

Final Report to the U.S. Environmental Protection Agency Enhancing Capacity of Wetland Programs Assistance ID NO. WD-83467501-0 June 2010 - October 2012

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PROJECT SUMMARY

With the support and partnership of the U.S. Environmental Protection Agency, Office of Wetlands, Oceans, and Watersheds Wetlands Division, the Chicago Horticultural Society (Chicago Botanic Garden) carried out the project, "Enhancing the Capacity of Wetland Programs to Assess and Manage Habitat for Secretive Marsh Bird Support" under Wetlands Program Development Grant WD-83467501-0.

The project was designed to assist state, tribal, and local wetland programs nationwide with meeting conservation targets for secretive marsh birds. Providing habitat for secretive marsh birds is a key wetland function. Unfortunately, challenges in monitoring marsh bird populations have resulted in this group being underrepresented in bird monitoring programs and in wetland programs' conservation planning. This is problematic, as several species are of conservation concern. The National Wetland Condition Assessment (NWCA) provides exceptional opportunities to gain information about wetland quality, but bird indicators have not been included in the NWCA to date. Furthermore, it is unknown how effective vegetation/habitat indicators of wetland condition (such as those measured in the NWCA) are as indicators of marsh bird support. This project integrated existing marsh bird data with intensive sampling of wetland habitats to provide technical assistance to wetland programs. Unique Level-3 marsh bird data were available through the first-ever statewide test of a planned nationwide monitoring program implemented in Wisconsin by partners of the proposed project. For a subset of Wisconsin's marsh bird monitoring sites, the project team supplemented Levels 1-2 site data and Level-3 marsh bird data with Level-3 vegetation/habitat data collected using NWCA protocols. The team assessed relationships between habitat variables and marsh bird diversity and abundance. Wetlands restored under USDA's Wetlands Reserve Program were included to assess effectiveness of restoration at meeting habitat needs of secretive marsh birds.

ACCOMPLISHMENTS

All project tasks were accomplished as specified in the work plan and results are detailed in *Appendix 1, Glisson Thesis*. The primary output of the project is the ongoing technical assistance provided to state, tribal, and local wetland programs on use of wetland monitoring and assessment data to advance secretive marsh bird conservation. Secondary outputs of the project include (1) communication to the scientific community about fundamental aspects of wetland and marsh bird ecology, (2) education of the public on how wetland conservation challenges and opportunities influence these highly valued animals, and (3) training of one master's student and several

undergraduates as wetland scientists. Activities included training and education, thesis and research presentations, and partnerships with wetland and wildlife managers as described below.

Scientific training and education

This project formed the basis for one graduate thesis, included as *Appendix 1*. Wesley Glisson received his master's degree in Plant Biology and Conservation from the joint Chicago Botanic Garden-Northwestern University graduate program for his work under this project.

Two undergraduate students gained wetland ecology experience by serving as paid field assistants for this project. These students, Tyr Wiesner-Hanks of Northwestern University and Evan Eifler of the University of Wisconsin-Madison, both intend to pursue graduate degrees in conservation/ecology-related fields.

Scientific products

Scientific products to date include Glisson's thesis and research presentations at the following science and management meetings:

Wisconsin Wetlands Association Conference. Lake Geneva WI, Feb 22–23, 2012.

Interagency Private Lands Meeting, Wisconsin Department of Natural Resources. Drummond WI, Jun 7, 2012.

Midwest Bird Conservation and Monitoring Workshop. Milwaukee WI, Jul 31-Aug 2, 2012.

Annual Meeting of the Ecological Society of America. Portland OR, Aug 5–10, 2012.

The first manuscript is at an advanced stage of preparation and will be submitted to either *Ecological Applications* or *Wetlands*. For preliminary results, see Appendix 1 (Glisson thesis) and Appendix 2 (Larkin et al. ESA presentation).

Partnerships with wetland and wildlife managers

Resource managers at the Wisconsin Department of Natural Resources (DNR) have been key partners throughout this project. In addition, the team has begun to work closely with partners from the U.S. Fish and Wildlife Service and other agencies through the Midwest Coordinated Bird Monitoring Partnership. Dr. Larkin has been sharing insights from this project as a member of the Midwest Marsh Bird Monitoring Working Group, through which he is advising the development of future large-scale monitoring and research efforts. Follow-on work to this project is being developed in collaboration with the Wisconsin DNR, Michigan Natural Features Inventory, Midwest Coordinated Bird Monitoring Partnership, and the Upper Mississippi River-Great Lakes Joint Venture. Larkin has also shared findings with the Integrated Waterbird Management and Monitoring Program.

Habitat requirements and restoration targets for secretive marsh birds in southeastern Wisconsin

A Thesis Submitted to the Graduate Faculty of Northwestern University

In partial fulfillment of the requirements for the degree of Master of Science in Plant Biology and Conservation

Northwestern University

by

Wesley James Glisson October 4, 2012

ABSTRACT

Due to concerns about population declines and habitat destruction, secretive marsh birds (SMBs) are of high conservation concern at state, regional, and national levels. Gaps in research on SMB habitat pose barriers to conservation and wetland restoration efforts. We conducted surveys for SMBs in 51 natural sites from 2009 – 2011 and 10 restored sites in 2011 in southeastern Wisconsin. We modeled occupancy of Virginia Rail, Sora, and American Bittern as a function of measured habitat variables at three levels of intensity: intensive (1-m² plots), rapid (100 m), and landscape (1 km) assessment. We compared ecologically relevant variables between natural and restored sites. Overall, SMB occupancy was strongly associated with cover and quality of wetland vegetation and intensive assessment variables were consistently selected over rapid and landscape variables. Regression tree analysis determined reed canarygrass dominance and mean C-value to be top negative and positive indicators of SMB occupancy, respectively, across all assessment levels. Rapid and landscape variables included in top ranking habitat models included: emergent herbaceous vegetation (Virginia Rail), Typha (Virginia Rail and Sora), open water (Sora), and agriculture within 1 km (Sora). Between natural and restored sites, rapid and landscape assessment variables were similar. Among intensive variables, reed canarygrass was significantly higher (P = 0.023) and mean C-value significantly lower (P = 0.023) <0.001) in restored sites, suggesting that in terms of top habitat variables, restored wetlands may not provide adequate SMB habitat. In order to support SMB habitat, wetland management and restoration in this region should focus on active management strategies to promote native species growth and reduce reed canarygrass dominance.

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INTRODUCTION

Secretive marsh birds (SMBs) are a group of marsh-dependent species that often exhibit a secretive or inconspicuous habit. Representative species include rails, bitterns, coots, moorhens, and grebes (Waterbird Conservation for the Americas 2006). Due to concerns about population stability and habitat destruction, SMBs are of high conservation concern at state, regional, and national levels (Conway 2009, Wires et al. 2010, WDNR 2012). Difficulty in monitoring has resulted in a general lack of knowledge about the status of SMB populations. Recent analysis shows range-wide and local declines for species such as American Bittern, Least Bittern, King Rail and Virginia Rail (Santisteban et al. 2011). Overall, most SMB populations appear to declining, while information remains inadequate to estimate trends for some species (Eddleman et al. 1988, Conway et al. 1994, Wires et al. 2010). Population declines coupled with drastic losses in emergent wetland area across the United States (Dahl 2006), present a significant challenge for conserving for these species. This is compounded by the fact that much is still unknown about habitat requirements for SMBs.

A national marsh bird monitoring program recently began to determine population status and trends for SMBs. As of 2011, a total of seven states have participated in the pilot phase, including Florida, Idaho, Kentucky, Michigan, New York, Ohio, and Wisconsin. Wisconsin was the first to begin monitoring efforts in 2008 and this program has provided unique state-wide data on SMB populations. This information has helped fill gaps in monitoring but does not provide a thorough understanding of the habitat requirements for SMBs. Gaps in research on SMB habitat pose critical barriers to effective conservation. Several research areas require special attention, including: (1) study of SMB habitat that includes comprehensive fine-scale vegetation characteristics along with local and landscape attributes (2) assessment of the effects

of invasive plant species on SMBs, (3) assessment of wetland restoration on SMB habitat suitability, and (4) study of SMB habitat in the state of Wisconsin.

Vegetation composition and structure are important components of SMB habitat suitability. Many studies have examined vegetation on a coarse scale (e.g., vegetation within 100 m), combining all emergent vegetation, or grouping plants into broad categories such as tall and short emergent vegetation, or robust and non-robust emergent vegetation (Fairbairn and Dinsmore 2001, Bolenbaugh et al. 2011, Valente et al. 2011). While SMB occupancy is not likely associated with the exact composition of plant species, it is likely influenced by other finescale vegetation characteristics. Several studies have included rigorous assessment of vegetation composition and structure to examine the influence of fine-scale vegetation attributes on SMBs. Fine-scale vegetation characteristics that have been found to influence SMB habitat use include availability of individual vegetation types/species (Manci and Rusch 1988, Flores and Eddleman 1995, Winstead and King 2006, Conway and Sulzman 2007), vegetation height (Zedler 1993, Lor and Malecki 2006), density of vegetation (Frederick et al. 1990, Lor and Malecki 2006), availability of standing senescent vegetation (Weller 1961, Stenzel 1982, Popper and Stern 2000), presence of woody vegetation or trees (Darrah and Krementz 2009, Pierluissi et al. 2010), and dominance of invasive plant species (Benoit and Askins 1999). However, while these studies have looked at a subset of fine-scale vegetation characteristics, few have attempted to incorporate an inclusive assessment of these variables. This has made it difficult to identify which of the these variables are most important to SMBs. Additionally, we have found no SMB study in the literature that has included fine-scale vegetation composition/structure with both local and landscape habitat characteristics to encompass three scales of habitat selection (e.g.,

first, second, and third-order selection; Johnson 1980). Thus, the relative importance of fine-scale vegetation compared to attributes at other scales is also largely unknown.

The threat of invasive species to SMBs has been raised as a topic of concern (Soulliere et al. 2007, Wires et al. 2010) but has rarely been looked at in depth. As habitat sinks, wetlands are particularly vulnerable to invasive species (Zedler and Kercher 2004). Anthropogenic drivers such as nutrient loading, vegetation removal, and altered hydrology give rise to opportunities for invasive species such as reed canarygrass (*Phalaris arundinacea*), and common reed (*Phragmites australis*; Galatowitsch et al. 1999). Species such as *Phragmites australis* can form dense monotypes that may negatively influence use of wetlands by SMBs (Benoit and Askins 1999, Gregory Shriver et al. 2004). Anthropogenic drivers may facilitate the change from one dominant native species to another, which can have negative consequences for SMBs (Winstead and King 2006). However, the effect of invasive species on SMB occupancy is largely unknown, especially for aggressive species such as reed canarygrass (*Phalaris arundinacea*).

While progress has been made in wetland restoration practices, challenges remain in recreating original vegetation and habitat structure (Zedler 2000, Zedler and Kercher 2005).

Restoration of original ecosystem components, including provision of habitat for wildlife, may simply be unrealistic (Zedler and Callaway 1999, Zedler and Kercher 2005). Restoration programs such as the Wetlands Reserve Program (WRP) were developed with the goals of providing wetland function and wildlife habitat. WRP is a voluntary program operated by the Natural Resources Conservation Service (NRCS) in which landowners sell a conservation easement or enter into a cost-share restoration agreement with the U.S. Department of Agriculture (USDA) to protect, restore, and enhance wetlands on their property (NRCS 2012).

The WRP has been shown to provide wetland habitat for waterbirds (Kaminski et al. 2006, King

et al. 2006), yet little information exists on whether WRP lands are meeting the specific habitat needs of SMBs. The WRP is a major driver of wetland restoration across the Midwest (Brinson and Eckles 2011). As of 2011, a total of 23,749 ha have been enrolled in the program in Wisconsin (NRCS 2012). Whether or not SMBs are utilizing potential habitat resources provided by WRP wetlands in Wisconsin, or across the Midwest, is unknown.

SMB habitat has been examined recently in Illinois (Darrah and Krementz 2009, Moore et al. 2009), Iowa (Harms 2011), and Missouri (Darrah and Krementz 2010). A recent study, Bolenbaugh et al. (2011), assessed SMB habitat associations and co-occurrence across the Midwest. This study included Illinois, Iowa, and Missouri, among other Midwest states, but did not include Wisconsin. Previous studies have shown that SMBs are using Wisconsin wetlands (Manci and Rusch 1988, Ribic 1999). However, there is a lack of current and rigorous studies regarding the condition of Wisconsin's wetlands to perform as SMB habitat. This is unfortunate, because despite an estimated loss of 1.8 million ha of original wetland cover across the state, Wisconsin boasts a relatively high percentage of remaining wetland (14.8%) compared to other Midwestern states: Illinois (3.5%), Iowa (1.2%), and Missouri (1.4%; Dahl 1990). Wetlands in the state of Wisconsin present a large and relatively understudied area of potential SMB habitat that could be a major refuge for SMBs across the Midwest.

These gaps in research present a challenge to SMB conservation and wetland restoration. Rigorous study is needed to advance our knowledge of SMB habitat requirements and increase the ability of wetland management and restoration to provide, conserve, and restore important SMB habitat. The objectives of this study were to: (1) examine the effects of wetland vegetation and habitat characteristics on SMB occupancy, (2) identify key vegetation and habitat variables

across multiple levels of wetland assessment, and (3) assess whether typical wetland-restoration efforts in the region are providing adequate SMB habitat.

METHODS

Study area and site selection

The study area consisted of wetlands within the Southeast Glacial Plains ecological landscape in southeastern Wisconsin (Fig. 1). This region is heavily developed and highly populated. The dominant land cover is agricultural cropland (58%), however the Southeast Glacial Plains contains extensive wetlands (12% of land cover) including marshes, fens, sedge meadows, wet prairies, tamarack swamps and floodplain forests (WDNR 2005). Many wetlands have been affected by hydrologic modifications from agriculture including ditching, diking, and tilling. Grazing, invasive plant infestation, and significant sediment and nutrient runoff from cropland also affect wetlands in this region (WDNR 2005).

