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Research Paper

Secretive marsh bird habitat associations in the Mississippi Flyway: a meta-analysis

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ABSTRACT. Secretive marsh birds, including rails and bitterns, have experienced widespread population declines due to the loss of wetland habitat on which they depend. Because of their cryptic behavior, secretive marsh birds are challenging to study and information on their habitat requirements is limited, especially across the full annual cycle. Quantifying habitat associations throughout the annual cycle and at broad geographic scales can advance a more comprehensive approach for secretive marsh bird conservation. The goal of this study was to quantitatively synthesize results from empirical studies that examined species-habitat relationships of secretive marsh birds in the North American Mississippi Flyway to identify general patterns and information gaps that can guide future management and conservation efforts. We performed a meta-analysis and incorporated results from 40 studies that quantitatively assessed habitat associations of American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), King Rail (*Rallus elegans*), Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*), and Yellow Rail (*Coturnicops noveboracensis*). Most studies examined breeding season habitat, whereas only 13% reported on habitat use during migration and none during winter. At landscape scales, breeding marsh birds were positively associated with amount of wetlands, especially in the Great Lakes region, and negatively associated with amount of urban land cover, particularly for American Bittern. At the local scale, breeding marsh birds were positively associated with cattail coverage (*Typha* spp) and other robust emergent vegetation. Overall, marsh birds were negatively associated with woody wetland vegetation, although effects were weaker in the Prairie region and varied among species. During autumn migration, moist-soil vegetation coverage was important for rails in the lower Midwest. The habitat use patterns we identified across studies provide a general characterization of marsh bird breeding habitat to aid in landscape-level multi-species conservation efforts. Our study also highlights the immediate research needs for full annual cycle conservation of secretive marsh bird habitat in North America: specifically, information during winter and migration.

Associations entre l'habitat et les oiseaux de marais discrets dans la voie migratoire du Mississippi : une méta-analyse

RÉSUMÉ. Les oiseaux de marais dits discrets, notamment les râles et les butors, ont connu une baisse généralisée de leurs populations en raison de la perte des milieux humides dont ils dépendent. Compte tenu de leur comportement cryptique, les oiseaux de marais discrets sont difficiles à étudier et les informations sur leurs besoins en matière d'habitat sont limitées, en particulier sur l'ensemble du cycle annuel. La quantification des associations avec l'habitat tout au long du cycle annuel et à de vastes échelles géographiques peut faire progresser une approche plus exhaustive de la conservation de ces oiseaux de marais. L'objectif de la présente étude était de réaliser une synthèse quantitative des résultats d'études empiriques qui ont examiné les relations entre les oiseaux de marais discrets et l'habitat dans la voie de migration nord-américaine du Mississippi, afin de déterminer les tendances générales et les lacunes en matière d'information qui pourraient guider les futures activités de gestion et de conservation. Nous avons effectué une méta-analyse et intégré les résultats de 40 études ayant évalué de façon quantitative les associations avec l'habitat du Butor d'Amérique (*Botaurus lentiginosus*), du Petit Blongios (*Ixobrychus exilis*), du Râle élégant (*Rallus elegans*), de la Marouette de Caroline (*Porzana carolina*), du Râle de Virginie (*Rallus limicola*) et du Râle jaune (*Coturnicops noveboracensis*). La plupart des études se sont penchées sur l'habitat pendant la saison de reproduction, tandis que seulement 13 % ont fait état de l'utilisation de l'habitat pendant la migration et aucune pendant l'hiver. À l'échelle du paysage, les oiseaux de marais nicheurs étaient positivement associés à la quantité de milieux humides, surtout dans la région des Grands Lacs, et négativement associés à la quantité de milieux urbains, surtout pour le Butor d'Amérique. À l'échelle locale, les oiseaux de marais nicheurs étaient positivement associés au couvert de quenouilles (*Typha* spp.) et d'autres espèces végétales émergentes robustes. Dans l'ensemble, les oiseaux de marais étaient associés négativement à la végétation ligneuse de milieux humides, bien que les effets aient été plus faibles dans la région des Prairies et aient varié selon les espèces. Pendant la migration automnale, le couvert végétal de sols humides était important pour les râles dans le Midwest inférieur. Les tendances de l'utilisation de l'habitat que nous avons déterminées à partir des études permettent d'avoir une caractérisation générale de l'habitat de reproduction des oiseaux de marais pour guider les efforts de conservation multi-espèces au plan du paysage. Notre étude met

également en évidence les besoins immédiats en matière de recherche pour la conservation de l'habitat d'oiseaux de marais discrets en Amérique du Nord durant le cycle annuel complet, en particulier les informations pendant l'hiver et la migration.

Key Words: *American Bittern*; *full annual cycle conservation*; *King Rail*; *Least Bittern*; *Sora*; *Virginia Rail*; *Yellow Rail*; *wetland birds*; *wetland habitat management*

INTRODUCTION

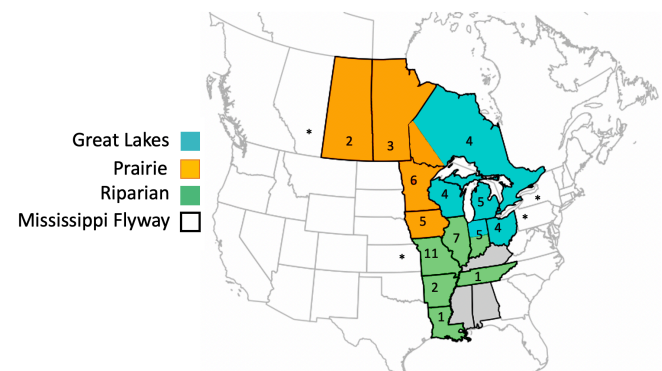
North America has experienced extensive wetland habitat loss over the past two centuries (Dahl 1990, Brinson and Malvárez 2002), contributing to population declines for many wetland-dependent avian species (Morrison et al. 1994, Tozer 2016, Sauer et al. 2020). For example, many states in the midwestern United States and Mississippi River watershed have lost at least 90% of wetland surface area since 1780, primarily through draining for agricultural production (Dahl 1990). Thus, migratory avian species that use interior portions of North America throughout their life cycle, such as secretive marsh birds, have likely been acutely affected by wetland habitat loss. Wetland habitat conservation efforts have predominantly focused on waterfowl (Family *Anatidae*) and contributed to restoration of substantial wetland habitat area in North America (North American Waterfowl Management Plan 2012, U.S. Fish and Wildlife Service 2018), but other wetland-dependent birds are often ignored in restoration efforts.

Secretive marsh birds, including rails and bitterns, are wetland-dependent species and designated species of conservation concern by many state, provincial, and federal natural resource agencies (U.S. Geological Survey 2021). Some secretive marsh bird species have experienced widespread population declines (Tozer 2016, Sauer et al. 2020), while other species' rarity and secretive nature precludes determination of their population trajectory. Secretive marsh birds can be challenging to study and monitor because they vocalize infrequently, are rarely seen, and their habitat is often inaccessible. North America's Mississippi Flyway contains critical habitat for several species of secretive marsh birds throughout their annual cycle. Breeding grounds for most of these species are located in the upper Midwest and Prairie Pothole regions, but the remainder of the Flyway provides critical migration and wintering habitats (Huschle et al. 2013, Fournier et al. 2017, Leston and Bookhout 2020).

Despite the challenges of studying secretive marsh birds, research has increased in the last decade and numerous studies have examined species-habitat relationships (Darrah and Kremenz 2011, Harms and Dinsmore 2013, Glisson et al. 2015, Tozer 2016, Tozer et al. 2020). Given the dynamic and cyclic nature of wetlands, researchers have learned that marsh birds are more likely to occupy wetlands with specific habitat conditions. Understanding species-habitat relationships is a central theme in conservation ecology (Guisan and Thuiller 2005, Guisan et al. 2013) and is essential for developing effective habitat management strategies for secretive marsh birds throughout their full annual cycle. Research and management that focuses exclusively on local habitat needs may ultimately contribute to a fragmented approach that fails to adequately address management and conservation efforts at a scale sufficient to promote sustainable populations (although funding priorities also play a role). Quantifying trends in habitat associations throughout the annual cycle and at broad geographic scales, such as the flyway scale, can advance a more

comprehensive approach for secretive marsh bird conservation (Martin and Finch 1995). Thus, the goal of this study was to quantitatively synthesize results from empirical studies that examined species-habitat relationships of secretive marsh birds in the Mississippi Flyway (Fig. 1) to identify general patterns and information gaps that can guide future management and conservation efforts. The flyway scale not only captures full life cycle habitat needs but is pragmatic from a conservation standpoint because the administrative flyways facilitate coordination of management and conservation actions among states and provinces within a flyway.

