breeding period across the northern coast of the GoM and, possibly, in tidal marshes along the Atlantic coast. However, for species that vocalize infrequently or do not flush readily (e.g., species in the family Rallidae such as Clapper Rails), our estimates may underrepresent true population sizes.

We recognize that, for species such as Red-winged Blackbirds, Common Yellowthroats, Swamp Sparrows, and Sedge Wrens that are not restricted to tidal marshes, our population estimates do not represent the entire non-breeding populations along the Mississippi Coast. Although estuarine marshes on barrier islands, ~3% of the estuarine marsh along the Mississippi Coast, were not surveyed, we do not believe that the inclusion of these areas in our study would have drastically changed our population estimates, species relative abundances, or vegetation associations. We also acknowledge that our 95% confidence intervals are wide and could likely be reduced with more detections or could reflect species with localized or patchy distributions in tidal marsh habitats due to high microhabitat-specificity (Conway and Droege 2006, Wiest et al. 2016). Due to time and logistical constraints, we employed a line-intercept approach to collect vegetation data because it was faster than quadrat data when there are few plant species and large areas to sample (Little 2013). However, this approach did not allow us to measure and characterize other potentially important vegetation variables such as spatial extent, height, and density that might influence marsh bird densities and vegetation associations.

This study, which provides robust population estimates and documents vegetation associations for non-breeding marsh birds found in coastal Mississippi tidal marshes, is the first of its kind in the Gulf of Mexico and forms the basis for future research into the ecology and conservation of tidal marsh birds. For example, our results show these tidal marshes provide winter habitat for several bird species of conservation concern (Woodrey et al. 2019), and thus provide critical habitat for both permanent resident and short-distance, intra-continental migrants during the non-breeding season. Understanding the ecological aspects and requirements of the full annual lifecycle of migratory birds is critical to our conservation of these mobile species (Marra et al. 2015). A prime example of the need for non-breeding distribution and abundance data to manage and conserve a species throughout the annual cycle is Nelson's Sparrows. Understanding potential linkages between interior breeding populations and the Gulf of Mexico wintering grounds is a critical first step in the development of a comprehensive conservation approach for this and several other short-distance marsh bird migrants of conservation concern including Yellow, Black, and King rails, American Bitterns, and Sedge and Marsh wrens (Woodrey et al 2019). A second example, particularly relevant to current marsh restoration efforts along the Gulf in response to the Deepwater Horizon Oil Spill, involves tracking the responses of marsh birds to the increasing use of dredge material to create and restore estuarine marshes. Our bird-vegetation associations can be used to plan and target vegetation communities to provide suitable habitat for specific suites of non-breeding marsh bird species of conservation concern. Additional critical uncertainties regarding marsh birds in the Gulf region that must be addressed for their long-term sustainability include their responses to habitat restoration, including the application of prescribed fire, the impacts of invasive species management, evaluating the effects of changing hydrologic regimes, and predator management while also conducting monitoring to improve our understanding of ecological processes such as natural disturbance regimes on marsh bird populations (Woodrey et al. 2019).

Targeted application of our winter marsh bird population estimates and vegetation-association data will support coastal marsh management and enhance future conservation planning efforts for the northern GoM. In addition, these data are crucial to making informed, science-based decisions when confronting continuing coastal issues such as rising sea levels, erosion, subsidence, and increasing urbanization. In a time of dwindling global coastal wetlands (Nicholls 2004, Dahl 2011, Davidson 2014), and an increasing call to focus research on the full annual cycle of migratory birds (Calvert et al. 2009, Hostetler et al. 2015, Marra et al. 2015), studies of bird communities overwintering in tidal marshes are more important than ever.

ACKNOWLEDGMENTS

We thank the many field technicians who helped conduct bird and vegetation surveys in the marsh. In addition, we also thank personnel from the Saltmarsh Habitat & Avian Research Program (SHARP) who provided advice for implementing a large-scale marsh bird survey. This work was funded with support from the Mississippi Department of Environmental Quality, via the National Fish and Wildlife Foundation Gulf Environmental Benefit Fund [Grant #335414] to Mississippi State University (RBI, KOE, MSW). Additional funding support included National Oceanic and Atmospheric Administration [Awards #NA17NOS4200045, #NA18NOS4200063] to the Mississippi Department of Marine Resources' Grand Bay National Estuarine Research Reserve (MSW), and the Mississippi Department of Marine Resources [Contract #8200025414] to Mississippi State University (MSW). This publication is a contribution of the Mississippi Agricultural and Forestry Experiment Station, Forest and Wildlife Research Center at Mississippi State University, and based upon work supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, Hatch project (MSW, JMF). An anonymous reviewer, along with the editor, provided valuable comments that helped improve the quality of this manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article at the publisher's website.