SMB survey locations were initially determined using a Generalized Random Tessellation Stratified (GRTS) design (Stevens and Olsen 2004) to acquire randomly selected, spatially balanced, and logistically clustered survey sites throughout Wisconsin. Using this design, primary sampling units (PSUs) were first selected from a grid of 40-km² hexagons covering the state. Then, within each PSU, individual survey points were randomly selected in defined marshbird habitat determined from digital layers of the Wisconsin Wetland Inventory (WWI). Each PSU contained 5 – 8 survey points. Survey points were separated by at least 375 m to avoid sampling the same individuals at multiple locations (Conway 2009) and included a mix of within-wetland and roadside survey locations. We selected 51 survey points within 7 PSUs as our "natural" sites (never converted to agriculture, or not farmed within at least the last 40 years). All natural sites were found within, or on private land adjacent to, the following Wisconsin

Department of Natural Resources (WDNR) State Wildlife Areas: Anthony Branch, Eldorado Marsh, Honey Creek, Mud Lake, Peter Helland, Rat River, and White River Marsh. Sites were located in permanent and semi-permanent palustrine wetlands classified by the Wisconsin Wetlands Inventory (WWI) as emergent-wet meadow, or emergent-wet meadow interspersed with shrub-scrub. Common emergent-wet meadow vegetation in this region includes: cattail (*Typha* spp.), sedges (*Carex* spp.), and grasses (Poaceae). Common scrub-shrub vegetation includes willows (*Salix* spp.), alders (*Alnus* spp.), and green ash (*Fraxinus pennsylvanica*; WDNR 1992).

Restored sites were located in 10 WRP easements within the Southeast Glacial Plains that were geographically grouped with natural PSUs. We selected restored sites by randomly placing a single SMB survey point in each WRP easement using ArcMAP 10.0 (ESRI 2010). Five pairs of restored sites were spatially grouped with five natural PSUs. The WRP easements in this study were passively restored by reestablishing historic hydrology and were completed between 1993 and 1999. No other habitat modification or supplemental plantings were performed. While a water control structure is present on one WRP easement, it was not being actively manipulated. No active hydrologic management was taking place at any of the restored sites in this study. Secretive marsh bird surveys

Call-broadcast surveys for SMBs were performed at natural and restored sites following the Standardized North American Marsh Bird Monitoring Protocol (Conway 2009) as modified by Brady (2011). A combination of trained volunteers, field technicians and WDNR biologists performed surveys. Natural sites were surveyed for SMBs 2 – 3 times a year from 2009 – 2011 between 3 May and 17 June. Due to logistical constraints, natural sites belonging to the Mud Lake PSU were not surveyed in 2011, and a single natural site from Honey Creek PSU was not

surveyed in 2010. Restored sites were surveyed 2 – 3 times in 2011 between 13 May and 2 June. Survey dates corresponded to peak breeding and vocalization periods in the southern half of Wisconsin (Brady 2011). Surveyors attempted to conduct each marshbird survey within a 10-day window (survey period) while maintaining two weeks between surveys. Survey periods were: May 1-10, May 17-27, and June 3-13. A mix of morning and evening surveys were performed; morning surveys were conducted from 30 minutes prior, to 3 hours after sunrise while evening surveys were conducted from 3 hours prior, to 30 minutes after sunset. Each marsh bird survey included a five-minute passive listening period followed by six successive one-minute broadcast periods. Broadcast periods consisted of 30 seconds of calls followed by 30 seconds of silence for each of six species in the following sequence: Least Bittern, Yellow Rail, Sora, Virginia Rail, King Rail, and American Bittern. Standardized pre-recorded calls for each species were broadcast with an MP3 player through a portable folding amplified speaker system at maximum volume (Brady and Paulios 2010). Distance to each marsh bird from the survey point was aurally and visually estimated by the surveyor and all SMBs were counted regardless of distance. Surveys were aborted if heavy rain, fog, or high wind speeds (>20 km/hr) were present.

Habitat sampling

Habitat sampling was performed on three levels of intensity to encompass multiple scales of SMB habitat and to elucidate which level of sampling is most important for SMBs. The three levels correspond with the EPA's 3-Level technical approach in wetland assessment (USEPA 2006) and included: intensive site assessment, rapid site assessment, and landscape assessment.

From each PSU we chose 2-4 survey sites to perform intensive assessment. These sites were selected to represent the range of habitat/vegetation types available at each PSU. We

implemented intensive site assessment at a total of 20 natural sites and all 10 restored sites 13 June – 5 Aug 2011. Intensive site assessment was performed using a modified version of the EPA's National Wetland Condition Assessment (NWCA) protocol supplemented with additional sampling plots (USEPA 2011). For a full description and diagram of this sampling design and the modifications included in this study, see Appendix A. Supplemental plots were added to ensure that vegetation composition and structure were adequately sampled, as the original NWCA protocol was not designed for the specific goals of this study. For SMB survey points that abutted inhospitable habitat (e.g., upland forest, highway, agriculture field), we moved the NWCA sampling area into the interior of the corresponding wetland at a minimal distance. At each 1-m² plot, we identified each vascular plant to species and estimated cover using arcsine square root transformed cover classes (Muir and McCune 1987). Average height of each species was estimated in one of six height classes: 0-0.5m, >0.5-2m, >2m-5m, >5-15m, >15-30m, >30m. Habitat variables assessed at each 1-m² plot included cover of: water, water covered with floating aquatic vegetation, total water (water plus water covered with floating aquatic vegetation), litter, and standing-dead vegetation. Water depth or litter depth was measured in the center of each 1-m² plot. Horizontal vegetation cover was visually estimated at 0.2 m, 0.5 m, and 0.7 m from the water/ground (Lor and Malecki 2006). For each site, we calculated importance values for all individual species and for species/genera that we suspected might influence SMB occupancy: Carex spp., Typha spp., Phalaris arundinacea (reed canarygrass), and woody species (e.g., Salix spp.). Importance value (hereafter referred to as "dominance") was calculated as the average of relative frequency and relative abundance for each species/genera (McCune and Grace 2002). To assess vegetation quality at each site, we calculated Shannon-Wiener diversity index (expressed as both H' and $e^{H'}$), mean coefficient of conservatism (mean C-value),

abundance-weighted mean C-value, and floristic quality index (FQI). We calculated a water index for each site as the sum of relative water cover and relative water depth across all sites that received intensive sampling (N = 30). A litter index was calculated in the same fashion. All other intensive habitat measurements were averaged across all $1-m^2$ plots at each site.

Rapid site assessment was performed for all study sites (N = 61) as specified in Conway (Conway 2009) and modified by Brady (2011). Rapid site assessment was performed at natural sites 4 May – 11 June 2011 and at restored sites 13 June – 5 Aug 2011. We visually estimated habitat within a 100-m radius circle while standing at the SMB survey point. Rapid site assessment variables included cover of: wetland, emergent herbaceous vegetation, trees, shrubs, open water, and cover of the two most dominant wetland herbaceous plant types: reed canarygrass, *Typha*, and/or grasses/sedges.

For landscape assessment, we first created a 1-km buffer around the center of each survey site using ArcMap 10.0 (ESRI 2010). Then, using 2010 digital orthophotos from the U.S. Department of Agriculture's National Agriculture Imagery Program (NAIP), along with wetland layer data from the WWI and the U.S. Fish and Wildlife Service's (USFWS) National Wetland Inventory (NWI), we classified land cover into one of nine types: agriculture, agriculture and grassland, grassland/pasture, forest, open water, residential, emergent wetland, forested wetland, and shrub wetland. Polygons were drawn for each land cover type and we calculated proportion of each cover type in the 1-km buffer. Land cover types were compiled to calculate a Land Disturbance Index (Brown and Vivas 2005) value for each survey site. Land Disturbance Index (LDI) is a land use based index that quantifies potential human disturbance at a wetland based on the intensity of human use in the landscape (Brown and Vivas 2005). Each land use type was given a LDI coefficient based on the intensity of land use and this was multiplied by the

percentage of 1-km buffer covered by that land use type. These values were then summed into a single LDI score for each site. For a measurement of total wetland cover we summed across all wetland types. Additionally to get a measure of total natural land cover, we summed across all natural land cover types: water, forest, and all wetland types. A full list of all variables used in subsequent analyses can be found in Appendix B.

Secretive marsh bird occupancy analysis

For occupancy modeling, we restricted all species detections in a given year to those occurring within 150 m of the survey point. If, however, a species was ever detected within 150 m of the survey point, we also included all detections for that species within 300 m across all years. This approach ensures that species were detected within the habitat that we measured, but relaxes the assumption that a species detected within 150 m must always be within 150 m (Valente et al. 2011). We performed subsequent analyses with each SMB species.

Using the program Presence (version 4.3, Hines 2006), we modeled species occupancy (Ψ) as a function of rapid and landscape assessment variables while simultaneously accounting for detection probability (p; MacKenzie 2002). For this analysis we used all natural sites for which rapid and landscape assessment data were collected (N = 51). Occupancy modeling in Presence was a multi-step process. We surveyed SMBs over multiple years so the first step was to understand the population dynamics (site fidelity) of each species. We modeled population dynamics and p simultaneously for each species while holding occupancy constant (MacKenzie et al. 2003). We constructed models to represent: random yearly changes in occupancy (low site fidelity), non-random yearly changes in occupancy (high site fidelity), or no yearly changes in occupancy (perfect site fidelity; MacKenzie et al. 2006: 205-208). The latter scenario reduces the multi-year model to a single-year model (MacKenzie et al. 2006). For the random and non-

random changes in occupancy models, we used parameterizations that directly estimated yearly occupancy (Mackenzie et al. 2006:199). These parameterizations enabled us to model year-specific occupancy as a function of habitat covariates. To account for p, for each type of population dynamics model, we included all combinations of the survey-specific covariates: survey period and year. We compared models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). The single top ranking population dynamics p model for each species was selected and incorporated into all subsequent habitat occupancy models.

Before proceeding to model species occupancy, we tested for correlation among measured habitat variables using Pearson's correlation coefficient in R version 2.15.1 (R Core Team 2012). When two or more variables were highly correlated ($r \ge 0.80$) we kept the variable that made the most biological sense. We examined Q-Q plots for each retained variable to determine normality. When necessary, an appropriate transformation was applied to improve normality. We selected the rapid assessment variables: emergent herbaceous vegetation, Typha, reed canarygrass, and open water; and landscape variables: total wetland, agriculture, and forest, to include in our occupancy models. We used a hierarchical model selection process following Johnson (1980), in which birds first select habitat on the landscape scale and then select sitescale characteristics. For each species, we created two separate sets of candidate models to test the effects of rapid site assessment variables and landscape variables. The top ranking landscape model was included in all rapid assessment models for each species. To understand the relative importance of each variable, we summed AIC weights (w) for all models containing that variable to get a cumulative weight for each variable. To determine the direction and magnitude of effect size for each habitat variable, we calculated model-averaged parameter estimates and

unconditional variance estimates across all models in the set that contained the given parameter using Eq. 4.1 and Eq. 4.9 in Burnham and Anderson (2002:150,162).

For no yearly change (single-season) occupancy models, we examined the fit of the global model by dividing the models' Pearson X^2 test statistic to an average X^2 test statistic from 10,000 bootstrap samples to calculate an overdispersion parameter (\hat{c} ; MacKenzie and Bailey 2004). For multi-season models, we determined \hat{c} by splitting the data into single years and calculating the global model Pearson X^2 test statistic and the bootstrap X^2 test statistic for each year. We then summed these values across all years, and divided the summed Pearson X^2 test statistic by the summed bootstrap X^2 test statistic (Jim Hines, USGS, personal communication). If $\hat{c} > 1$, a quasi-likelihood adjustment to AIC (QAIC) was used for model ranking and model variance was multiplied by a factor of \hat{c} .

To assess the effect of all measured habitat variables across all levels of assessment we created regression trees using the package rpart in R version 2.15.1 (R Development Core Team 2012, Therneau and Atkinson 2012). Regression trees use recursive partitioning to split a dataset into subsets based on given explanatory variables that maximally distinguish differences in the response variable (Crawley 2007). Regression trees are a robust tool for ecological data as they can handle many explanatory variables, do not rely on parametric assumptions, and are able to capture relationships that are difficult to resolve with conventional linear models (Urban 2002). For regression tree analyses, we used the proportion of years occupied ("occupancy" followed the 150 m guidelines outlined above) as the response variable to control for differences in the number of years surveyed.). We constructed trees using natural sites that included all variables across all three sampling levels (N = 20) and trees that included rapid and landscape variables only (N = 51). Trees were pruned to minimize error using a cost-complexity parameter (cp;

Urban 2002). We tested the significance of the variables determined from our regression trees using generalized linear models (GLMs) with a binomial error distribution. If overdispersion was detected (residual scaled deviance > residual degrees of freedom) we used a quasibinomial distribution. GLM analysis was performed in R version 2.15.1 (R Development Core Team 2012).

Comparison of natural and restored sites

To test for differences in ecologically relevant factors between natural and restored sites, we compared the mean values of variables that were of high importance in Presence and regression tree models between site types using a Wilcoxon rank-sum test. The Wilcoxon rank-sum test is a non-parametric and more conservative alternative to a t-test, used when errors are non-normal (Crawley 2007). All comparative analyses were performed in R version 2.15.1 (R Development Core Team 2012). Survey effort and SMB detections were much lower at restored sites compared to natural sites in 2011, so we did not formally compare occupancy between site types. Instead, we assessed relative occupancy of individual species between natural and restored sites in 2011 (natural N = 46, restored N = 10).

RESULTS

Occupancy analysis incorporating detection probability

Due to low detections, we only considered Virginia Rail and Sora occupancy for analysis in Presence. The top ranking population dynamics / p models included survey period, but not year, for all species/group considered (Table 1). Population dynamics for Virginia Rail was best represented by a perfect site fidelity model (single year parameterization) while Sora was best represented by a low site fidelity model (multi-year parameterization; Table 1). Complete population dynamics / p modeling results can be found in Appendix C.