Fig. 1. Map of United States and Canada showing the regions within the Mississippi Flyway and distribution of studies by state/province that were included in the meta-analysis of secretive marsh bird habitat associations. The Mississippi Flyway was delineated according to the United States Fish and Wildlife Service administrative boundary. Studies were included if > 50% of the sampling locations were within the boundaries of the Mississippi Flyway. Asterisks (*) indicate states or provinces where sampling took place as part of a study that was conducted in the Mississippi Flyway.



A meta-analysis is a quantitative and robust method to synthesize research findings across studies by enabling evaluation of the strength and heterogeneity in ecological patterns (Koricheva et al. 2013, Gurevitch et al. 2018). Meta-analyses that examine species-habitat associations are not common (but see Hagen et al. 2007, Hagen et al. 2013, Aubry et al. 2013) but for imperiled, understudied species, such as secretive marsh birds, a meta-analysis can be useful to wetland managers and conservation practitioners by providing insight on the broader applicability of results from individual studies. Additionally, a meta-analysis can statistically evaluate potential differences in habitat associations among factors of ecological interest, such as species, regions, or life history events, and identify information gaps that can guide future research efforts. Our objectives were to identify trends and information gaps as they relate to four main factors: 1) Species -

how do secretive marsh bird species differ in their habitat associations and are there species-specific information gaps? 2) Region - are there regional patterns in habitat associations or information gaps? 3) Spatial scale of measurement - is the spatial scale at which habitat is measured important for determining habitat associations, and if so, do previous studies encompass the most important scale? 4) Season - how do breeding season habitat associations differ from non-breeding season habitat associations and are there seasonal information gaps?

METHODS

Literature search and study selection

We located studies by searching three online databases: Web of Science, ProQuest Theses and Dissertations, and Google Scholar. We performed searches in February 2020 and searched the full text for the following phrase (“Least Bittern” OR “American Bittern” OR “Sora” OR “Virginia Rail” OR “King Rail” OR “Yellow Rail” OR “Black Rail”) and, within the same search, titles only for (“habitat” OR “ecology” OR “landscape”). To search for studies not published online, we emailed representatives of the Nongame Bird Technical Section of the Mississippi Flyway Council from each state and province within the United States Fish and Wildlife Service administrative boundaries of the Flyway. We requested representatives send us copies of reports that included any marsh bird studies carried out in their jurisdiction. Although this approach may have missed some relevant studies, it provided an unbiased method for collecting literature.

We then assessed the potential for each study to contribute quantitative data to our analysis. We initially screened studies based on titles and abstracts and excluded studies that obviously did not pertain to the subject of our search (i.e., the title or abstract indicated the study did not include our focal species, was not within the Mississippi Flyway, or did not pertain to habitat associations). Our focal species were Least Bittern (*Ixobrychus exilis*), American Bittern (*Botaurus lentiginosus*), Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*), King Rail (*Rallus elegans*), Yellow Rail (*Coturnicops noveboracensis*), and Black Rail (*Laterallus jamaicensis*). We further screened studies by skimming the methods and results, tables, and figures (Koricheva et al. 2013). We excluded studies not done in wetlands, studies that analyzed community metrics rather than individual species metrics, studies that provided qualitative rather than quantitative results (Koricheva et al. 2013), studies that condensed habitat variables into principal components, and studies that assessed relationships of our focal species only to habitat management actions rather than habitat features. We included studies where the response variable was any measure of population response by at least one of our focal species, including abundance, density, presence, nest presence, nest survival, or brood presence. We included studies in which the majority of sampling locations were within the United States Fish and Wildlife Service administrative boundaries of the Mississippi Flyway, even if some of the sampling locations were outside of the Flyway boundaries (Fig. 1). We excluded studies that did not report sufficient information to calculate an effect size or whose authors did not respond to our requests for missing information (Koricheva et al. 2013). We included peer-reviewed journal articles, theses and dissertations, agency reports, and

unpublished manuscripts. We compared titles and authors of all potential studies to avoid duplicate studies (i.e., including studies that were first reported in a thesis, dissertation, or report and then later published in a peer-reviewed journal). A thesis or dissertation chapter that was later published in a peer-reviewed journal was considered a single study. In these cases, we first looked to the peer-reviewed material and extracted what we could. However, if some of the information was missing from the peer-reviewed publication, we looked for it in the thesis or dissertation. If most of the information we needed came from the thesis or dissertation, we cited that (Reference A1) instead of the peer-reviewed publication.

Effect size extraction

Data to calculate effect sizes were extracted from in-text results, tables, or figures. We used Pearson correlation coefficient r between the species response variable and a habitat variable as our effect size estimate. Some studies reported r , but for many studies r was calculated from other reported values. Some studies reported means and variances for habitat variables among two groups (present vs. absent, used vs. available). For these studies, we first calculated the standardized mean difference (Hedges d ; Koricheva et al. 2013), then converted d to r following Koricheva et al. (2013). To calculate d we extracted the mean, standard deviation (SD), and n for both groups. If studies reported standard error or confidence/credible intervals, we converted those values to SD. We did not use partial R^2 or beta coefficients from multivariate models (Hullet and Levine 2003). For studies that reported results of models with multiple covariates rather than single covariates, we emailed authors and requested raw data to calculate r . Some studies incorporated detection probability of the focal species and although they reported results of models with multiple covariates, they indicated models with a single covariate were analyzed. In these cases, we contacted authors and asked them to share standardized beta coefficients from single-covariate models or alternatively the raw data. If authors shared standardized beta coefficients from logistic regression, we converted them to r as described in Polanin and Snilstveit (2016). If authors shared raw data, we calculated the standardized mean difference for each habitat variable between sites where each focal species was detected and sites where they were not detected, then converted the standardized mean difference to r .

When a study included species-specific results for multiple species, we treated these as separate observational units and extracted data for each species as independent effect sizes. Similarly, if a study was conducted during more than one annual season and presented season-specific results, we extracted data from each season as independent effect sizes. If a habitat variable was measured at multiple scales, we extracted scale-specific results as independent effect sizes. When a study was conducted across multiple years and presented results combined across years, we used the combined results. When a study presented results for individual years rather than years combined, we used results from the last year of the study (Koricheva et al. 2013). Accordingly, if authors sent us raw data in which birds and habitat were sampled at the same sites in multiple years, we used the last year of the data to calculate effect sizes.

The sample size (n) associated with each effect size was the number of locations where birds and habitat were surveyed. For studies

that compared habitat at locations where the focal species was detected versus random points, n was the total number of points from both groups combined where habitat was measured. The following data were also extracted from each study to use as potential explanatory variables of effect size direction and magnitude: 1) species - one of seven focal secretive marsh bird species; 2) location - most studies were conducted across many sites, but often within one or two states or provinces; 3) season - spring migration, breeding, autumn migration, or winter; 4) scale - the scale at which habitat variables were measured; 5) response variable - the population variable that was analyzed in relation to habitat variables; 6) bird survey method - the methods used to collect data on focal species; 7) habitat survey method - methods used to measure habitat variables.

We grouped studies into 3 regions within the Mississippi Flyway: Great Lakes, Prairie, and Riparian (Fig. 1). The regions were determined based on the geographic distribution of included studies and on broad differences in wetland hydrogeomorphology, which we expected to influence marsh bird habitat associations. Two studies included sampling points across more than one region and were not included in region-specific analyses.

Data analysis

Habitat variables varied across studies. Although we extracted data for every habitat variable reported in each study, we grouped and analyzed habitat variables only if the variable was measured and reported by at least 3 independent studies and was represented by at least 10 effect sizes (Higgins et al. 2020). Thus, sample sizes varied for each habitat variable. Some variables were named or measured differently across studies yet represented comparable or the same habitat feature such that we expected marsh birds to exhibit a similar association to these independent variables. For example, many studies assessed the relationship between marsh birds and the amount of emergent vegetation within a wetland, but study authors measured the amount of emergent vegetation in various ways including percent cover, density, or area of emergent vegetation within a radius around a survey point. Expecting equivalent or similar associations across different measures of the same habitat feature, we grouped these variables across studies for analysis (Table A1). Studies measured habitat at varying levels of specificity. For example, while most studies measured in some way the amount of emergent vegetation, some studies split this habitat feature into robust emergent vegetation and non-robust emergent vegetation or further into taxon-specific categories such as percent cover of *Typha spp* (cattail). We structured our analysis to reflect the hierarchy of measured variables (Table A2).

We grouped measurements across studies into 17 habitat variables (Tables A1 and A2). Five variables were typically measured at larger scales (median scale from 300 to 1,000 m) and represented the amount of 5 landcover types surrounding the survey point or focal wetland: wetland, forest, agriculture, urban, and open water. Other variables were measured at smaller scales, typically within the focal wetland, and included the amount of non-woody emergent vegetation, robust non-woody emergent vegetation, non-robust non-woody emergent vegetation, *Typha spp.*, woody emergent vegetation, shrubs, water depth, the interspersions of water and vegetation, wetland area, and vegetation height (Table 1).

