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Articles

Secretive Marsh Bird Species Co-Occurrences and Habitat Associations Across the Midwest, USA

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Abstract

Because secretive marsh birds are difficult to detect, population status and habitat use for these birds are not well known. We conducted repeated surveys for secretive marsh birds across 264 sites in the Upper Mississippi River and Great Lakes Joint Venture region to estimate abundance, occupancy, and detection probabilities during the 2008 and 2009 breeding seasons. We identified species groups based on observed species co-occurrences. Two species, least bittern *Ixobrychus exilis* and American bittern *Botaurus lentiginosus*, co-occurred with other species less often than expected by chance, and two species groups, rails (Virginia rail *Rallus limicola* and sora *Porzana carolina*) and open-water birds (pied-billed grebe *Podilymbus podiceps*, common moorhen *Gallinula chloropus*, and American coot *Fulica americana*; coots were only surveyed in 2009), co-occurred more often than expected by chance. These groupings were consistent between years. We then estimated the relation of these species and groups to landscape and local site characteristics by using zero-inflated abundance models that accounted for incomplete detection. At the landscape level (5-km radius), the amount of emergent herbaceous wetland was positively associated with least bittern occupancy, whereas the amount of woody wetland was negatively associated with least bittern, rail, and open-water bird occupancy. At the local level, habitat variables that were associated with abundance were not consistent among groups or between years, with the exception that both least bitterns and open-water birds had a strong positive association between abundance and water-vegetation interspersion. Land managers interested in marsh bird management or conservation may want to consider focusing efforts on landscapes with high amounts of emergent herbaceous wetland and low amounts of woody wetland, and managing for high amounts of water-vegetation interspersion within the wetland.

Keywords: marsh bird; Midwest; occupancy; abundance; habitat use; wetland; species co-occurrence

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Introduction

Secretive marsh birds include waterbirds that primarily inhabit marshes, are dependent upon wetlands for most of their life cycle, and are difficult to detect. Because most marsh birds have experienced widespread popula-

tion declines (Eddleman et al. 1988; Ribic et al. 1999), they have become a focus of conservation concern (North American Bird Conservation Initiative 2009). These population declines are thought to result primarily from wetland loss and alteration (Gibbs et al. 1992; Meanley 1992; Lor and Malecki 2002). By the 1970s, parts of the



U.S. lost more than 90% of their original wetland area, with the Midwest among the areas with greatest percentage loss of wetland (Tiner 1984). Emergent wetland loss has continued, although at a slower pace since the mid-1990s (Dahl 2006). Proper management of remaining wetlands is thus important for the conservation of marsh birds, and information on the habitat requirements of each species across its range is critical.

Given the secretive nature of most marsh birds, accurate population estimates and detailed information about habitat use are often lacking and difficult to obtain (Eddleman et al. 1988; Ribic et al. 1999; Conway and Gibbs 2005). Many researchers (see Cooper 2010) of secretive marsh birds currently use occupancy estimation (MacKenzie et al. 2002, 2003; MacKenzie and Royle 2005) to index species occurrence while accounting for imperfect detection. Recently, researchers have developed means of fully exploiting occupancy information to estimate an additional parameter, abundance (Royle and Nichols 2003; Wenger and Freeman 2008). These methods allow researchers to estimate abundance, occupancy, and detection simultaneously. There is also well-established methodology to model site occupancy as a function of habitat characteristics to determine habitat–use associations (MacKenzie et al. 2002, 2003).

We estimated abundance, occupancy, and detection for secretive marsh birds across the Upper Mississippi River and Great Lakes Joint Venture region (JV) of the United States. Joint ventures are partnerships of organizations that implement national or international bird conservation plans within a geographic area or for a specific taxonomic group (U.S. Fish and Wildlife Service [USFWS] 2010). The JV region has lost most of its original wetlands (five states have lost $\geq 85\%$ [Dahl and Allord 1997]) to agricultural development, urban and rural development, and river impoundments (Dahl 2006). Dahl (1990) reported the Midwestern farm belt states of Illinois, Indiana, Iowa, Michigan, Minnesota, Ohio, and Wisconsin lost more than 1.5 million ha of wetlands since European settlement. Gottgens et al. (1998) reported less than 5% of the original western Lake Erie marshes remain today. In Illinois, palustrine emergent wetlands have declined to approximately 16.1% of the state's total wetland area (Moore et al. 2009). In Iowa, 89% of native wetlands have been lost (Fletcher and Koford 2003).