Agriculture within 1 km, emergent herbaceous vegetation, Typha, and open water were included in the top ranking models across both species (Table 1). Agriculture was the single landscape variable selected for Sora, while none of the landscape variables were ranked in top models for Virginia Rail (Table 1, see Appendix C for full landscape models for each species). For Virginia Rail, emergent herbaceous vegetation was the most important covariate affecting occupancy (w = 0.71) and also had the greatest effect size (positive effect; Table 2, Fig. 2). Typha and reed canarygrass were the next most important (w = 0.41 and w = 0.30 respectively), while reed canarygrass had a greater effect size (negative effect) than Typha (positive effect; Table 2, Fig. 2). The covariates with the greatest relative importance and effect sizes for Sora occupancy included: agriculture (w = >0.99, negative effect), Typha (w = >0.99, positive effect) and open water (w = 0.60, positive effect; Table 2, Fig. 2).

Occupancy analysis using regression trees

Reed canarygrass dominance and mean C-value, both intensive assessment variables, were selected over rapid and landscape assessment variables in regression tree models involving all three levels of sampling intensity (N = 20; Fig. 3). We had sufficient detections to include Virginia Rail, Sora, and American Bittern in regression tree analyses. Reed canarygrass dominance was the most important variable for Virginia Rail and American Bittern occupancy (Fig. 3). Both Virginia Rail and American Bittern had a significant negative relationship with reed canarygrass dominance (Table 3, Fig. 4). Mean C-value was the most important variable for Sora occupancy (Fig. 3). Sora had a positive, but not significant relationship with mean C-value (Table 3, Fig. 5).

Two rapid assessment variables – emergent herbaceous vegetation and *Typha*, and no landscape variables were selected in regression trees which included rapid and landscape

assessment variables (N = 51; Fig. 6). Regression trees for Virginia Rail and American Bittern specified emergent herbaceous vegetation as the most important variable influencing occupancy (Fig. 6). Both species had a significant positive relationship with emergent herbaceous vegetation (Table 3). Typha was the most important variable for Sora occupancy and Sora had a significant positive relationship with Typha (Table 3).

Comparison of natural and restored sites

Restored sites had significantly higher reed canarygrass dominance (natural: 0.010 +/-0.031, restored: 0.252 +/-0.057, 1 SE; W = 152, P = 0.023; Fig. 7) and significantly lower mean C-values (natural: 4.86 +/-0.18, restored: 4.01 +/-0.14, 1 SE; W = 172, P = <0.001; Fig. 8) than natural sites. Natural and restored sites did not differ in *Typha* (W = 219.5, P = 0.49) or emergent herbaceous vegetation (W = 236.5, P = 0.72). Open water and agriculture within 1 km did not appear in regression tree models, but had large effect sizes and cumulative AIC weights in Presence models (Tables 1 and 2) so they were also compared between natural and restored sites. Restored sites had significantly more open water than natural sites (natural: 0.044 +/-0.016, restored: 0.057 +/-0.018, 1 SE; W = 166, P = 0.044). Agriculture within 1km of restored and natural sites was not significantly different between site types (W = 178, P = 0.14). In 2011, occupancy was 15%, 10%, and 8% greater at natural sites (N = 46) than restored sites (N = 10) for Sora (natural: 35%, restored: 20%), American Bittern (natural: 20%, restored: 10%), and Virginia Rail (natural: 28%, restored: 20%) respectively.

DISCUSSION

Habitat variables influencing SMB occupancy

Overall, SMB occupancy was strongly associated with cover and quality of wetland vegetation, including positive relationships with mean C-value, emergent herbaceous vegetation,

and *Typha*, and negative relationships with reed canarygrass cover and dominance (Table 2, Figs. 3 and 6). A positive association with emergent herbaceous vegetation is not surprising and is well known for Virginia Rail, American Bittern, Sora, and SMBs in general (Eddleman et al. 1988, Conway 1995, Melvin and Gibbs 1996, Fairbairn and Dinsmore 2001, Lowther et al. 2009, Poole et al. 2009). Preference for *Typha* spp. and other robust vegetation is also well documented for Sora (Manci and Rusch 1988, Ribic 1999, Lor and Malecki 2006). Much less is known about the effect of reed canarygrass on SMBs. Reed canarygrass is rarely included as a factor in SMB studies, or more often lumped with other "weak stemmed", "tall", or all "emergent herbaceous vegetation". A single study, Harms (2011), found a negative effect of reed canarygrass on Virginia Rail occupancy but the author explains that there was little to no actual effect due to large standard error. We found that both Virginia Rail and American Bittern had negative relationships with reed canarygrass with a particularly low threshold for American Bittern (Fig. 4).

There are several potential explanations for the negative relationship between reed canarygrass dominance and occupancy of Virginia Rail and American Bittern. Reed canarygrass invasion is associated with decreased native species richness, diversity, and biomass (Barnes 1999, Green and Galatowitsch 2002, Werner and Zedler 2002, Kercher and Zedler 2004, Spyreas et al. 2010). It grows aggressively and can quickly become a monotype in temperate wetlands (Galatowitsch et al. 1999). This creates a homogenous environment that may not provide adequate foraging and nesting habitat. Reduction in plant richness and diversity may reduce quantity and quality of available seeds, which are consumed by Virginia Rail (Conway 1995). Reed canarygrass invasion has also been shown to reduce richness and abundance of arthropods (Spyreas et al. 2010), which are consumed by both species (Conway 1995, Lowther et al. 2009).

The thick structure, high stem density, and abundant litter produced by reed canarygrass may impede movement of Virginia Rail (Johnson and Dinsmore 1986, Conway 1995). Thick vegetation and horizontal cover is important for both Virginia Rail and American Bittern (Lor and Malecki 2006), however, reed canarygrass may produce vegetation cover that is too thick to navigate. American Bittern requires tall, robust plants (Manci and Rusch 1988, Bolenbaugh et al. 2011). Culms of reed canarygrass are not considered robust and in the field they were often seen lying nearly flat, weighed down by morning dew (W. Glisson personal observation). Presence of robust vegetation may not be as strong of an influence for Virginia Rail; they have shown preference for both weak-stemmed vegetation and cattail (Fairbairn and Dinsmore 2001, Harms 2011). Thus, other factors influenced by reed canarygrass, including reduced diversity of vegetation types, may potentially play a larger role for Virginia Rail occupancy (Johnson and Dinsmore 1986). Our study incorporated several vegetation and habitat structure characteristics that could be influenced by reed canarygrass, including litter, litter depth, and horizontal cover. If these factors play a role in influencing SMB occupancy, their effects may be represented collectively through our measure of reed canarygrass dominance.

Reed canarygrass dominance in wetlands is also indicative of a suite of anthropogenic influences, including runoff, sedimentation, excess nutrients, flooding, and fluctuating water levels (Galatowitsch et al. 1999, Kercher and Zedler 2004, Zedler and Kercher 2004). Rails are sensitive to fluctuating water levels and flooding in different seasons (Rundle and Fredrickson 1981, Sayre and Rundle 1984). Contaminants from runoff can negatively affect reproductive success of rails and bitterns (Eddleman et al. 1988, Connell et al. 2003, Schwarzbach et al. 2006). Little is known about the specific effects on American Bittern and Virginia Rail, but it is generally believed that contaminants may have a significant impact on these species (Conway

1995, Lowther et al. 2009). These anthropogenic effects are difficult to measure directly and were not incorporated into our study. However, reed canarygrass dominance may be a proxy for their cumulative effects on Virginia Rail and American Bittern.

Occupancy was greater in sites with higher mean C-value for Sora according to regression tree analysis, although the trend was not significant (Table 3, Figs. 3 and 5). In addition to being a measure of vegetation quality, mean C-value is negatively correlated with anthropogenic disturbance and wetland degradation (Cohen et al. 2004, Bourdaghs et al. 2006). Another standard measure of vegetation quality at a site, FQI, was included in our regression tree analysis. While FQI is a strong indicator of local and landscape disturbance factors among similar wetland plant communities (Lopez and Fennessy 2002, Bourdaghs et al. 2006), mean Cvalue is potentially a more effective assessment measure (Rooney and Rogers 2002, Cohen et al. 2004). The advantages of mean C-value are that it is computationally less intensive than FQI and because it is a single variable as opposed to the product of two variables, it provides more straightforward results. In terms of mean C-value versus abundance weighted mean C-value, which we also examined, the response of these two variables to wetland disturbance and their ability to discriminate between sites is very similar (Bourdaghs et al. 2006). By not weighting by abundance, mean C-value is more sensitive to less abundant and less frequent species that may be representative of higher quality and less disturbed sites. These species would be given less weight with abundance weighted mean C-value and this could be the reason that mean C-value was selected as the more sensitive indicator of Sora occupancy. A single study involving mean C-value and the species in this study, O'Neal et al. (2008), found that mean C-value was not a strong predictor of habitat quality for waterbirds in restored wetlands in Illinois. Yet, these results likely do not reflect habitat preferences of SMBs, as this study was heavily influenced by

inclusion of waterfowl and shorebirds. While no other evidence relating Sora or SMBs to mean C-value was found in the literature, this measure could represent an indicator that integrates a range of anthropogenic stressors for SMBs.

Agriculture in the landscape and open water at the rapid assessment scale were two variables that had large effects on Sora occupancy in Presence models (Table 2). Agriculture has been found to negatively influence American Bittern occupancy (Hay and Manseau 2004). Valente et al. (2011) found a positive relationship with Least Bittern occupancy and agriculture in Louisiana, however, this result may have been due to landscape changes (e.g. flooding) between sampling periods. More often, wetland area/size, isolation, and distribution, are the focus of landscape analyses. SMBs vary in their response to wetland size; species such as American Bittern and Least Bittern tend to occupy larger wetlands, while Virginia Rail and Sora appear to be area-independent (Brown and Dinsmore 1986, Craig 2008, Tozer et al. 2010). For our study sites, agriculture and total wetland area within 1 km were correlated (r = 0.77), though not highly enough for either one to be excluded from analysis. Agriculture was selected above total wetland area in Presence models and subsequently the only landscape variable included in full habitat models for any species (Table 1, Appendix C). Thus, species like Sora, which may not be selecting wetlands of a specific size, appear to be avoiding wetlands surrounded by greater agriculture in the landscape.

Open water at the rapid scale was among the most important variables for Sora occupancy (Tables 1 and 2). Sora nest primarily shoreward, away from open water, and occupancy is largely unaffected by cover of open water at the local wetland (rapid assessment) scale (Lor and Malecki 2006, Bolenbaugh et al. 2011). The wetlands in this study did not have large expanses of open water. At the rapid assessment scale, open water was typically found in

pockets among emergent vegetation. In fact, open water only appeared in top ranking models when included as an additive effect with some measure of vegetation (e.g., *Typha*; Table 1). This distribution of vegetation and open water may be better described as a measure of the mix of vegetation and water (i.e., interspersion). Interspersion has been shown to positively influence abundance of Sora (Rehm and Baldassarre 2007). Other SMBs including Virginia Rail, American Bittern, and Least Bittern have also shown preference for high interspersion as it likely provides quality feeding habitat (Rehm and Baldassarre 2007, Moore et al. 2009).

Across all assessment levels (N = 20), intensive assessment variables were consistently selected over rapid and landscape variables (Table 3, Fig. 3). When analyzing across rapid and landscape assessment, rapid assessment variables were selected for all species (Table 3, Fig. 6). Several studies have shown that landscape characteristics do not play a substantial role in habitat selection for SMBs (Rehm and Baldassarre 2007, Craig 2008, Valente et al. 2011). In extreme cases, particular nest site characteristics may be crucial for nesting success such as with the Light-footed Clapper Rail in salt marshes of southern California (Zedler 1993). This type of situation is likely not the case with the species we examined. For more generalist species like Virginia and Sora, selection of fine-tuned structure, individual plant species, or distinct "high quality" communities is not likely a strong driver of occupancy. Instead, an index like mean Cvalue captures effects on multiple levels and likely summarizes both measured variables, along with variables we did not account for, across intensive, rapid, and landscape assessment. Reed canarygrass dominance also serves this function, as its spread is dependent on a number of disturbance factors found at local and landscape scales (Kercher and Zedler 2004). These two variables should not necessarily be considered the definitive determinants of occupancy, but rather, a proxy for a multitude of effects on SMB occupancy. An analysis of relationships

between these two variables and other variables we examined is beyond the scope of this study, but it is important to note that reed canarygrass dominance and mean C-value were not correlated (r = 0.21). Thus while reed canarygrass and mean C-value often represent similar disturbance factors, they may represent distinct effects on occupancy of different species (e.g., Virginia Rail and American Bittern as opposed to Sora).

Comparison of natural and restored sites

At the intensive assessment scale, wetland sites restored through the WRP did not appear adequate to support the SMB species we examined. Reed canarygrass dominance was significantly greater in restored sites while mean C-value was significantly lower. Reed canary grass had a significant relationship with two species we examined, and both variables and were seen at levels in restored sites beyond determined thresholds (Figs. 7 and 8). Others have observed higher mean C-values in natural wetlands than restored wetlands (Swink and Wilhelm 1994, Mushet et al. 2002, Matthews et al. 2009b). On average, mean C-values of both natural and restored wetlands in this study were greater than those found in North Dakota (Mushet et al. 2002) and Illinois (Swink and Wilhelm 1994), however, assigned Wisconsin C-values have been shown to produce greater mean C-values than other states (Bourdaghs et al. 2006). Reed canarygrass is found at high levels at both natural and restored wetlands (Galatowitsch and van der Valk 1996, Seabloom and van der Valk 2003, Evans-Peters et al. 2012). While reed canarygrass does not appear to have an affinity towards restored wetlands in general (Seabloom and van der Valk 2003), Balcombe et al. (2005) described high reed canarygrass cover in restored mitigation wetlands compared to no reed canarygrass found in reference wetlands in West Virginia. Also, wetlands that have undergone hydrologic restoration alone, as in this study, may be particularly vulnerable to reed canarygrass invasion. Evans-Peters et al. (2012)

determined reed canarygrass as an indicator species at unmanaged wetlands, but not passively and actively managed wetlands where hydrology had been restored. Mulhouse and Galatowitsch (2003) examined wetlands in which hydrology alone was restored, and found that over an 11-year timespan, reed canarygrass aggressively colonized previously uninvaded sites and cover increased 60-100% on nearly half of all sites.