We conducted random-effects meta-analyses for habitat variables that were represented by at least 10 data points and 3 studies. We first transformed correlation coefficients to Fisher's z scale (Sokal and Rohlf 1995, Koricheva et al. 2013). We included study ID as a random effect in every analysis because we considered our sample of studies to represent the larger group of marsh bird studies to which we wished to generalize our results and because it accounted for non-independence of multiple effect sizes that came from the same study (Stewart 2010, Gurevitch et al. 2018). We used the restricted maximum likelihood estimator (REML) and the Hartung-Knapp adjustment for all analyses (Viechtbauer 2007, IntHout et al. 2014). We conducted all analyses with the package *meta* (Schwarzer 2007, Balduzzi et al. 2019) in program R (version 3.6.2; R Core Team 2019).

To determine the summary weighted-mean effect size of a habitat variable, we initially included all data points for that variable across species, regions, seasons, and measurement scales. We used I^2 to measure the percent of variability in mean effect size estimates that is due to heterogeneity rather than sampling error (Higgins and Thompson 2002). If significant heterogeneity ($I^2 > 50\%$) was indicated by I^2 , then we tested for effects of moderator variables univariately, including the population response variable that studies measured and moderators of primary interest to this study: season, species, region, and spatial scale. We assessed differences among response variables, seasons, species, and regions based on whether 95% Confidence Intervals (CI) of mean effect sizes overlapped among groups. We tested the effect of the scale of measurement of each habitat variable as a continuous variable using meta-regression with $p < 0.05$ indicating a scale effect. If these effects explained significant variation, we reported the summary weighted-mean effect for each group that contained effect sizes from at least 3 independent studies. For each habitat variable, we subset the data by region and then analyzed each region independently for species effects. For some habitat variables, there were fewer than 3 studies representing some seasons, species, or regions and we did not report summary effects or make inference on habitat associations in those cases. We report mean effect sizes with 95% confidence intervals and consider mean effect sizes significant if confidence intervals do not overlap 0.

Publication bias can occur in meta-analyses when studies with significant results are more likely to be published and therefore are over-represented in a meta-analysis (Rothstein et al. 2005). Some of the studies included in this meta-analysis were theses and dissertations, or agency reports, which may be less subject to the potential bias of publication in peer-reviewed journals. Nonetheless, we tested for publication bias using visual assessment of funnel plots (Koricheva et al. 2013) and by Egger's test (Egger et al. 1997), which assesses the relationship between effect size and study sample size. When publication bias was indicated by the Egger's test, we used the trim and fill method to calculate an adjusted summary effect size (Duval and Tweedie 2000).

We used an influence analysis to test for outliers within statistically significant groups. We used the "leave-one-out" method and recalculated the mean effect size $n - 1$ times, each time removing one observation (Viechtbauer and Cheung 2010). If removing a single observation resulted in a mean effect size with CIs that did

Table 1. Meta-analysis results of habitat associations of secretive marsh birds in the Mississippi Flyway. Statistically significant mean effects are indicated with an asterisk. Species, region, and season effects are listed if there were at least three studies representing the group and the confidence interval for the group-specific mean effect did not overlap 0. Species codes are AMBI = American Bittern, LEBI = Least Bittern, SORA = Sora, VIRA = Virginia Rail, KIRA = King Rail, YERA = Yellow Rail. Region abbreviations are GL = Great Lakes region, P = Prairie region, R = Riparian region. I² indicates the percent of variability in mean effect size estimates of a habitat variable that is due to heterogeneity rather than sampling error. CI = confidence interval.

Habitat variable	Effect sizes	Studies	Mean effect size	Lower 95%CI	Upper 95%CI	I ²	Species	Regions	Seasons	Median scale (min, max) m
Agriculture	64	8	-0.012	-0.043	0.018	82.8%	AMBI, LEBI, SORA, VIRA	P	Breeding	900 (100, 6400)
Forest	49	6	-0.046*	-0.083	-0.01	70.9%	AMBI, LEBI, SORA, VIRA	GL	Breeding	1000 (100, 10,000)
Wetland	116	17	0.107*	0.083	0.131	79.2%	AMBI, LEBI, SORA, VIRA	GL, P	Breeding	1000 (100, 10,000)
Urban	57	6	-0.118*	-0.162	-0.074	84.7%	AMBI, LEBI, SORA, VIRA	GL	Breeding	800 (100, 6400)
Open water	59	16	-0.026	-0.067	0.016	82.4%	AMBI, LEBI, SORA, VIRA	GL, P, R	Breeding	275 (1, 10,000)
Wetland size	15	6	0.15*	0.052	0.245	90.8%	LEBI, SORA, VIRA	GL	Breeding	NA
Interspersion	16	6	0.075*	0.01	0.139	48.0%	LEBI	R	Breeding	50 (50, 1000)
Water depth	26	12	0.162*	0.014	0.304	95.8%	LEBI, SORA, VIRA, YERA	GL, R	Breeding, Autumn	5 (0, 100)
Vegetation height	16	7	0.118	-0.005	0.238	88.8%	LEBI, SORA, VIRA	R	Breeding	5 (0, 50)
Non-woody emergent veg.	129	26	0.087*	0.037	0.137	89.9%	AMBI, LEBI, SORA, VIRA, KIRA, YERA	GL, P, R	Breeding	25 (1, 400)
Robust emergent veg.	41	13	0.17*	0.025	0.307	94.3%	AMBI, LEBI, SORA, VIRA	GL, P, R	Breeding	50 (1, 100)
Typha	29	10	0.219*	0.098	0.334	92.6%	AMBI, LEBI, SORA, VIRA	GL, P	Breeding	50 (1, 100)
Non-robust emergent veg.	55	13	0.003	-0.042	0.048	88.3%	AMBI, LEBI, SORA, VIRA, YERA	GL, R	Breeding, Autumn	1 (1, 300)
Emergent veg. (non-specific)	15	8	0.165*	0.097	0.231	75.1%	AMBI, LEBI, SORA, VIRA	GL, R	Breeding	100 (50, 400)
Woody wetland veg.	71	18	-0.109*	-0.191	-0.025	87.8%	AMBI, LEBI, SORA, VIRA, KIRA, YERA	GL, P, R	Breeding	50 (1, 5000)
Shrubs	13	5	-0.075	-0.152	0.003	90.5%	AMBI, LEBI, SORA	GL	Breeding	50 (100, 200)
Woody wetland veg. (non-specific)	36	11	-0.139	-0.297	0.028	90.9%	AMBI, LEBI, SORA, VIRA, KIRA	GL, R	Breeding	50 (1, 5000)

not overlap the mean effect with all observations included, we considered that observation to be an outlier and re-analyzed the data without it.

RESULTS

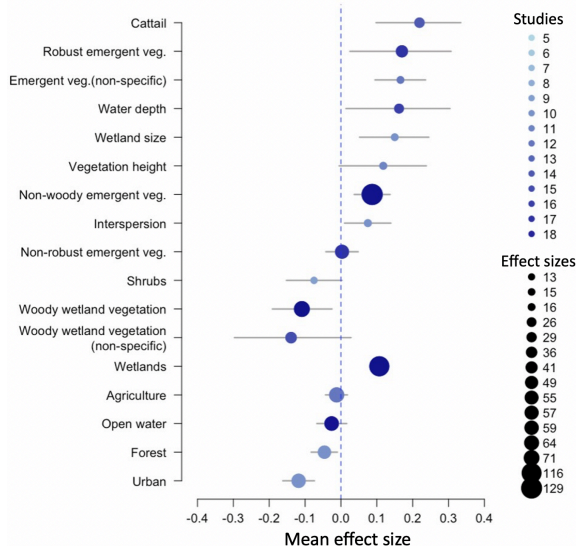
The literature search returned 1,304 articles. After screening titles and abstracts for relevance and duplicates, 150 articles were left. Of these, 69 quantitatively assessed habitat associations of at least one of our focal species in the focal region, although we were only able to obtain enough information to calculate effect sizes for 41 studies. Thus, 41 studies met all our inclusion criteria for the meta-analysis (Reference A1). These were from peer-reviewed journals ($n = 20$; 49%), theses or dissertations ($n = 15$; 37%), agency reports ($n = 5$; 12%) or unpublished manuscripts ($n = 1$; 2%). We obtained missing information via email from authors of 19 studies when we could not extract information to calculate an effect size from what was reported in the study.