Thus, our objectives were to develop species group associations for secretive marsh birds and to investigate their habitat use across the JV region. Because we knew that some marsh birds were more abundant (e.g., pied-billed grebe *Podilymbus podiceps*) than other marsh birds (e.g., king rail *Rallus elegans*), we recognized that developing habitat associations for less common marsh bird species would be difficult. Hence, we used species group associations (i.e., surrogates) so that we could take advantage of more abundant species to develop habitat associations for less common species (Raphael and Molina 2007; Rodrigues and Brooks 2007).

Methods

We conducted our study in the JV region that encompasses all or portions of Illinois, Indiana, Iowa,

Kansas, Michigan, Minnesota, Missouri, Nebraska, Ohio, and Wisconsin (Figure 1).

Site selection

In 2008, we used a landscape suitability index model developed for predicting king rail presence to select survey wetlands across the JV region (Souilliere et al. 2007). Souilliere et al. (2007) used geographic information systems (GIS) and spatial data from the National Land Cover Dataset (NLCD) to estimate landscape suitability index scores based on wetland cover type (emergent or woody wetland), wetland size (>20 ha or <20 ha), and distance from major river systems and the southern shores of Lake Erie and Lake Michigan. We used ArcGIS 9.2 (Environmental Systems Research Institute Inc. [ESRI] 2006) and the Hawth's Tools application (Beyer 2004) to randomly select 100 sites each for landscape suitability index habitat suitability scores equal to or greater than 80 (high), 50–80 (moderate), or less than 50 (low). We defined a site as a coordinate (i.e., point) located within a wetland of a given habitat suitability. We excluded Wisconsin from the random selection because the Wisconsin Department of Natural Resources was independently conducting similar secretive marsh bird surveys statewide (Paulios and Brady 2010).

In 2009, wetland site values were averaged by 5×5 -km blocks, rather than scoring each individual wetland separately within the landscape as we had done in 2008. We did this because in 2008, moderate suitability sites were often located adjacent to high suitability sites within the same wetland complex, thereby making both suitability habitats susceptible to flooding. We used 5×5 -km blocks because that was the unit size used for the landscape suitability index model (Souilliere et al. 2007). We then used GIS and spatial data from the National Wetlands Inventory (NWI) to randomly select 133 wetlands each for high, moderate, and low suitability habitats. We increased the number of randomly selected sites in 2009 because we wanted additional sites in case of access issues. We chose to use data from the NWI rather than the NLCD because NWI data are considered more spatially accurate and better at identifying wetland cover types (B. Potter, USFWS, personal communication). The NWI provides finer thematic and spatial resolution for wetlands than satellite imagery and allows researchers to distinguish differences in representation of wetlands that would not be distinguishable using the NLCD (Niemuth et al. 2006). A drawback to using the NWI is that it is 20–30 y older than the NLCD and contains many wetlands less than 0.4 ha that may have been more prone to loss or change in cover type; for example, 85% of all freshwater wetlands lost between 1998 and 2004 were wetlands less than 2 ha, and 52% were wetlands less than 0.4 ha (Dahl 2006). Because of the disproportionate loss of smaller wetlands and because Brown and Dinsmore (1986) found the frequency of occurrence of pied-billed grebes, American bitterns *Botaurus letiginosus*, least bitterns *Ixobrychus exilis*, Virginia rails *Rallus limicola*, and soras *Porzana carolina* were all greater in wetlands more than 5 ha than in wetlands less than 1 ha, we decided to restrict selected wetland size to equal to or greater than 5 ha.