Rapid and landscape assessment variables showed mixed results when compared between natural and restored sites. In terms of rapid assessment, restored sites appear to provide important SMB vegetation. It may simply be the case that basic vegetation is largely similar in natural and restored wetlands within the study area. Another explanation is that rapid assessment variables are simply too imprecise to distinguish differences between natural and restored sites (Matthews et al. 2009a). Among rapid assessment variables, only open water showed any difference between the two site types, but due to relatively large and overlapping standard errors, we have little confidence in this result. It is more likely that no difference exists between natural and restored sites. Among landscape variables, agriculture within 1 km was similar between natural and restored sites. This was to be expected, as natural and restored sites were geographically clustered and agriculture surrounding sites should not differ significantly. Thus, the negative effects of agriculture on SMB occupancy (Table 2) appear to be independent of site type.

Restored sites had lower occupancy for each of the species we examined. This is consistent with our findings that intensive scale vegetation requirements are not likely being met at WRP wetlands. However, because detections were low at restored sites, long term, extensive SMB monitoring of restored wetlands is needed to provide more conclusive results. Restored wetlands in general have been shown to provide habitat for SMBs (Hickman 1994, VanRees-Siewert and Dinsmore 1996, Brown and Smith 1998, Balcombe et al. 2005, Hapner et al. 2011).

Interestingly, Balcombe et al. (2005) reported that Virginia Rail and Sora were found only in restored wetlands and not in reference wetlands in West Virginia. Species such as Sora and Virginia Rail can colonize restored sites quickly, while American Bittern and Least Bittern show delayed responses to restoration (VanRees-Siewert and Dinsmore 1996, Brown and Smith 1998). In terms of WRP restorations, several studies have simply included WRP sites in their analyses without distinguishing between restored and natural wetlands (Darrah and Krementz 2009, Budd and Krementz 2010, Valente et al. 2011). SMBs have been shown to use WRP wetlands and wetlands restored through the similar Conservation Reserve Enhancement Program (CREP; Kaminski et al. 2006, O'Neal et al. 2008). Whether or not restored sites can provide equivalent habitat and sustain SMB populations is still unclear and whether individual species or SMBs in general actually show preference for natural or WRP wetlands has yet to be specifically addressed. Regional context also needs to be considered, as WRP wetlands in other regions, such as the Mississippi River Alluvial Valley, may not have comparable management regimes or similar outcomes as those in Wisconsin or the upper Midwest (King et al. 2006). An example being that the WRP wetlands in our study were not managed for hydrology, whereas Kaminski et al. (2006) showed that hydrological management in WRP wetlands increased waterbird abundance and number of waterbird taxa. The benefits of managing hydrology has also been shown for rails (Rundle and Fredrickson 1981). Thus, the potential provision of SMB habitat by the WRP, as well as characteristics of local WRP wetlands, needs to be taken in a regional and management context before making conclusions for the program as a whole.

Conclusions and management implications

While basic SMB habitat needs of emergent herbaceous vegetation, *Typha* spp. cover, and open water are essential, it is important to look beyond these characteristics to more

intensive measures of habitat quality. Our results demonstrate SMB sensitivity to fine-scale plant-community composition, with reed canarygrass dominance and mean C-value as top negative and positive indicators of occupancy, respectively. In terms of these variables, restored wetlands did not appear to provide adequate SMB habitat. These are novel findings that provide challenges and opportunities based on the current state of wetlands and wetland restoration in this region. Reed canarygrass invasion is a considerable problem for wetland managers in Wisconsin. It dominates nearly 500,000 ha of wetlands throughout the state and 27% of all emergent wetlands (Hatch and Bernthal 2008). From our findings, this extensive area of wetlands may be inadequate for some SMBs. Thus, it is likely that functional wetland area for these SMBs is substantially lower than actual wetland area across the state. Presence of emergent wetland is the criteria for selecting SMB habitat and subsequent survey points for the Wisconsin SMB monitoring program. Thus, roughly a quarter of selected sites may be inadequate for SMBs. Continued surveys at these locations may not be helpful for understanding their statewide status and population trends, which are primary goals of the statewide monitoring program (Brady and Paulios 2010). Eliminating sites dominated by reed canarygrass can potentially free up time and resources for surveying other wetland sites. Mean C-value is often used as a measure of wetland restoration success. As our findings suggest, it may provide a measure of habitat quality for SMBs as well. The relationship between vegetation quality and SMB occupancy can be seen as a useful application for wetland managers and wildlife biologists in that management practices that improve wetland condition can also potentially improve habitat for SMBs. Local and national vegetation based monitoring efforts such as the NWCA can potentially "hit two [secretive marsh] birds with one stone" by providing information on wetland

quality as well as a proxy for SMB habitat. This is a win-win situation for wetland restoration and management.

While our results show the strength of fine-scale vegetation characteristics on SMBs, they must be considered in the context of an anthropogenic and agriculturally dominated landscape. The effects of reed canarygrass, mean C-value, and agriculture on SMBs are not mutually exclusive. Reed canarygrass can be seen as a driver as well as passenger of change in wetlands with high anthropogenic inputs. Wetlands in anthropogenic landscapes face constant propagule pressure and inputs that support growth of invasive species such as reed canarygrass and drive down vegetation quality. Moreover, the anthropogenic effects of grazing and fire suppression, common to Midwest agricultural landscapes, can pose a threat to SMB occupancy (Stenzel 1982, Conway et al. 2010, Richmond et al. 2012). These issues pose a continuous challenge for wetland managers and wetland restorations which often do not meet desired goals (Zedler and Callaway 1999). In order to support adequate SMB habitat, wetland management and restoration in this region should focus on eliminating reed canarygrass where it dominates. Active management strategies including prescribed fire, planting native species, and controlling hydrology to promote native species growth and reduce reed canarygrass dominance should also be considered.

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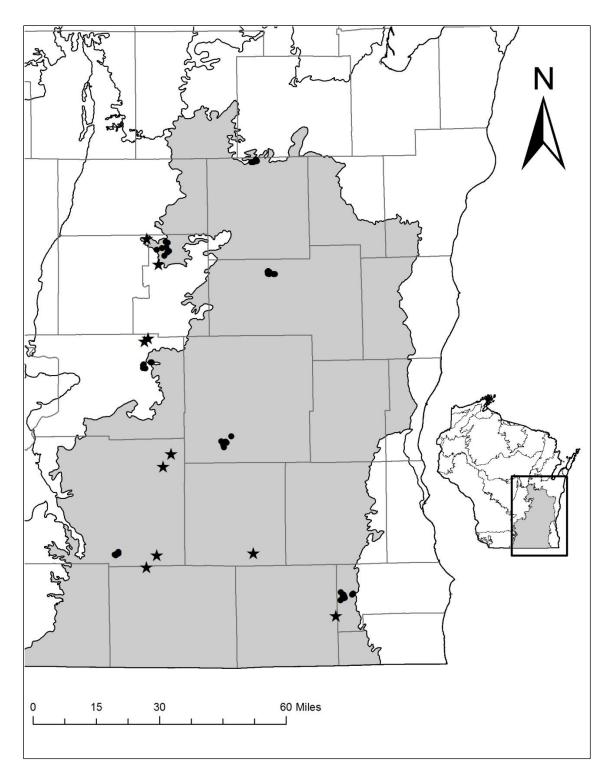


FIG. 1. Map of study area in southeastern Wisconsin where secretive marsh bird and habitat surveys were performed 2009 - 2011. Shaded region represents Southeast Glacial Plains ecological landscape. Natural sites are displayed as points, restored sites as stars.

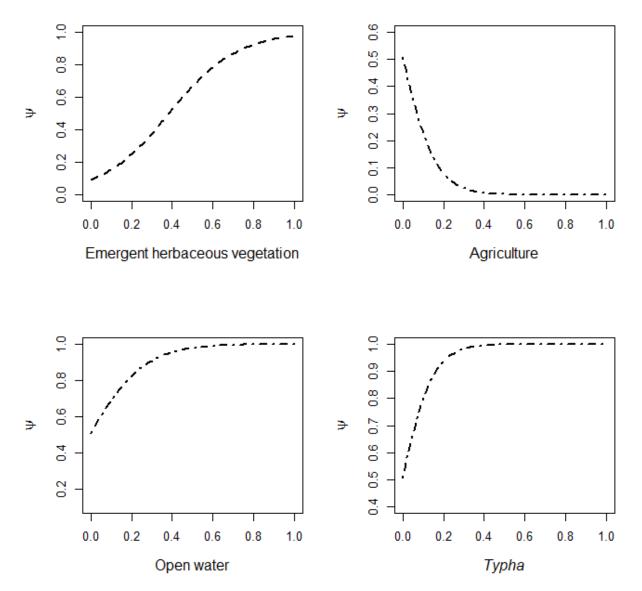
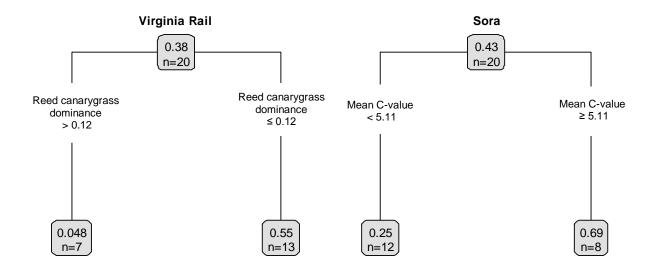


FIG. 2. Relationships between rapid and landscape assessment variables and occupancy (Ψ) of secretive marsh bird species in southeastern Wisconsin 2009 – 2011. Lines represent Virginia Rail (dashed) and Sora (dot-dash). Note different y-axes.



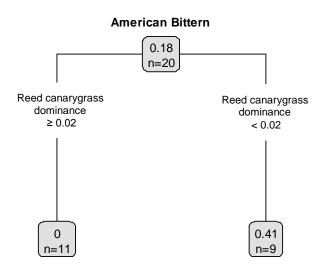


FIG. 3. Pruned regression trees for Virginia Rail, Sora, and American Bittern. All variables across three levels of sampling intensity were included in tree construction (N = 20; Appendix B). Boxes at tree nodes (leaves) show size of each group and mean proportion of years occupied. A minimum split value of N = 20 was used, constricting trees to a maximum of two branches. $R^2 = 0.40$ (Virginia Rail), 0.35 (Sora), and 0.39 (American Bittern).

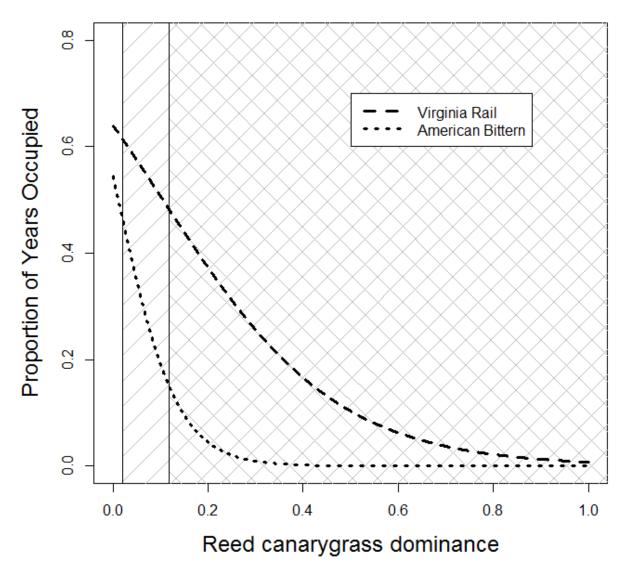


FIG. 4. Virginia Rail and American Bittern occupancy (measured as proportion of years occupied) as a function of reed canarygrass dominance. Vertical lines represent reed canarygrass dominance thresholds determined from regression tree analysis for American Bittern and Virginia Rail occupancy (Fig. 3). Diagonal lines represent levels of reed canarygrass beyond the threshold for American Bittern occupancy. Cross-hatched lines represent levels of reed canary grass beyond the threshold of American Bittern *and* Virginia Rail occupancy.

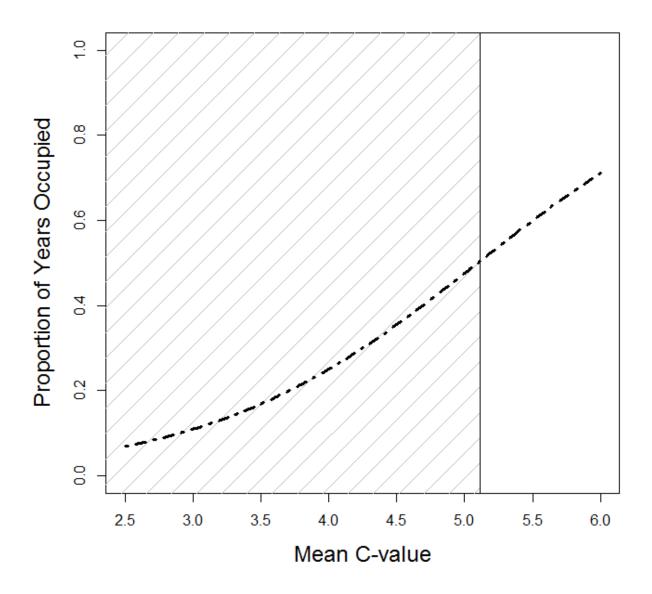
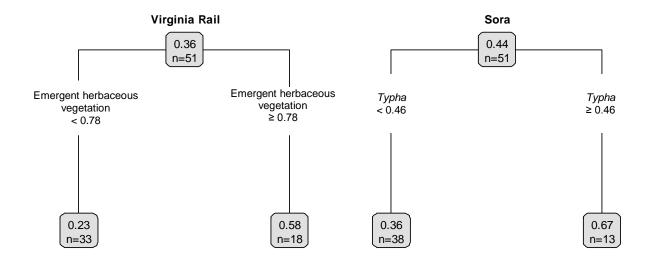


FIG. 5. Sora occupancy (measured as proportion of years occupied) as a function of mean C-value. Vertical line represents mean C-value threshold determined from regression tree analysis (Fig. 3). Shaded region represents mean C-values lower than the threshold for Sora occupancy.