Most studies took place during the breeding season ($n = 35$; 85%), with the remainder occurring during autumn migration ($n = 3$; 7%), spring migration ($n = 1$; 2%) or during spring migration and breeding with results combined for both seasons ($n = 2$; 5%). None of the studies took place during winter. A majority of studies were conducted during or after 2010 ($n = 28$; 68%), whereas others took place from 2000-2009 ($n = 8$; 20%) and before 2000 ($n = 5$; 12%). Thirty-six studies (88%) sampled locations entirely within the Mississippi Flyway, while 5 (12%) included a minority of points in neighboring states or provinces (Fig. 1). Fifteen studies (37%) were conducted in the Great Lakes region, eight (20%) in the Prairie region, and 17 (41%) in the Riparian region (Fig. 1). Two studies (5%) were conducted across more than 1 region and were not included in region-specific analyses. Black Rail was the only focal species that was not included in any study and thus not included in our analyses.

To examine trends across 17 habitat variables, we analyzed 620 effect sizes. Habitat variables were measured using remote sensing techniques or directly in the field. The number of studies and effect sizes analyzed for different habitat variables ranged from 5-26 and 13-129, respectively (Table 1). We removed two effect sizes as outliers. We calculated most effect sizes from marsh bird detection/non-detection data (335, 54%), followed by detection-adjusted occupancy (183, 30%), detection-adjusted abundance (86, 14%), and nest success data (16, 3%). Most studies surveyed birds using a call-broadcast point count method. We did not find evidence that effect sizes were different for any habitat variable based on the population response variable that was measured (CIs overlapped among response variables).

Across studies, secretive marsh birds were positively associated with the amount of non-woody emergent vegetation (mean effect size = 0.087, CI = 0.037 - 0.137, $I^2 = 89.9\%$), the amount of robust non-woody emergent vegetation (mean effect size = 0.170, CI = 0.025 - 0.307, $I^2 = 94.3\%$), the amount of *Typha spp.* (mean effect size = 0.219, CI = 0.098 - 0.334, $I^2 = 92.6\%$), the amount of wetlands in the landscape (mean effect size = 0.107, CI = 0.083 - 0.131, $I^2 = 79.2\%$), wetland size (mean effect size = 0.15, CI = 0.052 - 0.245, $I^2 = 90.8\%$), and water depth (mean effect size = 0.162, CI = 0.014 - 0.304, $I^2 = 95.8\%$). Secretive marsh birds were negatively associated with the amount of urban landcover in the landscape (mean effect size = -0.118, CI = -0.162 - -0.074, $I^2 = 84.7\%$), amount of forest in the landscape (mean effect size = -0.046, CI = -0.083 - -0.01, $I^2 = 70.9\%$), and amount of woody emergent vegetation (mean effect size = -0.109, CI = -0.191 - -0.025, $I^2 = 87.8\%$; Fig. 2, Table 1). I^2 indicated heterogeneity was substantial among studies for every habitat variable except interspersions (Higgins and Thompson 2002; Table 1).

Fig. 2. Mean effect sizes (Fisher’s z) representing the association of secretive marsh birds with 17 habitat variables based on meta-analysis of studies conducted in the Mississippi Flyway. Lines around the mean represent 95% confidence intervals. Sample size is indicated by shade (number of studies) and size (number of effect sizes) of points.



Based on the 3-study minimum, we examined region-specific associations of marsh birds to 14 habitat variables in the Great Lakes region, 7 in the Prairie region, and 10 in the Riparian region (Table 2). In the Great Lakes region water depth and the amount of *Typha spp.* were strongly positively associated with marsh birds (water depth mean effect size = 0.333, CI = 0.076 - 0.549, $I^2 = 91.5$; *Typha spp.* mean effect size = 0.217, CI = 0.128 - 0.303, $I^2 = 40.8$). The amount of wetlands in the landscape, wetland size, and amount of emergent vegetation (non-specific) were also positively associated with marsh birds in the Great Lakes region, whereas the amount of forest and urban landcover and the amount of shrubs were negatively associated with marsh birds in this region (Table 2; Table A3). In the Prairie region, the amount of all non-woody emergent vegetation was strongly associated with secretive marsh birds (mean effect size = 0.219, CI = 0.01 - 0.41, $I^2 = 95.9$). Amount of wetlands in the landscape was also positively associated with marsh birds in the Prairie region whereas the amount of open water habitat in the landscape was negatively associated (Table 2; Table A4). In the Riparian region, marsh birds were positively associated with the amount of all non-woody emergent vegetation and specifically robust emergent vegetation and negatively associated with woody emergent vegetation (Table 2; Table A5).

Table 2. Region-specific habitat associations of secretive marsh birds in the Mississippi Flyway based on meta-analysis. “...” means there were not at least 3 studies representing a species-habitat association, “0” means 95% confidence intervals overlapped zero, “+” indicates a significant positive relationship and “-” indicates a significant negative relationship.

Habitat variable	Great Lakes	Prairie	Riparian
Agriculture	...	0	...
Forest	-
Wetland	+	+	...
Urban	-
Open water	0	-	0
Wetland size	+
Interspersion	0
Water depth	+	...	0
Vegetation height	0
Non-woody emergent veg.	0	+	+
Robust emergent veg.	0	0	+
<i>Typha</i>	+	0	...
Non-robust emergent veg.	0	...	0
Emergent veg. - non-specific	+	...	0
Woody wetland veg.	0	0	-
Shrubs	-
Woody veg. - non-specific	0	...	-

Most variables for which we could compare across regions did not differ significantly by region (95% CIs overlapped; Appendix Figure 1). The association of marsh birds with the amount of wetlands in the landscape was significantly greater in the Great Lakes region relative to the Prairie region, although significant positive associations were present in both regions (Fig. A1).

At the species level, the number of habitat variables we examined varied by species, with few habitat variables for King Rail (3) and Yellow Rail (4), but considerably more for American Bittern (13), Least Bittern (17), Sora (16) and Virginia Rail (15; Table 3). Species differed significantly in their associations with the amount

of agriculture in the landscape and amount of forest in the landscape (Fig. 3). Both bittern species were negatively associated with agriculture whereas Sora was positively associated with agriculture. American Bittern and Sora were negatively associated with amount of forested habitat on the landscape, whereas Virginia Rail exhibited a positive association. There were also significant differences in the magnitude of associations with the amount of wetlands in the landscape, with Virginia Rail having a significantly weaker association, although American Bittern, Least Bittern, Sora, and Virginia Rail all had significant positive associations (Fig. 3). Similarly, although all species had significant negative associations with the amount of urban landcover in the landscape, American Bittern had a significantly stronger negative association (Fig. 3).

Table 3. American Bittern (AMBI), Least Bittern (LEBI), Sora (SORA), Virginia Rail (VIRA), King Rail (KIRA) and Yellow Rail (YERA) associations with habitat variables based on meta-analysis of secretive marsh bird habitat associations in the Mississippi Flyway. “...” means there were < 3 studies representing a species-habitat association. “0” means 95% confidence intervals overlapped zero. “+” indicates a significant positive relationship and “-” indicates a significant negative relationship.

Habitat variable	AMBI	LEBI	SORA	VIRA	KIRA	YERA
Agriculture	-	-	+	0
Forest	-	0	-	+
Wetland	+	+	+	+
Urban	-	-	-	-
Open water	0	0	0	0
Wetland size	...	0	0	0
Interspersion	...	+
Water depth	...	0	0	0	...	0
Vegetation height	...	+	0	0
Non-woody emergent veg.	0	0	+	+	0	0
Robust emergent veg.	0	0	+	+
Typha	0	0	0	+
Non-robust emergent veg.	0	0	0	0	...	0
Emergent veg. - non specific	0	0	0	+
Woody wetland veg.	-	0	0	0	0	0
Shrubs	0	0	0
Woody veg. - non-specific	-	0	0	0	0	...

Because we found few studies outside of the breeding season, we could only test for seasonal differences in marsh bird associations with two habitat variables: water depth and non-robust emergent vegetation (Table 1). The mean effect size of water depth was not different between breeding and autumn migration, whereas the mean effect size of non-robust emergent vegetation was significantly positive during autumn migration (mean effect size = 0.12, CI = 0.055 - 0.184, $I^2 = 89.1$) but neutral during the breeding season (mean effect size = -0.039, CI = -0.081 - 0.002, $I^2 = 58.6$). We did not detect differences in habitat associations according to the scale of measurement, except for the variable representing the amount of all non-woody emergent vegetation,

which had a weak positive relationship to the measurement scale ($\rho = 0.0012$, p -value = 0.025) indicating marsh bird association strength increased as measurement scale increased.