Table S1. Number of marsh birds detected that could be identified to species-level during non-breeding line transect surveys within estuarine, emergent tidal marsh along coastal Mississippi.

Table 1. Results of hierarchical distance sampling model selection for species of marsh birds detected during line transect surveys conducted during the non-breeding period in estuarine, emergent tidal marsh along coastal Mississippi using package unmarked (Fiske and Chandler 2011) in the statistical software program R (R Core Team 2018).

Species	**λ**	**φ**	***p***	**Key function**	**Data type**	**ΔAIC**
Marsh Wren	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS	visit	wind+ordinal+observer+JURO+SPAL+CLMA+SPCY+SPPA	Hazard-rate	NB	0
Red-winged Blackbird	year+complex+JURO+(JURO^2)	visit	wind+ordinal+observer	Hazard-rate	NB	0
	year+complex+JURO+(JURO^2)+CLMA	visit	wind+ordinal+observer	Hazard-rate	NB	0.8
Seaside Sparrow	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS		wind+ordinal+observer	Hazard-rate	NB	0
Clapper Rail	year+complex+JURO+SPAL+CLMA+SEGS	visit	wind+ordinal+observer+JURO+SPAL+CLMA+SPCY+SPPA	Half-normal	NB	0
Nelson's Sparrow	year+complex+JURO+SPAL+CLMA	visit	observer	Hazard-rate	NB	0
	year+complex+JURO+SPAL+CLMA+SEGS	visit	observer	Hazard-rate	NB	0.45
	year+complex+JURO+SPAL+CLMA	visit	observer	Hazard-rate	P	0.69
	year+complex+JURO+SPAL+CLMA+SEGS	visit	observer	Hazard-rate	P	1.16
Swamp Sparrow	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS		wind+ordinal+observer	Half-normal	NB	0
Sedge Wren	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS	visit	wind+ordinal+observer+JURO+SPAL+CLMA+SPCY+SPPA	Hazard-rate	NB	0
Common Yellowthroat	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS	visit	wind	Hazard-rate	NB	0
	year+complex+JURO+SPAL+CLMA+SPPA+SPCY+SEGS	visit	wind+ordinal	Hazard-rate	NB	1.13

Only models within ΔAIC < 2 are shown in the table. Abbreviations: λ = density, φ = availability, *p* = detection, JURO = *Juncus roemerianus*, SPAL = *Spartina alterniflora*, CLMA = *Cladium mariscus*, SPPA = *Spartina patens*, SPCY = *Spartina cynosuroides*, SEGS = the number of vegetation ecotone changes per 100 meters along a transect, NB = negative binomial distribution, and P = Poisson distribution.

Table 2. Estimated mean species-specific densities per hectare by marsh complex (± SE), along with estimated population sizes (including a 95% confidence intervals) for the Mississippi Coast in estuarine emergent tidal marsh. The number of individuals of each species detected in each marsh complex is given below the density estimate. The amount of estuarine emergent marsh in each complex is given in brackets below the complex name.