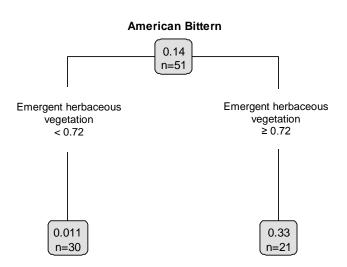


FIG. 6. Pruned regression trees for Virginia Rail, Sora, and American Bittern. All measured rapid and landscape assessment variables were included in tree construction (N = 51; Appendix B). Boxes at nodes show size of each group and mean proportion of years occupied. Trees used a minimum split value of N = 20; a sample size of 20 was needed to make an additional split beyond the initial split. $R^2 = 0.23$ (Virginia Rail), 0.17 (Sora), and 0.30 (American Bittern).

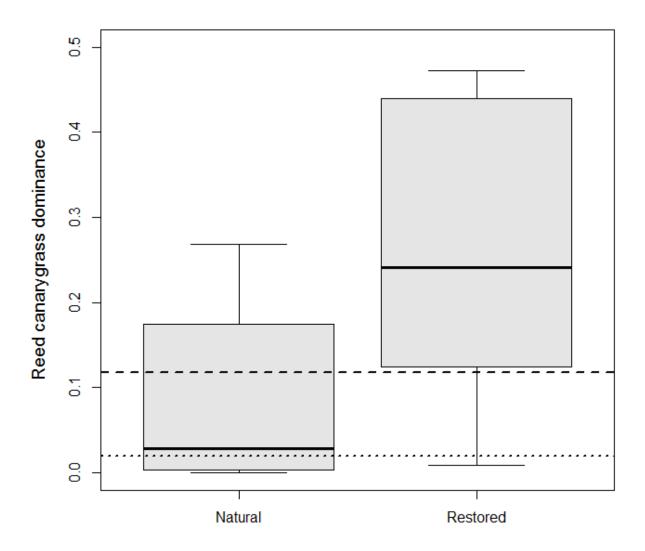


FIG. 7. Comparison of reed canary grass dominance in natural (N = 51) and restored (N = 10) wetland sites in southeastern Wisconsin. Boxes represent the range of data between the first and third quartiles. Horizontal lines within each box represent median values. Error bars represent the smaller value of either the most extreme data point or 2 standard deviations. Horizontal lines across boxes indicate reed canary grass dominance thresholds identified from regression trees for occupancy of Virginia Rail (dashed) and American Bittern (dotted; Fig. 3).

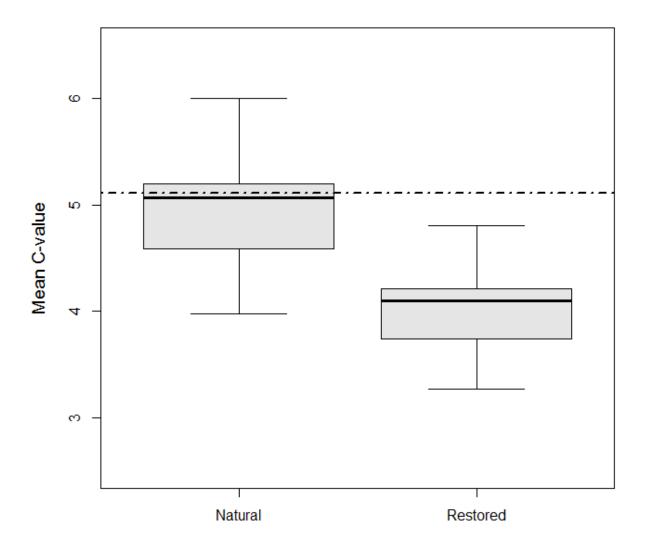


FIG. 8. Comparison of mean C-value in natural (N = 51) and restored (N = 10) wetland sites in southeastern Wisconsin. Boxes represent the range of data between the first and third quartiles. Horizontal lines within each box represent median values. Error bars represent the smaller value of either the most extreme data point or 2 standard deviations. The horizontal line across boxes indicates a threshold mean C-value identified from regression tree analysis for the Sora occupancy (Fig. 3).

TABLE 1. Model selection results for Virginia Rail and Sora occupancy (Ψ) in southeastern Wisconsin 2009 – 2011.

Model		$QAIC_c$	$\Delta QAIC_c$	W	Model likelihood
Virginia Rail					_
$\Psi(Ehv)$, $p(survey)$	5	208.10	0.00	0.25	1.00
$\Psi(\text{Ehv} + \text{Typha}), p(\text{survey})$	6	209.54	1.44	0.12	0.49
Ψ (Typha), p (survey)	5	209.63	1.53	0.11	0.47
$\Psi(\text{Ehv} + \text{Rcg}), p(\text{survey})$	6	209.81	1.71	0.10	0.43
$\Psi(\text{Ehv} + \text{OpenWater}), p(\text{survey})$	6	209.95	1.85	0.10	0.40
Sora ^a					
Ψ (Ag + Typha + OpenWater), γ (.), ε=1- γ , p (survey)	8	266.46	0.00	0.34	1.00
Ψ (Ag + Typha), γ (.), ε=1- γ , p (survey)	7	267.99	1.53	0.16	0.47

Notes: Global models for all species showed evidence of overdipersion, but not a distinct lack of fit ($\hat{c} < 2$), thus QAIC was used for model selection. ΔQAIC_c is the relative difference in QAIC_c compared to the best ranking model. Only models with $\Delta \text{QAIC}_c \le 2$ shown for each species. K is the number of parameters estimated in a model and w is the Akaike weight, which is the weight of evidence that a given model is the best approximating model. Covariates represent emergent herbaceous vegetation (Ehv), agriculture within 1 km (Ag), cover of Typha spp. within 100 m (Typha), cover of reed canarygrass within 100 m (Rcg), open water within 100 m (OpenWater), and survey period (survey).

^a Sora was modeled with a multi-year, low site fidelity parameterization: γ is colonization rate, ϵ is the extinction rate. Note that as ϵ =1- γ , colonization and extinction are the complement of one another (i.e., probability of occupancy in a given year does not depend on occupancy in the previous year).

TABLE 2. Untransformed model averaged parameter estimates of habitat variables included in occupancy modeling for each species (Table 1).

Parameter	Estimate	SE
Virginia Rail		
Intercept	-2.30	1.87
Agriculture ^a	-	-
Emergent herbaceous veg.	5.99	2.76
Typha	3.20	2.00
Rcg	-4.11	3.34
OpenWater	2.17	2.87
Sora		
Intercept	0.03	1.84
Agriculture	-12.33	5.03
Emergent herbaceous veg.	-3.87	3.55
Typha	13.36	4.98
Rcg	6.45	5.54
Open water	7.57	4.05

Note: Model averaged parameter estimates were averaged over all models in the model set that contained the given parameter (Table 1, Appendix C).

^a Agriculture was not included in the top ranking landscape model for Virginia Rail.

TABLE 3. Results of generalized linear models comparing variables determined from regression tree analysis (Figs. 3 and 6) and occupancy (proportion of years occupied) for secretive marsh birds in wetlands in southeastern Wisconsin 2009 – 2011.

Assessment level included in regression tree	N	Variable selected from regression tree	Variable intensity	Р
Virginia Rail				
Intensive, Rapid, Landscape	20	Reed canarygrass dominance s	Intensive	0.031
Rapid, Landscape	51	Emergent herbaceous veg. ^a	Rapid	< 0.001
Sora	•			0.150
Intensive, Rapid, Landscape	20	Mean C-value	Intensive	0.129
Rapid, Landscape	51	Typha ^a	Rapid	0.002
American Bittern				
Intensive, Rapid, Landscape	20	Reed canarygrass dominance ^s	Intensive	0.009
Rapid, Landscape	51	Emergent herbaceous veg. ^a	Rapid	< 0.001

Note: N =sample size used in each regression tree.

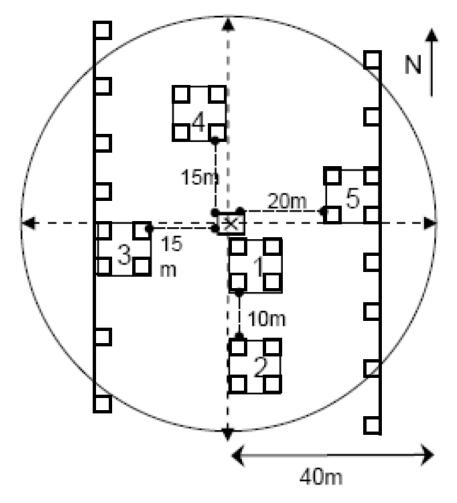
^s Variable was square root transformed to improve normality

^a Variable was arcsine square root transformed to improve normality

APPENDIX A. Description and diagram of vegetation and habitat sampling design modified from NWCA protocol.

The NWCA protocol uses five 100-m² plots which are positioned in the cardinal directions around a center point (AA Center). We positioned these plots in the same manner around the SMB survey point (the center of the study site). In cases where the SMB survey point abutted inhospitable habitat (e.g., upland forest, highway, agriculture field), we moved the NWCA sampling area into the interior of the corresponding wetland at a minimal distance. The original protocol includes two 1-m² plots within each 100-m² plot: one in the NE corner and the other in the SW corner. We placed two additional 1-m² plots within each 100-m² plot in the remaining corners. Additionally, we placed six 1-m² plots, nine meters apart, along a 64-m transect that abutted the original East and West 100-m² plots, such that all 1-m² plots were in line along this transect. The diagram below shows the original NWCA plot layout (from USEPA 2011) overlain with the 32 total 1-m² plots used for this study.

Plate 1. Standard Veg Plot Layout – Circular AA (1/2 hectare)



Place Veg Plots at specified locations on plot placement lines oriented through the AA CENTER on cardinal directions. Veg Plot 1 is placed 2m from the CENTER.

APPENDIX B. Table of all measured and calculated vegetation and habitat variables across three levels of assessment used to evaluate habitat for secretive marsh birds. See text for explanation of variables.

Assessment Level	Variable	Range
Intensive (NWCA)	Horizontal cover 0.2m	0 - 8
	Horizontal cover 0.5m	0 - 8
	Horizontal cover 0.7m	0 - 8
	Standing dead vegetation	0 - 8
	Litter cover	0 - 8
	Litter depth	0 -
	Litter index	0 - 1
	Water cover	0 - 8
	Water with floating aquatic vegetation (WaterFAV)	0 - 8
	Water total (Water + WaterFAV)	0 - 8
	Water depth	0 -
	Water index	0 - 1
	Carex spp. dominance	0 - 1
	Typha spp. dominance	0 - 1
	Reed canarygrass dominance	0 - 1
	Woody species dominance	0 - 1
	Vegetation height	0 - 6
	Mean C-value	0 - 10
	Weighted mean C-value	0 - 10
	FQI	0 -
	H'	0 -
	$e^{H'}$	0 -
Rapid (100 m)	Wetland cover	0 - 1
	Emergent herbaceous vegetation	0 - 1
	Open water	0 - 1
	Trees	0 - 1
	Shrubs	0 - 1
	Woody (Trees + Shrubs)	0 - 1
	Typha	0 - 1
	Grasses and Sedges	0 - 1
	Reed canarygrass	0 - 1
Landscape (1 km)	Agriculture	0 - 1
• • • •	Forest	0 - 1
	Grassland	0 - 1
	Agriculture + Grassland	0 - 1
	Water	0 - 1
	Residential	0 - 1
	Emergent wetland	0 - 1
	Forested wetland	0 - 1
	Shrub wetland	0 - 1
	Total wetland	0 - 1
	Total natural land	0 - 1
	LDI	0 - 7

APPENDIX C. Model selection results for population dynamics / detection probability (p), landscape, and complete assessment models for Virginia Rail and Sora.

APPENDIX C-1. Model selection results for Virginia Rail population dynamics and detection probability (p) in southeastern Wisconsin 2009 - 2011.

Model	K	AIC_c	ΔAIC_c	w	Model likelihood
$\Psi(.)$, $p(\text{survey})$	4	347.53	0.00	0.62	1.00
$\Psi(.), \gamma(.), p(\text{survey})$	5	349.34	1.81	0.25	0.40
$\Psi(.), p(.)$	2	352.18	4.65	0.06	0.10
$\Psi(.)$, $p(\text{survey} + \text{year})$	7	353.75	6.22	0.03	0.04
$\Psi(.), \gamma(.), p(.)$	3	354.17	6.64	0.02	0.04
$\Psi(.)$, p(year)	4	355.46	7.93	0.01	0.02
$\Psi(.)$, $\gamma(.)$, $p(\text{survey} + \text{year})$	8	356.03	8.50	0.01	0.01
$\Psi(.), \gamma(.), p(year)$	5	357.70	10.17	0.00	0.01
Ψ (.), γ (.), ε=1- γ , p (survey)	5	364.77	17.24	0.00	0.00
$\Psi(.)$, $\gamma(.)$, $\varepsilon=1-\gamma$, $p(.)$	3	370.11	22.58	0.00	0.00
Ψ (.), γ (.), ε=1- γ , p (survey + year)	8	371.93	24.40	0.00	0.00
Ψ(.), γ (.), ε =1- γ , p (year)	5	373.99	26.46	0.00	0.00

APPENDIX C-2. Landscape model selection results for Virginia Rail occupancy (Ψ) in southeastern Wisconsin 2009-2011.