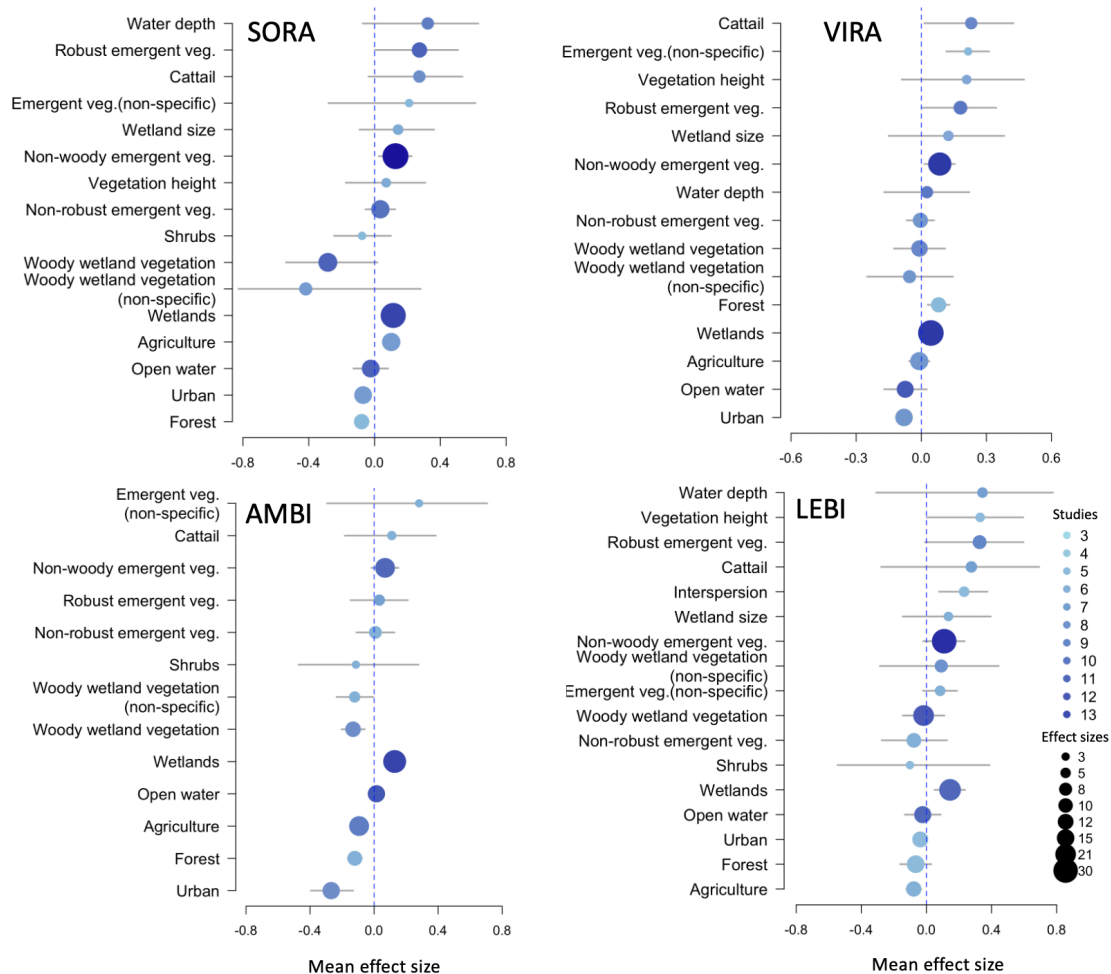
The Egger’s test indicated publication bias occurred in the sample of studies used to analyze 5 habitat variables: amount of forest in the landscape, amount of all non-woody emergent vegetation, amount of non-robust emergent vegetation, vegetation height, and interspersion. We recalculated the mean effect sizes after using the trim and fill method to account for publication bias and found that although the magnitude of the effects changed, the overall conclusions drawn remained consistent (i.e., confidence intervals still either did or did not overlap 0). The performance of the trim and fill method may be poor when between-study heterogeneity exists, as is the case for these 5 variables, or when publication bias is absent (Peters et al. 2007). We report the original mean estimates rather than trim-and-fill revised estimates.

DISCUSSION

Our study is the first quantitative synthesis of multiple studies on secretive marsh bird habitat associations and we provide a general characterization of suitable breeding habitat to aid in landscape-level multi-species conservation. Our study also highlights the immediate research needs for full annual cycle conservation of secretive marsh bird habitat: specifically, information during winter and migration periods of the annual cycle. We found breeding season habitat associations of secretive marsh birds were generally similar among the Great Lakes basin, Prairie, and Riparian regions of the Mississippi Flyway, although there were several important differences in habitat associations among species. Across studies throughout the Flyway, secretive marsh birds were positively associated with wetlands in the landscape and robust non-woody emergent vegetation but negatively associated with urban landcover and woody emergent vegetation.

Across studies, regions, species, and spatial scales we found secretive marsh birds were positively associated with the amount of wetland habitat in the landscape during the breeding season. Additionally, we found a positive association of secretive marsh birds with wetland size, although our inference is mostly limited to the Great Lakes region for this result. These findings align with previous work suggesting landscape composition and configuration are important considerations for waterbird conservation (Brown and Dinsmore 1986, Haig et al. 1998, Webb et al. 2010, Beatty et al. 2014, Quesnelle et al. 2015). For example, previous researchers have found isolated wetlands, even large ones, had lower species richness than wetlands that were part of a complex or near other wetlands (Brown and Dinsmore 1986, Smith and Chow-Fraser 2010) and landscape connectivity of wetlands fosters waterbird use (Guadagnin and Maltchik 2007). Although it has not been well-studied, wetland connectivity could be important for breeding secretive marsh birds because it enables within-season movements, allowing access to resources at multiple wetland sites within a complex that may not be present within a single wetland (Haig et al. 1998). Small wetlands may exclude area-dependent marsh bird species although a cluster of smaller wetlands may provide greater benefit to marsh bird populations than a single large wetland (Brown and Dinsmore 1986). Climate change may lead to further losses of wetland

Fig. 3. Mean effect sizes (Fisher's z) representing the associations of Sora (SORA), Virginia Rail (VIRA), American Bittern (AMBI), and Least Bittern (LEBI) with habitat variables based on meta-analysis of studies conducted in the Mississippi Flyway. Lines around the mean represent 95% confidence intervals. Sample size is indicated by shade (number of studies) and size (number of effect sizes) of points.



habitat as drought directly affects wetlands via drying and indirectly by intensifying other threats such as draining for agriculture (Erwin 2009). Restoration plans would benefit from incorporating potential wetland losses due to climate change.

We found negative associations with urban landcover across studies and species, although most studies were from the Great Lakes region. Similarly, distribution models developed for the breeding range of fourteen secretive marsh bird species indicated broad support for negative effects of urban development on species occupancy probability (Stevens and Conway 2020). While some wetland avian species have adapted to urban life (Martin et al. 2012, Murray et al. 2018), secretive marsh birds may be sensitive to the range of anthropogenic disturbances in urban landscapes (DeLuca et al. 2004, Schwarzbach et al. 2006, Hale et al. 2019). For instance, the natural dynamics of wetland hydrology are often disrupted in urban areas and subsequent changes in the plant community are likely to follow (Owen 1999, Wright 2005).

Our results suggest hydrological changes that diminish non-woody emergent vegetation, in addition to wetland isolation, would make urban wetlands inhospitable for secretive marsh birds. Avoidance of urban wetlands could also be due to changes in urban predator communities (Sorace and Gustin 2009), perceived predation risk (Hua et al. 2013, Malone et al. 2017), or increased competition from generalists (DeLuca et al. 2004). Furthermore, urban wetlands are exposed to surface run-off (Owen 1998) and pollution (Hale et al. 2019), which changes the nutrient composition, plant community (Owen 1999), and the invertebrate community on which secretive marsh birds prey and could expose them to direct lethal or sub-lethal risks (i.e., ingesting trash or toxins; Blus et al. 1977, De Luca-Abbott et al. 2001, Schwarzbach et al. 2006).

We found secretive marsh birds were positively associated with robust non-woody emergent vegetation, particularly *Typha*, and negatively associated with woody emergent vegetation. Robust,

perennial, non-woody emergent vegetation provides critical resources for secretive marsh birds during the breeding season, including protection from predators, nesting habitat (Lor and Malecki 2006), and food (Melvin and Gibbs 2020). Robust emergents like cattail provide ideal structure for secretive marsh birds to build above-water nesting platforms (Lor and Malecki 2006) and for above-water perching and foraging areas. Woody emergent vegetation excludes non-woody emergent vegetation and may not provide appropriate nesting substrate or cover for adults (Lor and Malecki 2006). Shrubs may provide habitat for predators (With 1996), including perching spots for avian predators like corvids (*Corvidae*). Thus, secretive marsh birds may avoid woody vegetation to avoid adult or nest predation by certain predators (With 1996, Winter et al. 2000, Ruth and Skagen 2017). We were unable to separate relationships of marsh birds with non-native, invasive wetland plant species from those with native wetland plant species. Non-native, invasives such as some types of cattail (e.g. *Typha angustifolia*) have expanded in range and may provide the robust structure that marsh birds prefer (Glisson et al. 2015).