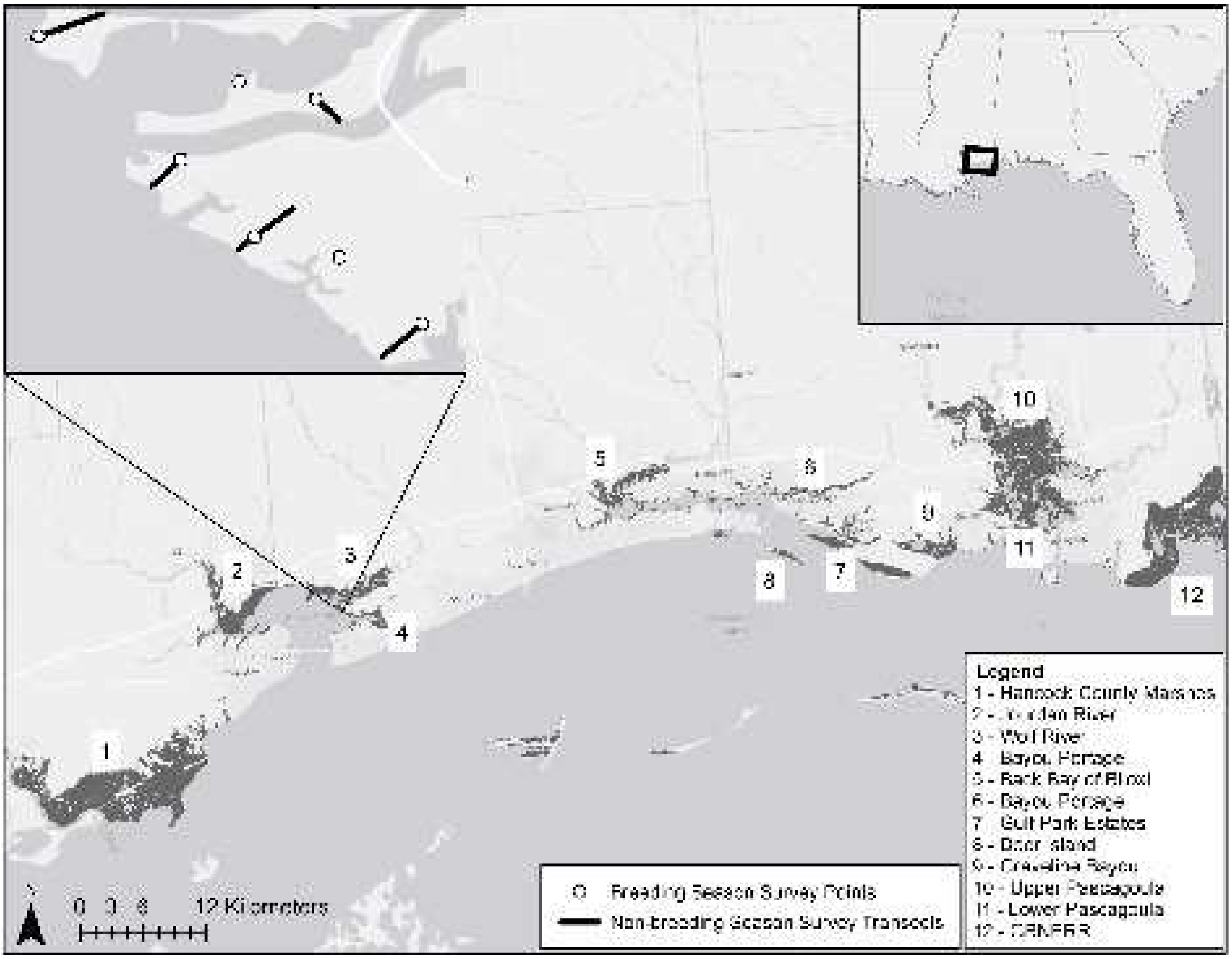
	Hancock County [6788 ha]	**Jourdan River** [1525 ha]	**Wolf River** [920 ha]	**Bayou Portage** [301 ha]	**Back Bay of Biloxi** [1208 ha]	**Deer Island** [119 ha]	**Old Fort Bayou** [419 ha]	**Gulf Park Estates** [537 ha]	**Graveline Bayou** [1027 ha]	**Lower Pascagoula** [3555 ha]	**Upper Pascagoula** [2744 ha]	**Grand Bay National Estuarine Research Reserve** [4166 ha]	**Statewide mean density estimate**	**Statewide population estimate**
Clapper Rail	1.1 ± 0.3 (*N* = 98)	0.7 ± 0.3 (*N* = 23)	0.7 ± 0.2 (*N* = 64)	0.6 ± 0.2 (*N* = 16)	0.3 ± 0.1 (*N* = 22)	2.0 ± 1.4 (*N* = 30)	0.6 ± 0.2 (*N* = 22)	0.9 ± 0.5 (*N* = 14)	0.9 ± 0.3 (*N* = 62)	0.4 ± 0.1 (*N* = 75)	0.4 ± 0.1 (*N* = 26)	0.7 ± 0.2 (*N* = 154)	0.7 ± 0.2	17,000 [10,000 – 32,000]
Sedge Wren	0.3 ± 0.2 (*N* = 2)	0.8 ± 0.6 (*N* = 4)	0.5 ± 0.3 (*N* = 5)	1.9 ± 1.0 (*N* = 25)	0.2 ± 0.2 (*N* = 2)	0 (*N* = 1)	0 (*N* = 0)	0 (*N* = 0)	0 (*N* = 1)	0.4 ± 0.2 (*N* = 42)	0 (*N* = 0)	1.2 ± 0.5 (*N* = 17)	0.5 ± 0.3	10,000 [4000 – 33,000]
Marsh Wren	4.7 ± 0.8 (*N* = 178)	3.5 ± 0.8 (*N* = 59)	3.9 ± 0.7 (*N* = 143)	8.1 ± 1.8 (*N* = 113)	6.8 ± 1.2 (*N* = 127)	7.6 ± 2.9 (*N* = 74)	8.4 ± 1.7 (*N* = 94)	2.2 ± 0.8 (*N* = 16)	4.1 ± 0.8 (*N* = 105)	3.4 ± 0.5 (*N* = 203)	3.7 ± 0.7 (*N* = 100)	5.3 ± 0.8 (*N* = 381)	4.6 ± 0.8	106,000 [75,000 – 150,000]