Model	K	$QAIC_c$	$\Delta QAIC_c$	w	Model likelihood
Ψ (.), p (survey)	4	251.26	0.00	0.36	1.00
Ψ (Wetland), p (survey)	5	252.57	1.31	0.19	0.52
$\Psi(\text{Forest}), p(\text{survey})$	5	253.01	1.75	0.15	0.42
$\Psi(Ag)$, $p(survey)$	5	253.31	2.05	0.13	0.36
$\Psi(\text{Wetland} + \text{Forest}), p(\text{survey})$	6	255.12	3.86	0.05	0.15
Ψ (Wetland + Ag), p (survey)	6	255.22	3.96	0.05	0.14
$\Psi(Ag + Forest), p(survey)$	6	255.27	4.01	0.05	0.13
Ψ (Wetland + Ag + Forest), p (survey)	7	257.95	6.69	0.01	0.04

APPENDIX C-3. Complete model selection results for Virginia Rail occupancy (Ψ) in southeastern Wisconsin 2009 – 2011.

Model	K	QAIC _c	$\Delta QAIC_c$	W	Model likelihood
Ψ(Ehv), p (survey)	5	208.10	0.00	0.25	1.00
$\Psi(\text{Ehv} + \text{Typha}), p(\text{survey})$	6	209.54	1.44	0.12	0.49
Ψ (Typha), p (survey)	5	209.63	1.53	0.11	0.47
$\Psi(\text{Ehv} + \text{Rcg}), p(\text{survey})$	6	209.81	1.71	0.10	0.43
$\Psi(\text{Ehv} + \text{OpenWater}), p(\text{survey})$	6	209.95	1.85	0.10	0.40
$\Psi(\text{Ehv} + \text{Rcg} + \text{OpenWater}), p(\text{survey})$	7	211.43	3.33	0.05	0.19
Ψ (.), p (survey)	4	211.57	3.47	0.04	0.18
Ψ (Typha + Rcg), p (survey)	6	211.66	3.56	0.04	0.17
$\Psi(\text{Ehv} + \text{Typha} + \text{OpenWater}), p(\text{survey})$	7	211.74	3.64	0.04	0.16
$\Psi(\text{Ehv} + \text{Typha} + \text{Rcg}), p(\text{survey})$	7	211.77	3.67	0.04	0.16
$\Psi(Rcg)$, $p(survey)$	5	212.14	4.04	0.03	0.13
Ψ (Typha + OpenWater), p (survey)	6	212.33	4.23	0.03	0.12
$\Psi(\text{Ehv} + \text{Typha} + \text{Rcg} + \text{OpenWater}), p(\text{survey})$	8	213.96	5.86	0.01	0.05
Ψ (OpenWater), p (survey)	5	214.06	5.96	0.01	0.05
Ψ (Typha + Rcg + OpenWater), p (survey)	7	214.46	6.36	0.01	0.04
$\Psi(\text{Rcg} + \text{OpenWater}), p(\text{survey})$	6	214.83	6.73	0.01	0.03

APPENDIX C-4. Model selection results for Sora population dynamics and detection probability (p) in southeastern Wisconsin 2009 - 2011.

Model	K	AIC_c	ΔAIC_c	w	Model likelihood
Ψ(.), γ (.), ε =1- γ , p (survey)	5	354.17	0.00	0.68	1.00
Ψ (.), γ (.), p (survey + year)	8	357.30	3.13	0.14	0.21
Ψ (.), γ (.), ε =1- γ , p (survey + year)	8	358.20	4.03	0.09	0.13
Ψ (.), γ (.), p (survey)	5	358.46	4.29	0.08	0.12
Ψ (.), p (survey + year)	7	362.70	8.53	0.01	0.01
Ψ (.), p (survey)	4	369.76	15.59	0.00	0.00
Ψ (.), p (year)	4	420.62	66.45	0.00	0.00
Ψ (.), γ (.), p (year)	5	421.97	67.80	0.00	0.00
Ψ (.), γ (.), ε =1- γ , p (.)	3	422.85	68.68	0.00	0.00
Ψ (.), γ (.), ε =1- γ , p (year)	5	424.55	70.38	0.00	0.00
$\Psi (.), \gamma (.), p(.)$	3	428.16	73.99	0.00	0.00
$\Psi (.), p(.)$	2	428.74	74.57	0.00	0.00

APPENDIX C-5. Landscape model selection results for Sora occupancy (Ψ) in southeastern Wisconsin 2009 – 2011.

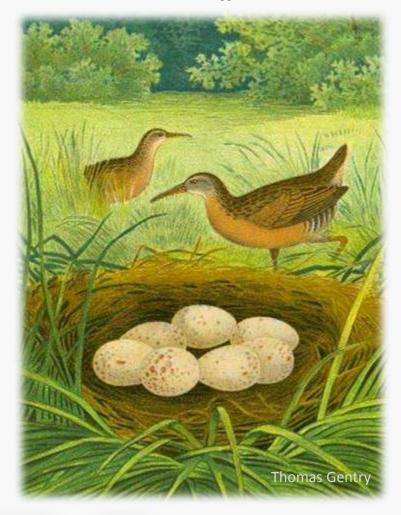
Model	K	$QAIC_c$	$\Delta QAIC_c$	W	Model likelihood
Ψ(Ag), γ (.), ε =1- γ , p (survey)	6	351.57	0.00	0.43	1.00
Ψ(Wetland + Ag), $\gamma(.)$, ε =1- γ , p (survey)	7	353.90	2.33	0.13	0.31
Ψ (Ag + Forest), gam(.), γ (.), ε=1- γ , p (survey)	7	354.01	2.44	0.13	0.30
Ψ (.), gam(.), γ (.), ε=1- γ , p (survey)	5	354.17	2.60	0.12	0.27
Ψ(Wetland), gam(.), γ (.), ε =1- γ , p (survey)	6	355.20	3.63	0.07	0.16
Ψ(Wetland + Ag + Forest), γ (.), ε =1- γ , p (survey)	8	355.21	3.64	0.07	0.16
Ψ(Forest),gam(.), γ (.), ε =1- γ , p (survey)	6	356.55	4.98	0.04	0.08
Ψ(Wetland + Forest), γ (.), ε =1- γ , p (survey)	7	357.85	6.28	0.02	0.04

APPENDIX C-6. Complete model selection results for Sora occupancy (Ψ) in southeastern Wisconsin 2009 – 2011.

Model	K	QAIC _c	$\Delta QAIC_c$	W	Model
					likelihood
Ψ (Ag + Typha + OpenWater), γ (.), ε=1- γ , p (survey)	8	266.46	0.00	0.34	1.00
Ψ (Ag + Typha), γ (.), ε=1- γ , p (survey)	7	267.99	1.53	0.16	0.47
Ψ (Ag + Typha + Rcg + OpenWater), γ (.), ε=1- γ , p (survey)	9	268.61	2.15	0.12	0.34
Ψ (Ag + Ehv + Typha + OpenWater), $\gamma(.)$, ε =1- γ , p (survey)	9	268.67	2.21	0.11	0.33
Ψ (Ag + Typha + Rcg), γ (.), ε=1- γ , p (survey)	8	268.73	2.27	0.11	0.32
Ψ (Ag + Ehv + Typha), γ (.), ε=1- γ , p (survey)	8	269.45	2.99	0.08	0.22
Ψ (Ag + Ehv + Typha + Rcg), γ (.), ε=1- γ , p (survey)	9	270.64	4.18	0.04	0.12
Ψ(Ag + Ehv + Typha + Rcg + OpenWater), $γ$ (.), $ε$ =1- $γ$, p (survey)	10	271.23	4.77	0.03	0.09
Ψ (Ag + Ehv + OpenWater), γ (.), ε=1- γ , p (survey)	8	279.86	13.40	0.00	0.00
Ψ (Ag), γ (.), ε=1- γ , p (survey)	6	280.42	13.96	0.00	0.00
Ψ (.), γ (.), ε=1- γ , p (survey)	5	281.77	15.31	0.00	0.00
Ψ (Ag + Ehv), γ (.), ε=1- γ , p(survey)	7	281.91	15.45	0.00	0.00
Ψ (Ag + Ehv + Rcg + OpenWater), γ (.), ε=1- γ , p (survey)	9	281.94	15.48	0.00	0.00
Ψ (Ag + OpenWater), γ (.), ε=1- γ , p (survey)	7	282.30	15.84	0.00	0.00
Ψ (Ag + Rcg), γ (.), ε=1- γ , p (survey)	7	283.23	16.77	0.00	0.00
Ψ (Ag + Rcg + OpenWater), γ (.), ε=1- γ , p (survey)	8	284.46	18.00	0.00	0.00
Ψ (Ag + Ehv + Rcg), γ (.), ε=1- γ , p (survey)	8	284.85	18.39	0.00	0.00

Habitat requirements and restoration targets for secretive marsh birds in southeastern Wisconsin

Dan Larkin, Wes Glisson, Ryan Brady, and Andy Paulios









Secretive marsh birds

- Wetlanddependent
- Non-colonial
- Non-waterfowl
- Discreet behavior

Rails, bitterns, coots, gallinules, grebes, moorhens

Kushlan et al. 2002, Waterbird Conservation for the Americas 2006









Habitat affinities

Presence can differ with:

- Water depth
- Cover and height of emergent vegetation
- Interspersion

Zedler 1993, Fairbairn and Dinsmore 2001, Lor and Malecki 2006, Rehm and Baldassarre 2007



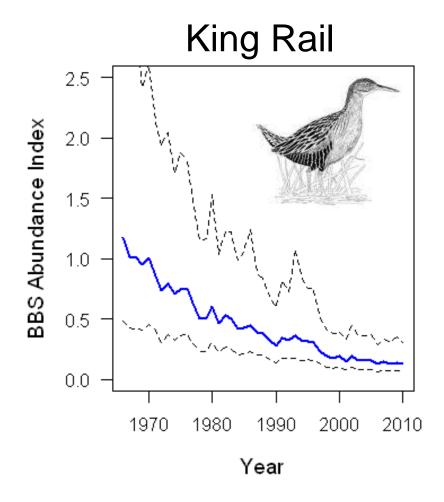


Photos: CCNAB, : D L'Hoste

Conservation challenges

- Several species declining
- Unknown trends for others
- Difficult to survey/study
 - Not well sampled by omnibus monitoring (e.g. BBS)
- Uncertain responses to changing wetland condition, management, and restoration

Eddleman et al. 1988, Kushlan et al. 2002, Soullierre et al. 2007, Conway 2009



Wetland degradation

Wetland condition has changed dramatically in much of upper Midwest

Agriculture + other land-use impacts →

Monotypes of invasive spp. (reed canarygrass, hybrid cattail, *Phragmites*)

Effects on SMBs of assoc. changes in habitat structure?

Galatowitsch et al. 1999, Zedler and Kercher 2004, Bowles and Jones 2006



Wetland restoration

Major investments being made to return wetland area and assoc. services

Especially NRCS' Wetlands Reserve Program in this study region

Brinson and Eckles 2011

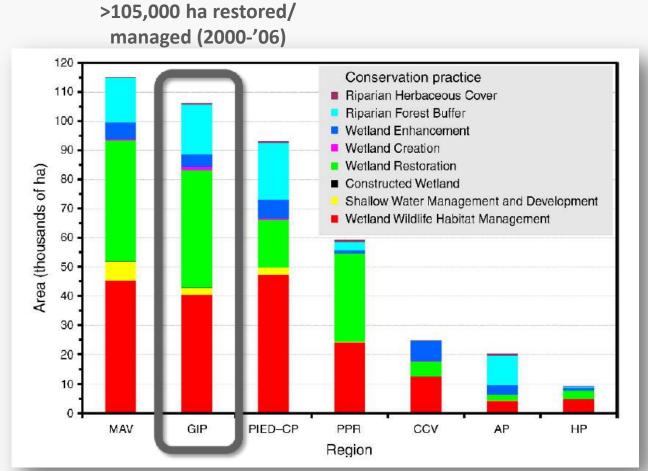




Photo: W Glisson

Research questions



Habitat selection

- How is SMB occupancy influenced by invasion-driven changes in wetland structure?
- Are typical wetland-restoration approaches meeting SMB needs?





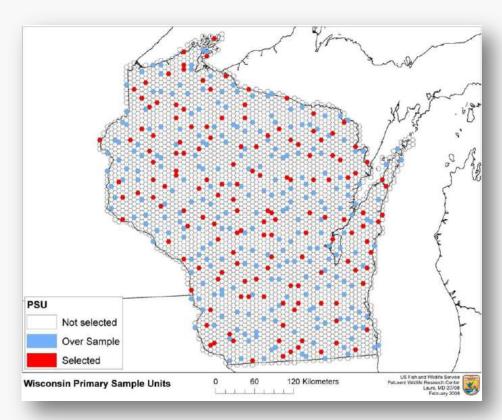


Photos: G Fewless, W Glisson, T Grey

Methods—Bird monitoring

- Marsh birds monitored throughout Wisc. 2009-'11
- Standardized natl. protocol: passive and playback
- Stratified, random site selection (GRTS)

Conway 2005, Johnson et al. 2009





Methods—Wetland assessment

Sampled subset of sites in SE Glacial Plains (2011) using three-tiered assessment:

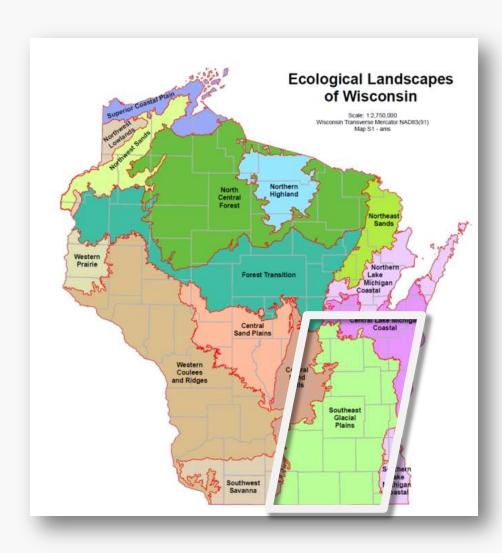
Rapid

Level 1. GIS land cover (n=51)

<u>Level 2</u>. Rapid site assessment (*n*=51)

Intensive

Level 3. EPA NWCA protocol (n=20)



Methods—WRP sites

- 10 sites, spatially clustered w/ natural sites
- All restored in the 1990s
- Bird monitoring and wetland assessment in 2011

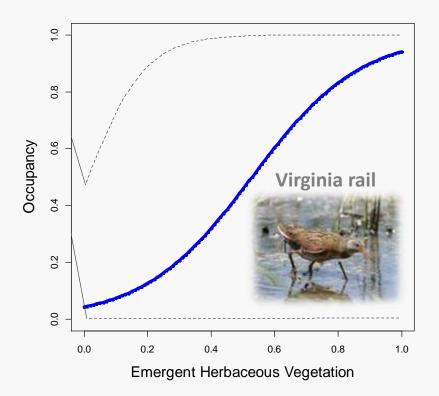


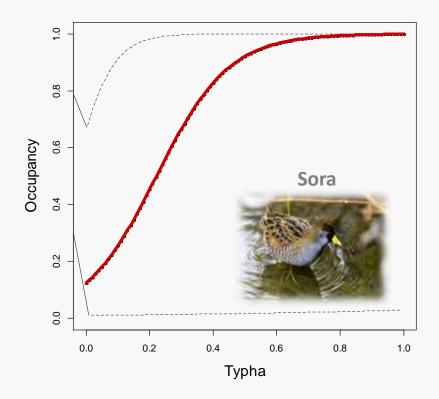
Photo: Kenosha Co.