Across studies, we found that secretive marsh birds were positively associated with water depth during breeding and autumn migration. The relationship is likely non-linear, with a negative trend at depths beyond those often found in emergent marsh habitat (> 50cm), although we were unable to explore those trends in our study. The positive association with water depth likely reflects food and nest site availability as well as predator deterrence (Lowther et al. 2020). Additionally, greater water depths may be indicative of favored vegetative cover; deeper, more permanent water may allow establishment of robust emergent vegetation (Kantrud and Stewart 1984), which is preferred by secretive marsh birds.

Habitat interspersions, which is often measured as the ratio of vegetative cover to open water (high interspersions = 50:50 ratio), has been suggested as an important factor in secretive marsh bird site use (Weller and Spatcher 1965, Weller and Fredrickson 1973). We found a small but significant positive effect of interspersions, although because many studies we reviewed did not measure interspersions, our inference is limited to only the Least Bittern in the Riparian region of the Mississippi Flyway. However, Lor and Malecki (2006) found Least Bittern favored lower cover to water ratios relative to American Bittern, Sora, and Virginia Rail, suggesting interspersions may not be important to species other than Least Bittern. Virginia Rail use wetlands with 100% cattail cover and thus no interspersions (Harms and Dinsmore 2013) as well as wetlands with hemi-marsh, or high interspersions, conditions (Conway 1994).

Full annual cycle habitat conservation of migratory birds depends on understanding species-habitat associations during the non-breeding season. Eighty-five percent of the studies we included in the meta-analysis were from the breeding season; thus, we were unable to quantitatively assess broad trends for many habitat associations during migration and none during winter. Least Bitterns winter south of our focal region, but other secretive marsh bird species' winter ranges include the southernmost portion of the Mississippi Flyway. There have been several non-breeding studies that were screened from our analysis that provide insight on localized habitat associations. Pickens and King (2014)

found water depth and vegetation density were important for over-wintering Sora and American Bittern, respectively, along the Gulf Coast. Morris et al. (2017) examined habitat associations of Yellow Rail wintering in Mississippi and Alabama and found the only important predictor in their analysis was a site management characteristic - fire return interval. A Missouri study on Sora and Virginia Rail migration found that spring migrant rails were most commonly associated with dead emergent stems of beggars-tick (*Bidens frondosa*) and broomsedge bluestem (*Andropogon virginicus*), or emerging sedges and rushes, while autumn migrants were associated with pure and mixed stands of composites and annual grasses (*Panicum*, *Echinochloa*; Sayre and Rundle 1984).

From the three fall migration studies included in our meta-analysis (Fournier et al. 2017, Fournier 2017, Clark-Schubert 2009), we concluded that annual, non-robust vegetation was positively associated with marsh birds during fall migration. However, the geographic and taxonomic scope of our conclusion is still limited; all three migration studies were conducted in Missouri and involved only two of our target species (Sora and Virginia Rail). Detecting secretive marsh birds is especially challenging during non-breeding seasons (Conway et al. 1993, Conway and Gibbs 2001), although new survey methods may address this issue and facilitate future non-breeding season studies (Fournier and Kremetz 2017). E-bird, a community science database, is a promising data source for mapping occurrence of rare species (Muller et al. 2018, Johnston et al. 2019) and could provide additional avenues for winter and migration habitat studies on secretive marsh birds.

Standardizing habitat measurement for marsh bird habitat studies may facilitate more collaboration and better comparison across studies (Connelly et al. 2003). The standardized marsh bird monitoring protocol (Conway 2011) was used in many of the studies we reviewed and likely influenced the increase in breeding season studies on secretive marsh birds within the last decade. Similar application of standardized marsh bird habitat measurements may have enabled our meta-analysis to investigate additional habitat characteristics, broadening the inference of this study. The large variation we found in many of the mean effect size estimates may be at least partially due to variation in metrics and methods across individual studies. With standardized habitat measurements, clearer patterns may emerge from future meta-analyses and provide additional guidance for wetland management practitioners.

CONCLUSIONS

Multi-species conservation efforts in the Mississippi Flyway, at least for American Bittern, Least Bittern, Virginia Rail, and Sora during the breeding season, may benefit by focusing on wetlands in high-density wetland landscapes or on re-connecting isolated wetlands to existing wetland complexes. Wetlands near developed or urban landcover may not be ideal targets for restoration unless conservationists find ways to make urban wetlands more hospitable to secretive marsh birds. Further research is needed to investigate the mechanisms affecting secretive marsh birds in urban wetlands and those that deter them from using wetlands near urban areas.

Based on habitat associations of marsh birds nesting in the Great Lakes region, Grand et al. (2020) developed a spatial

prioritization to identify specific wetlands as conservation priorities. Other regions, such as the U.S. Prairie Pothole Region, have taken species-specific approaches to spatial prioritization of waterbirds (Prairie Pothole Joint Venture 2017). Similar efforts would benefit other regions of the Flyway and beyond and help prevent further loss and degradation of wetlands that provide habitat for secretive marsh birds and for a broader suite of wetland-dependent taxa. At the wetland scale, habitat management practices that promote non-woody robust emergent vegetation and minimize woody emergent vegetation (i.e., burning, disking) are likely to meet habitat requirements for multiple marsh bird species. Finally, in order to advance conservation of secretive marsh birds, more research on secretive marsh bird distributions and their habitat associations during winter and migration would fill in existing information gaps during the full annual cycle.

Responses to this article can be read online at:
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Author Contributions:

EBW, DM, LK, AEM, and SWM conceived the study. All authors contributed to study design. KMM collected data, performed analyses, and wrote the first draft of the manuscript. All authors contributed substantial edits to the manuscript.

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1 APPENDIX

2 Appendix 1. Supplementary material on the variables examined, region-specific results, and
 3 studies included in the meta-analysis.

4

5 **Table A1.** Landscape habitat variables examined for associations with marsh birds in the
 6 Mississippi Flyway and the specific metrics used across studies that were grouped for meta-
 7 analyses.

Habitat variable	Study
Amount of agriculture	
Percent cover cultivated land	Hay and Manseau 2007
Percent cover agriculture	Valente et al. 2011, Martin 2012, Tozer 2016, Harms et al. 2017, Saunders et al. 2019, Tozer et al. 2020
Patch density of agriculture	Harms et al. 2017
Cropland area	Prairie Habitat Joint Venture 2014
Amount of wetlands	
Percent cover marsh	Hay and Manseau 2007, Smith-Cartwright and Chow-Fraser 2012, Tozer et al. 2020
Percent cover wet meadow	Hay and Manseau 2007, Hansen 2019
Percent cover emergent wetland	Scott 2010, Monfils and Corace 2018, Saunders et al. 2019
Percent cover wetland	Budd and Kremenz 2010, Kahler 2013, Glisson et al. 2015, Tozer 2016, Harms et al. 2017
Area of wetland habitat	Harms and Dinsmore 2013, Prairie Habitat Joint Venture 2014, Tozer 2016
Percent cover marsh/fen	Martin 2012
Wetland count	Prairie Habitat Joint Venture 2014
Wetland density	Mushanski 2015
Amount of forest	
Percent cover forest	Budd and Kremenz 2010, Smith-Cartwright and Chow-Fraser 2012, Kahler 2013, Glisson et al. 2015, Tozer et al. 2020
Percent cover mixed wood forest	Martin 2012
Amount of open water	
Percent cover open water	Winstead and King 2006, Scott 2010, Bolenbaugh et al. 2011, Harms and Dinsmore 2013, Glisson et al. 2015, Hill Chpt 2 2015, Tozer 2016, Monfils and Corace 2018
Percent cover water	Hay and Manseau 2007, Clark-Schubert 2009, Valente et al. 2011, Harms et al. 2017, Hansen 2019,
Area open water	Moore 2000
Percent aquatic bed/open water wetland	Kahler 2013
Largest patch index of water	Harms et al. 2017
Water area	Prairie Habitat Joint Venture 2014
Amount of urban	

Percent cover urban	Smith-Cartwright and Chow-Fraser 2012, Tozer 2016, Tozer et al. 2020
Percent cover development	Saunders et al. 2019
Percent cover developed (low-intensity)	Monfils and Corace 2018
Area of urban, road, built- up, or barrenland	Prairie Habitat Joint Venture 2014

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10 **Table A2.** Local scale habitat variables examined for associations with marsh birds in the
 11 Mississippi Flyway and the specific metrics used across studies that were grouped for meta-
 12 analyses.
 13