Seaside Sparrow	3.4 ± 0.8 (*N* = 145)	1.1 ± 0.5 (*N* = 10)	0.7 ± 0.2 (*N* = 19)	1.6 ± 0.6 (*N* = 16)	0.5 ± 0.2 (*N* = 9)	1.0 ± 0.6 (*N* = 14)	0.8 ± 0.3 (*N* = 11)	0 (*N* = 0)	0.2 ± 0.1 (*N* = 7)	1.3 ± 0.3 (*N* = 79)	0.1 ± 0.1 (*N* = 2)	1.2 ± 0.3 (*N* = 98)	1.6 ± 0.4	37,000 [22,000 – 62,000]
Nelson's Sparrow	0.5 ± 0.3 (*N* = 9)	0.4 ± 0.3 (*N* = 5)	0.7 ± 0.4 (*N* = 8)	1.6 ± 1.0 (*N* = 12)	0.9 ± 0.4 (*N* = 15)	0.9 ± 0.7 (*N* = 6)	1.5 ± 1.1 (*N* = 4)	0 (*N* = 0)	0.6 ± 0.4 (*N* = 3)	0.8 ± 0.4 (*N* = 23)	0.2 ± 0.2 (*N* = 2)	0.8 ± 0.5 (*N* = 22)	0.6 ± 0.4	14,000 [4000 – 47,000]
Swamp Sparrow	0.4 ± 0.2 (*N* = 12)	0.9 ± 0.4 (*N* = 49)	0.3 ± 0.1 (*N* = 26)	3.8 ± 1.8 (*N* = 38)	2.0 ± 0.8 (*N* = 45)	0 (*N* = 6)	3.0 ± 1.4 (*N* = 21)	2.2 ± 1.4 (*N* = 4)	0 (*N* = 0)	0.6 ± 0.2 (*N* = 37)	0.8 ± 0.3 (*N* = 40)	0.2 ± 0.1 (*N* = 8)	0.7 ± 0.3	15,000 [6,000 – 37,000]
Red-winged Blackbird	7.4 ± 3.3 (*N* = 74)	4.3 ± 2.5 (*N* = 184)	3.5 ± 1.8 (*N* = 63)	9.5 ± 5.5 (*N* = 85)	7.1 ± 3.5 (*N* = 60)	3.3 ± 4.6 (*N* = 5)	7.4 ± 5.1 (*N* = 25)	24.9 ± 17.1 (*N* = 25)	6.6 ± 4.2 (*N* = 47)	2.8 ± 1.5 (*N* = 197)	4.5 ± 2.3 (*N* = 68)	2.3 ± 1.2 (*N* = 108)	5.4 ± 2.8	127,000 [46,000 – 362,000]
Common Yellowthroat	0.2 ± 0.1 (*N* = 6)	0.2 ± 0.1 (*N* = 21)	0.1 ± 0.0 (*N* = 14)	0.4 ± 0.3 (*N* = 22)	0.1 ± 0.1 (*N* = 3)	0 (*N* = 0)	0.3 ± 0.2 (*N* = 5)	0 (*N* = 0)	0 (*N* = 0)	0 (*N* = 0)	0.1 ± 0.1 (*N* = 10)	0 (*N* = 1)	0.1 ± 0.1	2000 [1000 – 10,000]