- Detections low overall
- Only Sora and Virginia Rail had sufficient records for occupancy modeling
 - AIC model ranking incorporating detectability, Program PRESENCE
- Level 1: Surrounding land cover had no explanatory power



- Detections low overall
- Only Sora and Virginia Rail had sufficient records for occupancy modeling
 - AIC model ranking incorporating detectability, Program PRESENCE
- Level 1: Surrounding land cover had no explanatory power
- Level 2: ↑ Occupancy w/ ↑ cover emergent herbaceous veg. and cattails





Regression tree analysis

- Non-parametric method good for messy data
- Recursively partitions data based on most-discriminating variables
- Can yield complex trees w/ many "branches" and "leaves"

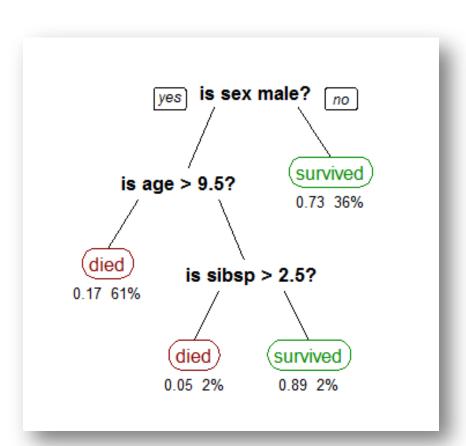
Regression tree analysis

- Non-parametric method good for messy data
- Recursively partitions data based on most-discriminating variables
- Can yield complex trees w/ many "branches" and "leaves"

Survival of passengers on the Titanic, function of:

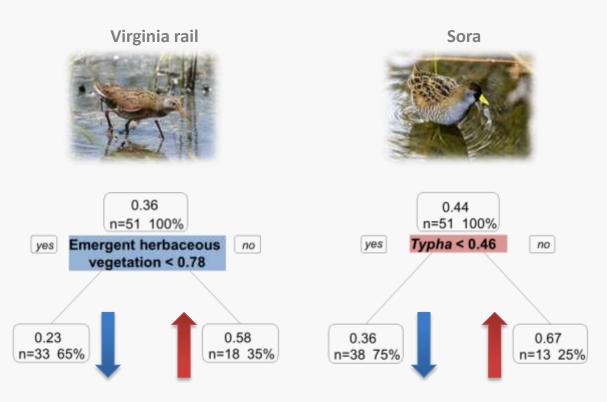
 Gender, age, # close relatives on board

Wikipedia



Regression tree analysis

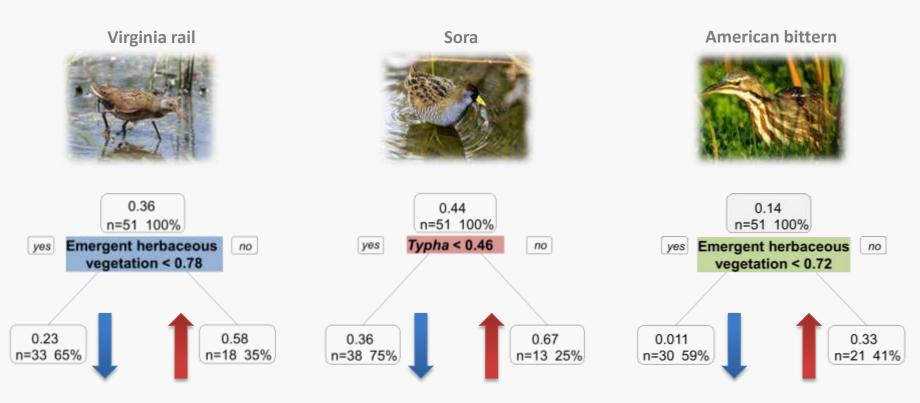
 Thresholds of ↑emergent veg. and cattail assoc. w/ ~1–30-fold ↑occupancy



Dependent var.: Proportion of years sites occupied

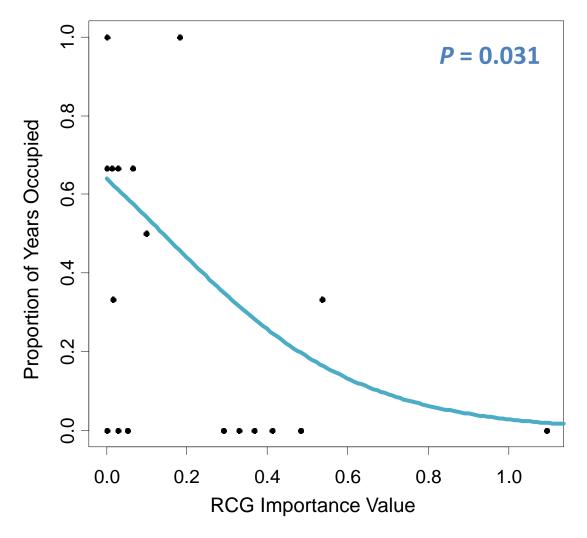
Regression tree analysis

 Thresholds of ↑emergent veg. and cattail assoc. w/ ~1–30-fold ↑occupancy



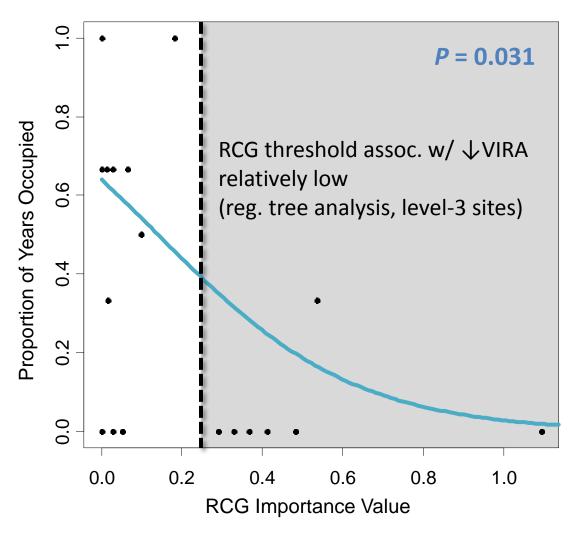
Dependent var.: Proportion of years sites occupied

Virginia Rail occupancy ↓w/ ↑RCG



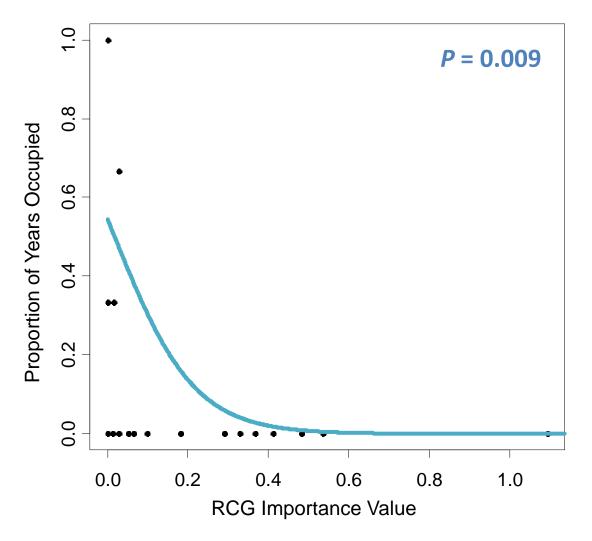


Virginia Rail occupancy ↓w/ ↑RCG

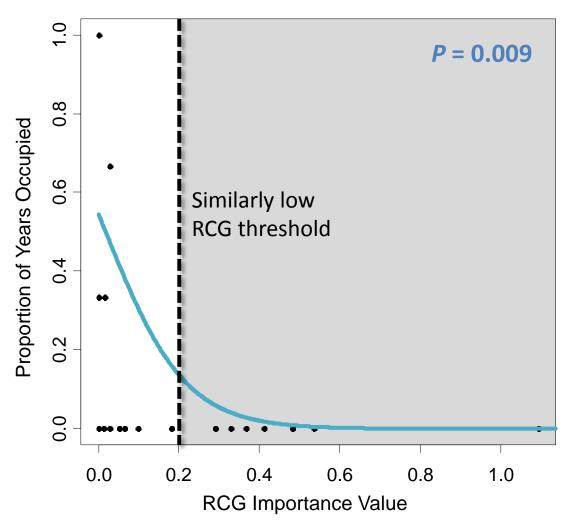




American Bittern also ↓w/ ↑RCG

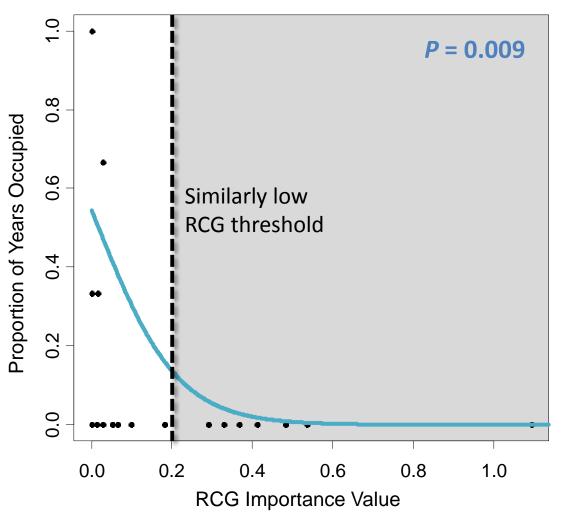


American Bittern also ↓w/ ↑RCG



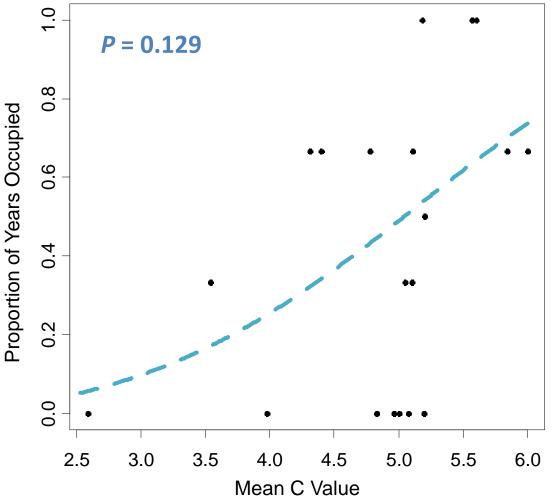


Not a water-level artifact: RCG ~ water, P = 0.20



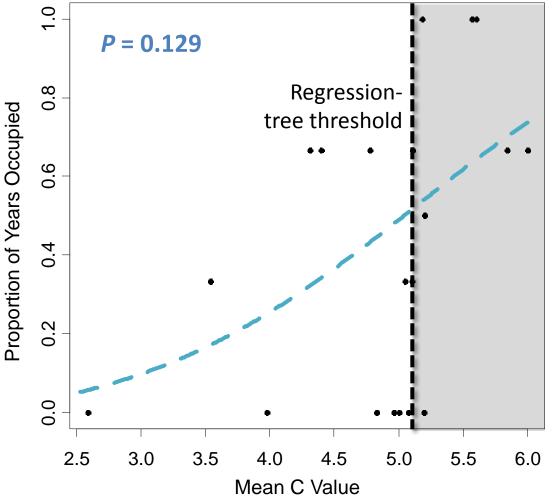


Intriguing but N.S. correlation between Sora occupancy and mean coefficient of conservatism



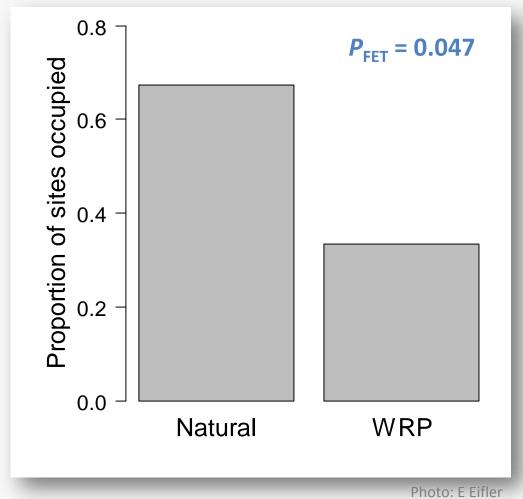


Intriguing but N.S. correlation between Sora occupancy and mean coefficient of conservatism