Habitat variable	Study
Wetland Size	
Wetland size	Chandler and Weiss 1995, Tozer et al. 2010, Smith-Cartwright and Chow-Fraser 2012, Harms and Dinsmore 2013, Mushanski 2015, Tozer 2016
Interspersion	
Interspersion of water and vegetation	Darrah and Krementz 2009, Bolenbaugh et al. 2011
Edge density of wetland	Harms et al. 2017
Edge density of water	Harms et al. 2017
Percent cover interspersion	Darrah and Krementz 2010
Robust emergent vegetation edge	Moore 2000
Edge index	Moore 2000
Open water edge	Moore 2000
Soil-water interface	Clark-Schubert 2009
Vegetation interface	Clark-Schubert 2009
Water Depth	
Water depth	Johnson and Dinsmore 1986, Reid 1989, Clark-Schubert 2009, Tozer et al. 2010, Darrah and Krementz 2011, Martin 2012, Austin and Buhl 2013, Harms and Dinsmore 2013, Hill Chpt 1 2015, Hill Chpt 2 2015, Fournier 2017, Monfils and Corace 2018, Hansen 2019
Water depth in cover	Moore 2000
Vegetation Height	
Vegetation height	Johnson and Dinsmore 1986, Clark-Schubert 2009, Martin 2012, Hill Chpt 1 2015, Hill Chpt 2 2015,
Maximum vegetation height	Martin 2012, Harms and Dinsmore 2013, Monfils and Corace 2018
Non-woody emergent vegetation	
Robust	
Area robust emergent cover	Moore 2000
Percent cover cattails and bulrush	Mushanski 2015
Percent cover persistent deep-water emergents	Monfils and Corace 2018,
Percent cover persistent shallow-water emergents	Monfils and Corace 2018,
Percent cover persistent vegetation	Hansen 2019
Percent cover persistent emergent vegetation	Blake-Bradshaw 2018

Percent cover robust emergent vegetation	Valente et al. 2011
Percent cover bulrush	
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<i>Typha</i>	
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Percent cover <i>Typha spp</i>	Chandler and Weiss 1995, Moore 2000, Kirk et al. 2001, Hay and Manseau 2007, Brittain and Thieme 2011, Martin 2012, Harms and Dinsmore 2013, Glisson et al. 2015, Hansen 2019
<i>Typha spp</i> stems	Brittain and Thieme 2011
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Non-robust	
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Percent cover non-robust short emergent vegetation < 0.75m	Valente et al. 2011
Percent cover non-robust tall emergent vegetation > 0.75m	Valente et al. 2011
Percent cover non-persistent vegetation (non-woody)	Hansen 2019
Percent cover annual moist soil vegetation	Fournier 2017
Percent cover non-persistent emergent vegetation	Blake-Bradshaw 2018
Percent cover perennial moist soil vegetation	Fournier 2017
Percent cover <i>Polygonum spp.</i>	Clark-Schubert 2009
Percent cover <i>Echinochloa spp.</i>	Clark-Schubert 2009
Percent cover <i>Eleocharis spp.</i>	Clark-Schubert 2009
Percent cover <i>Phalaris spp.</i>	Glisson et al. 2015
Percent cover <i>Carex spp.</i>	Monfils and Corace 2018
Percent cover grass/weeds	Valente et al. 2011
Percent cover sedge-bluejoint grass	Austin and Buhl 2013
Percent cover non-persistent shallow-water emergents	Monfils and Corace 2018
Percent cover sedge	Brittain and Theime 2011, Harms and Dinsmore 2013
Sedge stems	Brittain and Theime 2011
Herb stems	Brittain and Theime 2011
Percent cover grass	Kirk et al. 2001, Brittain and Theime 2011
Percent cover forbs	Martin 2012
Grass stems	Brittain and Theime 2011
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Emergent vegetation (non-specific)	
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Percent cover emergent herbaceous wetland	Scott 2010
Percent cover emergent herbaceous vegetation	Glisson et al. 2015, Tozer 2016
Percent cover other emergents	Winstead and King 2006
Percent cover short emergent (<1m)	Darrah and Krementz 2009

Percent cover tall emergent (>1m)	Darrah and Krementz 2009, Darrah and Krementz 2010
Percent cover emergent vegetation	Kirk et al. 2001, Hill Chpt 2 2015,
Proportion rank emergent vegetation (<i>Typha, Carex, Juncus, Schoenoplectus</i>)	Budd and Krementz 2010
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Woody emergent vegetation	
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Shrubs	
<hr/>	
Percent cover trees/shrubs	Kirk et al. 2001, Tozer 2016
Proportion cover scrub/shrub wetland	Monfils and Corace 2018
Percent cover trees <3m	Valente et al. 2011
Percent cover shrubs	Martin 2012
<hr/>	
Non-specific	
<hr/>	
Percent cover woody vegetation	Winstead and King 2006, Darrah and Krementz 2009, Darrah and Krementz 2010, Bolenbaugh et al. 2011, Brittain and Thieme 2011, Harms and Dinsmore 2013, Monfils and Corace 2018, Hansen 2019
Woody stems	Brittain and Thieme 2011
Woody wetland area	Bolenbaugh et al. 2011
Proportion forested wetland	Monfils and Corace 2018
Percent cover woody wetland	Bolenbaugh et al. 2012
Percent cover lowland woody	Austin and Buhl 2013
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15 **Table A3. Great Lakes region:** Summary effect sizes for the relationships of habitat to secretive marsh birds in the Great Lakes
 16 region. Asterisks indicate statistically significant mean effect sizes (95% confidence intervals did not overlap 0). Values are not
 17 reported when there were < 3 studies for a variable or species. Species codes are AMBI = American Bittern, LEBI = Least Bittern,
 18 SORA = Sora, VIRA = Virginia Rail. I^2 indicates the percent of variability in mean effect size estimates of a habitat variable that is
 19 due to heterogeneity rather than sampling error.

Habitat variable	Number of		Mean effect size	I^2	Mean effect size for species			
	Effect sizes	Studies			AMBI	LEBI	SORA	VIRA
Agriculture	36	2	-	-	-	-	-	-
Forest	47	4	-0.041* (-0.077; -0.004)	71.3%	-0.12* (-0.164; -0.076)	-0.053 (-0.152; 0.048)	-0.079* (-0.105; -0.052)	0.08* (0.03; 0.129)
Wetland	64	8	0.147* (0.112; 0.181)	78.0%	0.183* (0.13; 0.235)	0.205* (0.069; 0.334)	0.151* (0.108; 0.193)	0.059* (0.02; 0.098)
Urban	39	4	-0.162* (-0.225; -0.098)	86.7%	-0.409* (-0.546; -0.25)	-0.037* (-0.072; -0.003)	-0.078* (-0.092; -0.064)	-0.123* (-0.147; -0.1)
Open water	21	5	-0.02 (-0.102; 0.064)	88.3%	0.0080 (-0.080; 0.095)	-	-0.006 (-0.254; 0.243)	-0.132 (-0.347; 0.097)
Wetland size	12	4	0.194* (0.077; 0.306)	92.0%	-	0.265* (0.171; 0.355)	0.175 (-0.156; 0.47)	0.161 (-0.237; 0.513)
Interspersion	0	0	-	-	-	-	-	-
Water depth	13	5	0.333* (0.076; 0.549)	91.5%	-	-	0.446 (-0.376; 0.875)	0.104 (-0.302; 0.478)
Vegetation height	5	2	-	-	-	-	-	-
Non-woody emergent veg.	40	7	0.106 (-0.024; 0.233)	91.7%	0.102 (-0.085; 0.281)	0.273 (-0.188; 0.635)	0.139 (-0.064; 0.331)	0.111 (-0.03; 0.248)
Robust emergent veg.	18	5	0.1 (-0.179; 0.365)	93.5%	-	-	0.255 (-0.217; 0.63)	0.167 (-0.067; 0.383)
Typha	9	4	0.217* (0.128; 0.303)	40.8%	-	-	0.136 (-0.057; 0.32)	0.31* (0.132; 0.469)
Non-robust emergent veg.	13	5	0.016 (-0.134; 0.165)	83.6%	-	-	0.0001 (-0.273; 0.273)	-
Emergent veg. (non-specific)	9	3	0.18* (0.087; 0.27)	82.9%	0.281 (-0.294; 0.707)	-	-	0.216* (0.115; 0.312)
Wetland woody veg.	21	5	-0.208 (-0.466; 0.082)	95.4%	-0.12 (-0.29; 0.057)	0.274 (-0.949; 0.983)	-0.473 (-0.921; 0.515)	-0.146 (-0.409; 0.134)
Shrubs	13	3	-0.111* (-0.166; -0.054)	89.5%	-0.132 (-0.336; 0.084)	-	-0.079 (-0.174; 0.017)	-
Wetland woody veg. (non-specific)	11	3	-0.302 (-0.727; 0.29)	96.9%	-	-	-	-