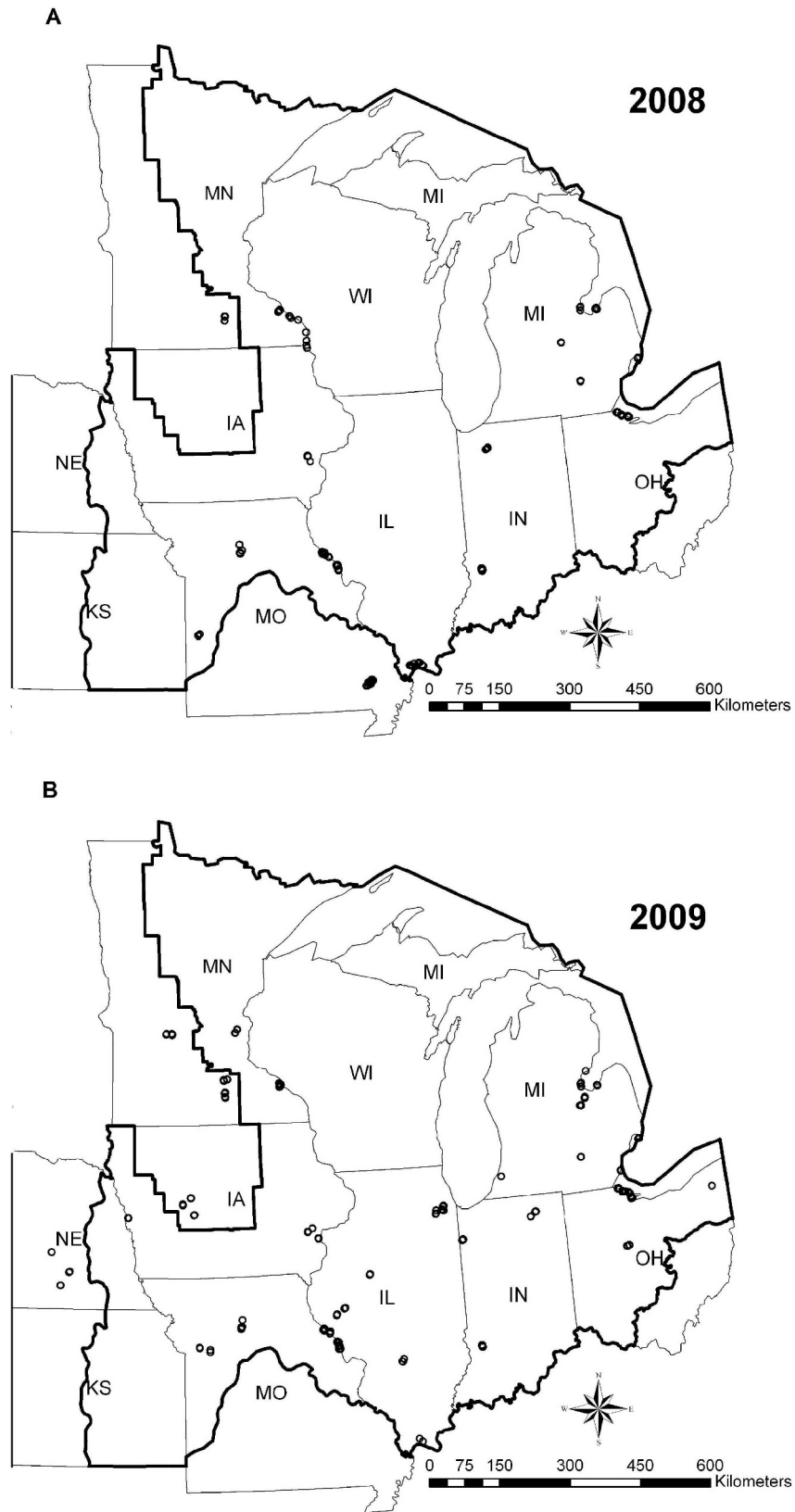


Figure 1. Outline of the Upper Mississippi River and Great Lakes Joint Venture region with sites ($n = 264$ each year) surveyed for marsh birds during breeding seasons of 2008 (A) and 2009 (B). Each point can represent variable numbers of sites surveyed.

The JV region experienced above-average rainfall in 2008. Regions of the JV received up to 203–406 mm above-average rainfall during May, June, and July 2008 (National Oceanic Atmospheric Administration [NOAA] 2010). The heavy rainfall resulted in extensive flooding that inundated 44 high and 55 moderate suitability sites in Illinois, Indiana, Iowa, and Missouri. As a result of the flooding, we were forced to select 99 alternate sites that were accessible. We attempted to relocate sites to the nearest wetland possible; however, the flooding was so extensive that low suitability sites were often the only nearby replacements for moderate and high suitability sites. In addition, we sometimes had to travel outside of the JV region to locate replacement sites (Figure 1). Of the 264 sites surveyed in 2008, 84 were high suitability, 29 were moderate suitability, and 151 were low suitability sites. In 2009, of the 264 sites surveyed, 103 were high suitability, 67 were moderate suitability, and 94 were low suitability sites.