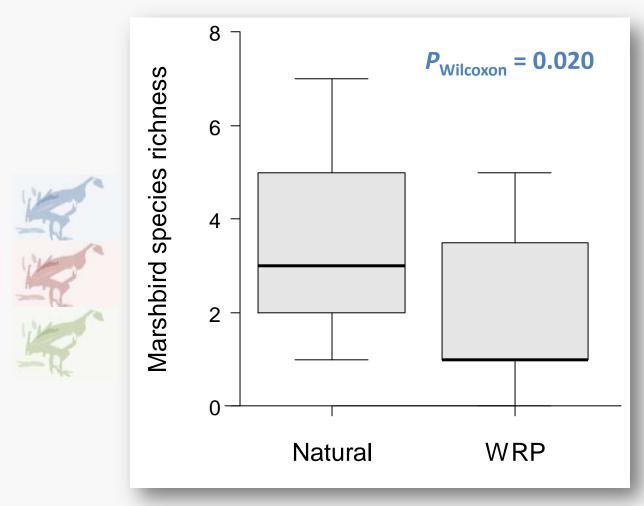




WRP sites less likely to have SMBs









↑ RCG in WRP sites

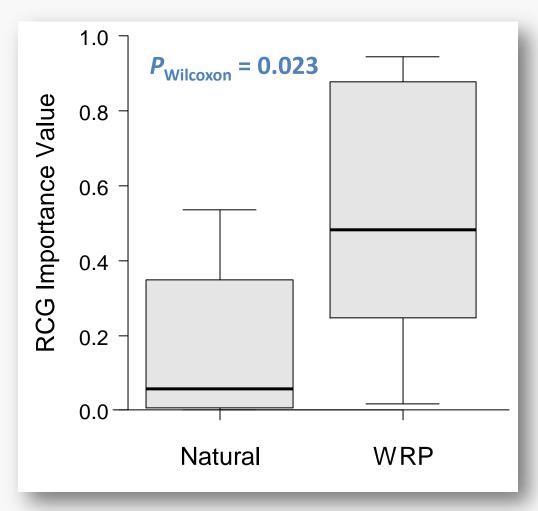




Photo: http://plants.ifas.ufl.edu

↑ RCG in WRP sites

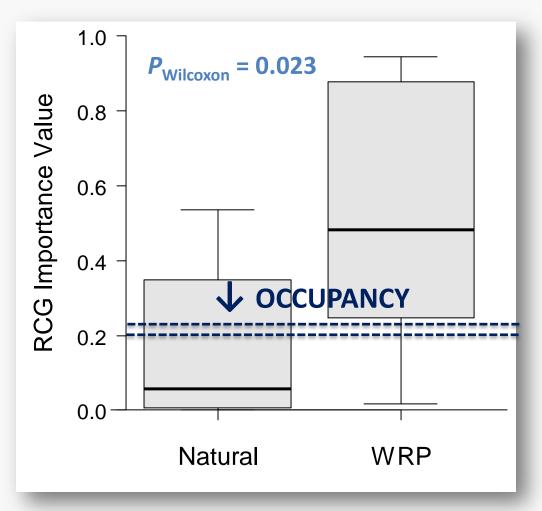


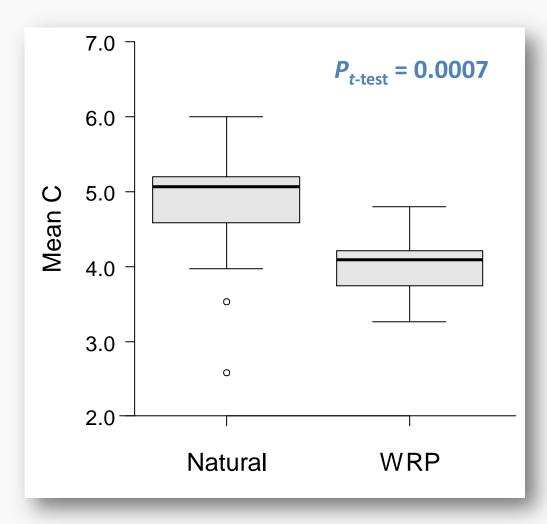


Photo: http://plants.ifas.ufl.edu

 ↓ Mean coefficient of conservatism in WRP sites



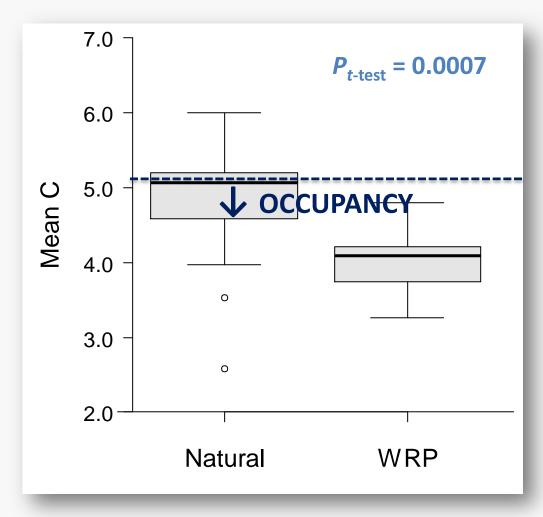
Photo: L Mehrhoff

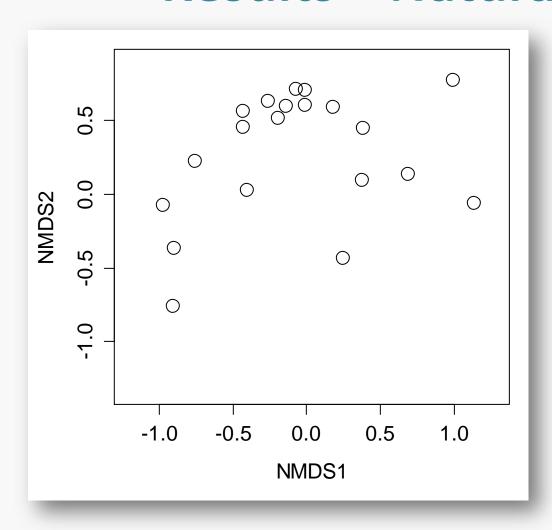


 ↓ Mean coefficient of conservatism in WRP sites



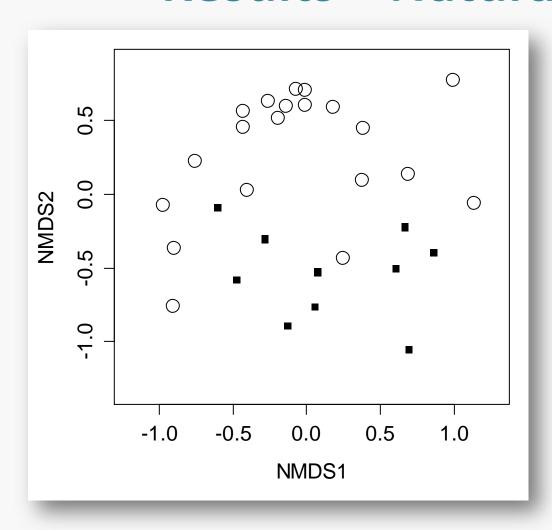
Photo: L Mehrhoff





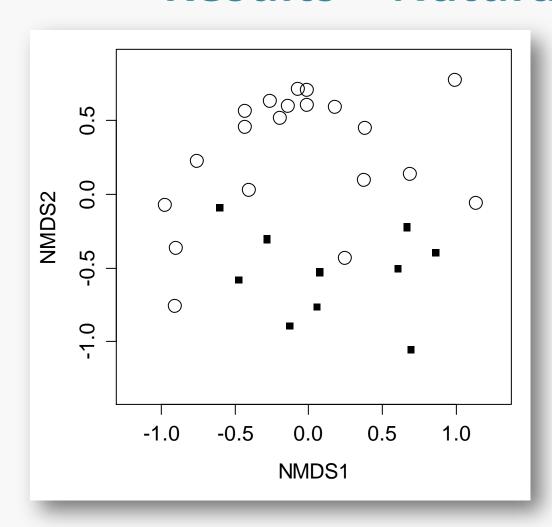
Plant-community composition

20 natural sites



- 10 WRP sites
- Distinct plantcomm. comp.

PERMANOVA: P = 0.0006

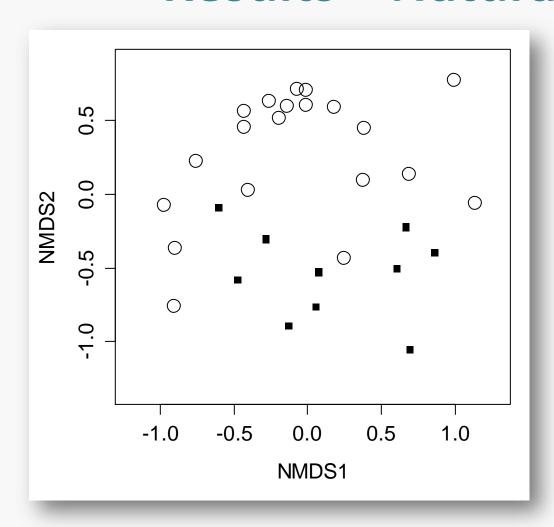


Sig. correlation between plant- and bird-comm. comp.

MANTEL tests

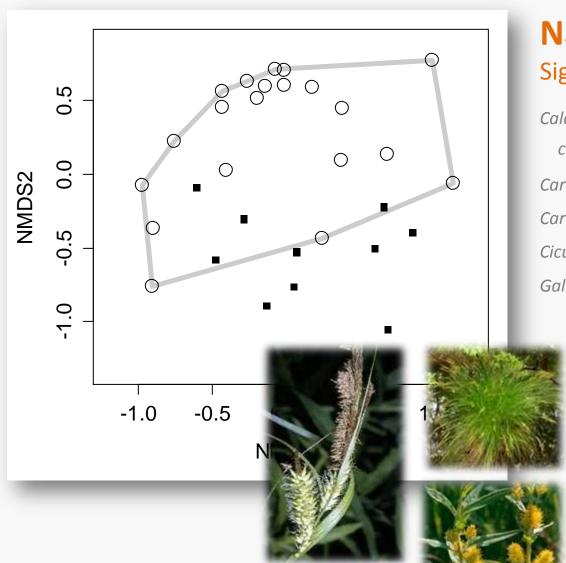
- Natl. sites: P = 0.049

- All sites : P = 0.045



Distinguishing species?

INDICATOR SPECIES ANALYSIS



Natural wetlands

Sig. indicators ($\alpha \le 0.05$)

Calamagrostis Lysimachia thyrsiflora

canadensis Rumex orbiculatis

Carex lacustris Scutellaria

Carex stricta galericulata

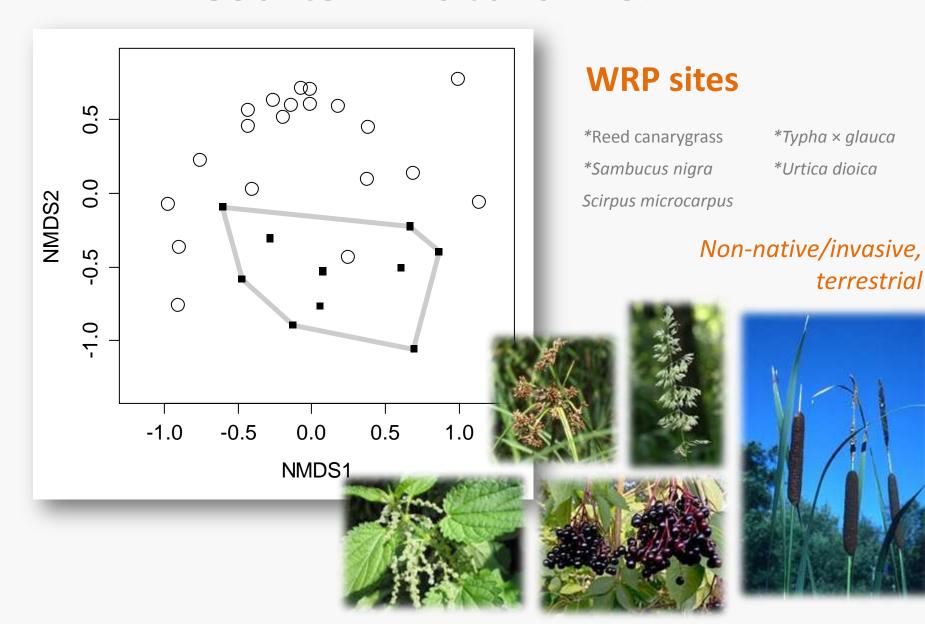
Cicuta bulbifera Sium suave

Galium trifidum

Native, wetland-dependent, fairly conservative







SMBs sensitive to plant-community composition



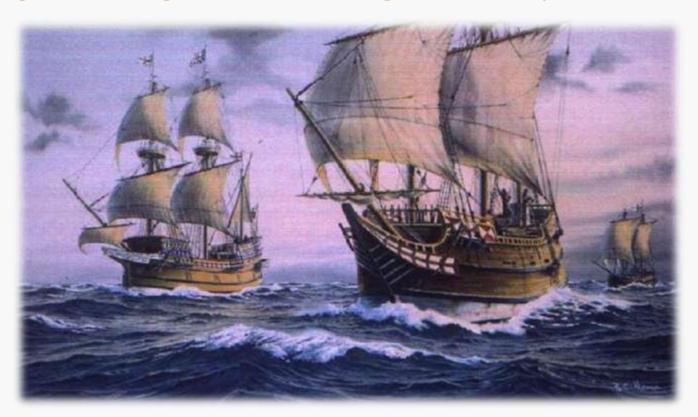
- SMBs sensitive to plant-community composition
 - SMBs and veg. not coupled but covary w/ other aspects of wetland condition



- SMBs sensitive to plant-community composition
 - SMBs and veg. not coupled but covary w/ other aspects of wetland condition
 - Morphology of dom. veg. influences sites' refuge/ forage/reproductive support



- The good news: A rising tide lifts all boats
 - Vegetation-based monitoring (e.g., NWCA) may provide proxy information for SMBs
 - Veg-focused goals and management may benefit SMBs



- The bad news:
 - Tide's not likely to rise anytime soon
 - Statewide RCG dominance
 - → <u>functional</u> wetland area for SMBs < actual wetland area
 - Difficult to restore highquality wetlands in ag. landscapes