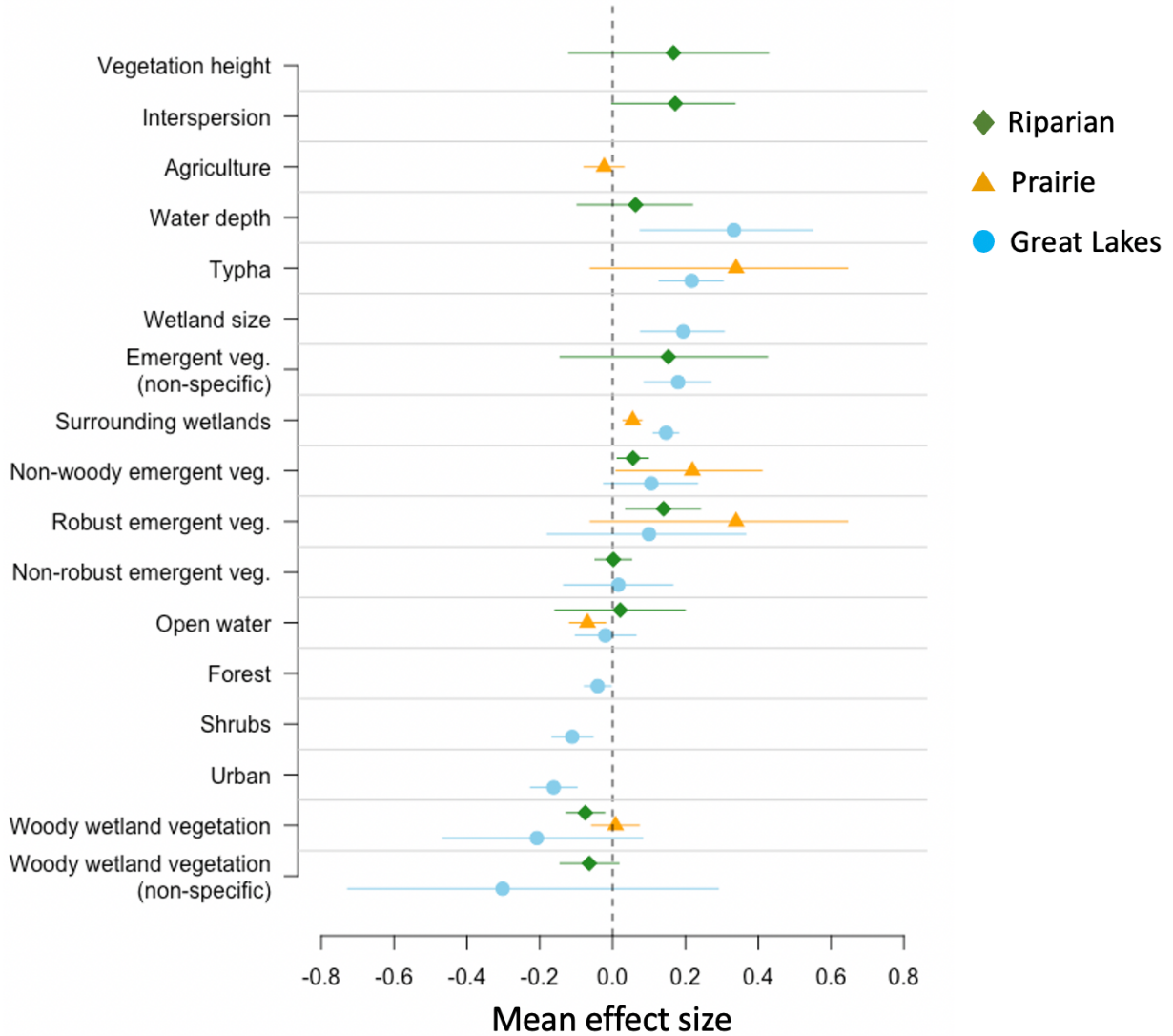
20 **Table A4. Prairie region.** Summary effect sizes for the relationships of habitat to secretive marsh birds in the Prairie region.
 21 Asterisks indicate statistically significant mean effect sizes (95% confidence intervals did not overlap 0). Values are not reported when
 22 there were < 3 studies for a variable and species. Species codes are AMBI = American Bittern, LEBI = Least Bittern, SORA = Sora,
 23 VIRA = Virginia Rail. I^2 indicates the percent of variability in mean effect size estimates of a habitat variable that is due to
 24 heterogeneity rather than sampling error.

Habitat variable	Number of		Mean effect size	I^2	Mean effect size for species			
	Effect sizes	Studies			AMBI	LEBI	SORA	VIRA
Agriculture (percent cover)	31	5	-0.023 (-0.078; 0.031)	89.7%	-0.17* (-0.225; -0.113)	-	0.122* (0.055; 0.188)	0.0004 (-0.093; 0.094)
Forest (percent cover)	1	1	-	-	-	-	-	-
Wetland (percent cover)	50	7	0.055* (0.029; 0.08)	61.9%	0.076* (0.013; 0.139)	-	0.077* (0.044; 0.110)	0.036 (-0.007; 0.079)
Urban (percent cover)	18	2	-	-	-	-	-	-
Open water (percent cover)	26	4	-0.069* (-0.118; -0.019)	93.6%	0.007 (-0.031; 0.044)	-	-	-0.063 (-0.196; 0.072)
Wetland size	3	2	-	-	-	-	-	-
Interspersion	5	1	-	-	-	-	-	-
Water depth	4	2	-	-	-	-	-	-
Vegetation height	4	2	-	-	-	-	-	-
Non-woody emergent veg. (percent cover)	17	4	0.219* (0.01; 0.41)	95.9%	-	-	-	-
Robust emergent veg.	9	4	0.339 (-0.061; 0.645)	97.5%	-	-	-	-
Typha	9	4	0.339 (-0.061; 0.645)	97.5%	-	-	-	-
Non-robust emergent veg.	4	2	-	-	-	-	-	-
Emergent veg. (non-specific)	0	0	-	-	-	-	-	-
Wetland woody veg. (percent cover)	6	3	0.008 (-0.057; 0.073)	0%	-	-	-	-
Shrubs	2	1	-	-	-	-	-	-
Wetland woody veg. (non-specific)	2	1	-	-	-	-	-	-

26 **Table A5. Riparian region.** Summary effect sizes for the relationships of habitat to secretive marsh birds in the Great Lakes region.
 27 Asterisks indicate statistically significant mean effect sizes (95% confidence intervals did not overlap 0). Values are not reported when
 28 there were < 3 studies for a variable or species. Species codes are AMBI = American Bittern, LEBI = Least Bittern, SORA = Sora,
 29 VIRA = Virginia Rail. I^2 indicates the percent of variability in mean effect size estimates of a habitat variable that is due to
 30 heterogeneity rather than sampling error.

Habitat variable	Number of		Mean effect size	I^2	Mean effect size for species			
	Effect sizes	Studies			AMBI	LEBI	SORA	VIRA
Agriculture (percent cover)	3	1	-	-	-	-	-	-
Forest (percent cover)	1	1	-	-	-	-	-	-
Wetland (percent cover)	2	2	-	-	-	-	-	-
Urban (percent cover)	0	0	-	-	-	-	-	-
Open water (percent cover)	8	6	0.021 (-0.158; 0.199)	66.6%	-	-0.031 (-0.259; 0.199)	-	-
Wetland size	0	0	-	-	-	-	-	-
Interspersion	7	4	0.172 (-0.002; 0.336)	75.5%	-	-	-	-
Water depth	9	5	0.063 (-0.097; 0.219)	96.7%	-	-	0.174 (-0.424; 0.666)	-
Vegetation height	7	3	0.167 (-0.12; 0.428)	92.0%	-	-	-	-
Non-woody emergent veg. (percent cover)	66	13	0.056* (0.013; 0.098)			0.036 (-0.086; 0.157)	0.084* (0.003; 0.165)	
Robust emergent veg.	14	4	0.14* (0.036; 0.241)	57.7%	-	0.243 (-0.111; 0.542)		
Typha	11	2	-	-	-	-	-	-
Non-robust emergent veg.	38	5	0.002 (-0.048; 0.052)	85.7%	-	-	0.058 (-0.045; 0.159)	-
Emergent veg. (non-specific)	5	4	0.153 (-0.144; 0.425)	63.9%	-	0.098 (-0.182; 0.363)	-	-
Wetland woody veg. (percent cover)	38	8	-0.075* (-0.127; -0.022)	57.5%	-	-0.05 (-0.104; 0.003)	-0.211* (-0.353; -0.061)	-
Shrubs	1	1	-	-	-	-	-	-
Wetland woody veg.	14	5	-0.064 (-0.144; 0.017)	49.9%	-	-0.085 (-0.218; 0.051)	-	-

32 **Figure A1.** Mean effect sizes (Fisher's z) representing the association of secretive marsh birds
 33 with 17 habitat variables based on meta-analysis of studies conducted within three regions
 34 (Riparian, Prairie, and Great Lakes) in the Mississippi Flyway. Lines around the mean represent
 35 95% confidence intervals.
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 38

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