Except for Deer Island, estimates do not include barrier islands. All estimates are rounded to the nearest thousand. Marsh complexes are listed from west to east.

FIGURE CAPTIONS

Fig. 1. Map showing the Mississippi Coast with the 12 marsh complexes included in our study. The inset image at upper left illustrates how line transects were distributed based on breeding marsh bird sample point locations placed using a Generalized Random Tessellation Stratified (GRTS) design. GBNERR = Grand Bay National Estuarine Reserve.

Fig. 2. Associations of eight marsh bird species detected during non-breeding line transect surveys within estuarine, emergent tidal marsh along coastal Mississippi with the availability of the top five most abundant vegetation types. Vegetation acronyms: JURO = *J. roemerianus*, SPAL = *S. alterniflora*, CLMA = *C. mariscus*, SPCY = *S. cynosuroides*, SPPA = *S. patens*, and SEGS = the number of dominant vegetation ecotone segments per 100 m along transects. Legend in upper-right most plot. Y axis represents the change in density (birds/ha) as the standardized x-axis covariate changes. All covariates were scaled to a mean of zero.



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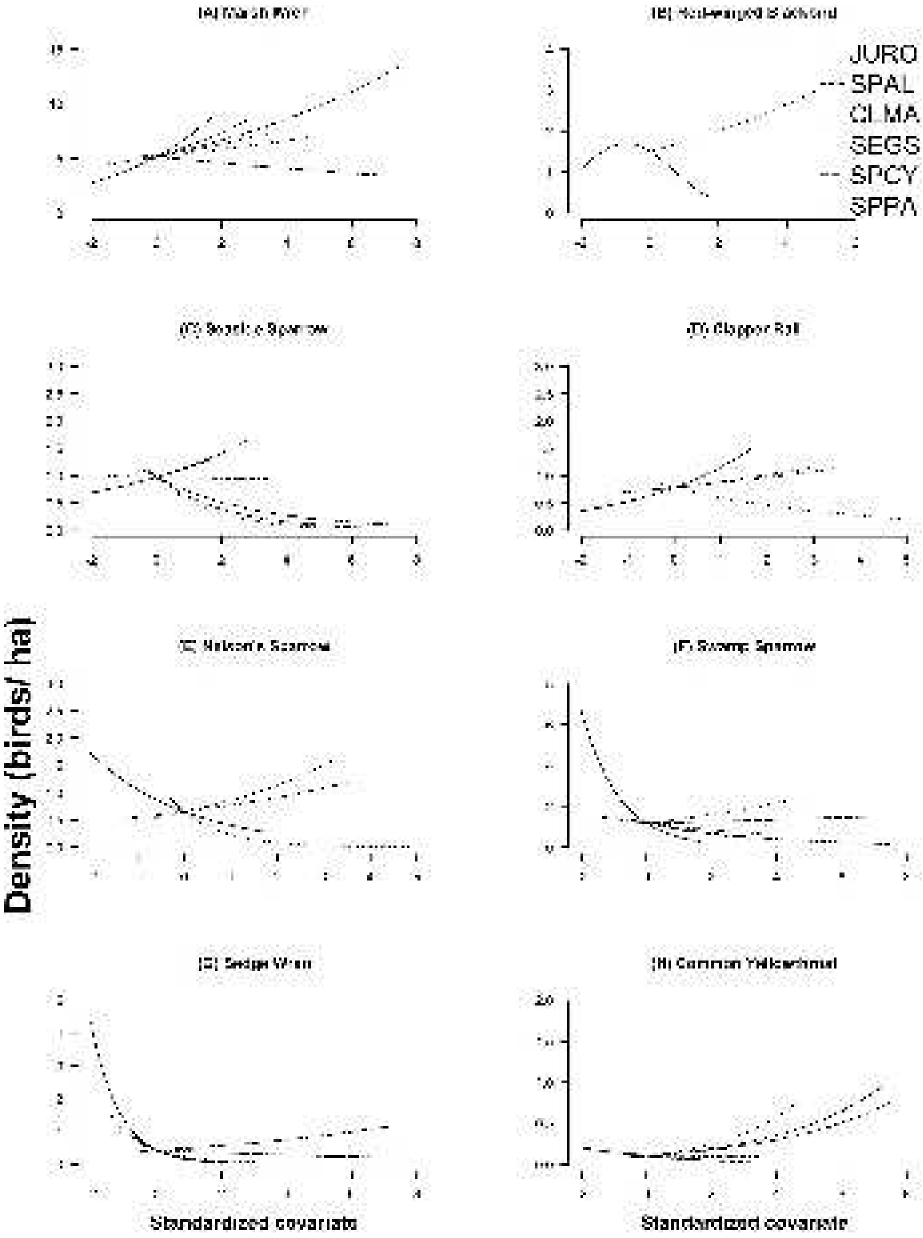

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