Marsh bird surveys

We conducted three surveys per site; each survey was approximately 20 d apart. We conducted surveys from May 5 to July 10, 2008, and from May 4 to 9 July, 2009, following the North American Marsh Bird Monitoring Protocol (Conway 2008). We broadcast breeding and territorial calls for the following species in 2008: least bittern, yellow rail *Coturnicops noveboracensis*, king rail, Virginia rail, sora, and common moorhen *Gallinula chloropus*, and included the American bittern, American coot *Fulica americana*, and pied-billed grebe in the call-playback survey in 2009. We conducted surveys from 30 min before sunrise until 1000 hours and from 1830 hours until 30 min after sunset. We did not conduct surveys during periods of high wind (≥ 19 km/h) or heavy rain or fog. We separated each survey site by ≥ 400 m to avoid double counting individuals. In 2008 we had 24 wetlands with more than one survey site each (103 total) and in 2009 we had 17 wetlands with more than one survey site each (40 total).

Habitat measurements

To estimate relations among landscape variables on marsh bird occupancy, we used FRAGSTATS 3.3 (McGarigal and Marks 1995) and spatial data from the NLCD to calculate the total area (hectares) of emergent herbaceous wetlands (includes both palustrine emergent wetlands and palustrine aquatic bed wetlands) and woody wetlands (includes both palustrine forested wetlands and palustrine scrub-shrub wetlands) within a 5-km buffer centered at the midpoint of all survey sites within a given survey area (e.g., conservation area). We used the 5-km scale because Brown and Dinsmore (1986) found the total area of marshland within 5 km of a survey site had stronger relation with species richness than marshland within 1 km.

To estimate the effects local habitat variables had on marsh bird abundance, we collected habitat measurements in a 30-m (2008) and 50-m (2009) radius circle centered at the surveyor. In 2009, we chose to collect habitat measurements at a larger scale in an attempt to

capture more habitat data indicative of the entire wetland area. We estimated the percentage of cover for the following habitat variables: open water, short emergent vegetation (< 1 m tall, e.g. smartweeds, spikerushes, and arrowleaves), tall emergent vegetation (> 1 m tall, e.g. cattails and bulrushes), and woody vegetation (e.g., buttonbushes, willows, and privets). In 2009, the approximate area of cover types in each 50-m plot was sketched, a grid was placed behind each sketch, and the number of squares containing a water-vegetation edge was summed to estimate interspersions (Rehm and Baldassarre 2007).

Data analysis

Species-group classification. We classified our marsh birds into groups based on their frequencies of co-occurrence. To accomplish this, we followed the procedures of Azeria et al. (2009) by combining null models of species co-occurrence with cluster analysis to identify groups whose members co-occurred more often than expected. This approach works best for those species who were detected at more than 5% or less than 95% of the sites (Azeria et al. 2009); species that are either very rare or ubiquitous provide little information on species co-occurrences and are difficult to place into species groups. The first step of the Azeria et al. (2009) approach was to define a “dissimilarity matrix” of the observations (Dis_{Obs}), which we did separately for each of the 2 y of the study. A dissimilarity matrix is a pairwise matrix of all species–site combinations. Two species that are never present in the same site will have a very high dissimilarity (1), whereas two species that are always present in the same site will have a low dissimilarity (0). We used the Sorensen-based coefficient of dissimilarity (Dis ; Sorensen 1948); this coefficient defines the distance between species pairs as $Dis = (b + c)/(2a + b + c)$, where a is the number of sites where both species were detected, b is the number of sites where the first species was detected but the second species was not detected, and c is the converse. This index was chosen because it is symmetric, meaning that it is the same for species A and B as for species B and A, and it is not affected by the inclusion of sites not occupied by either species (Hubálek 1982).

The second step was to calculate expected species co-occurrence patterns based on an assumption of random occurrence. This step was necessary so that the species co-occurrence matrix could be compared with that expected by chance. For this step, we created 1,000 null matrices in EcoSim 7.0 (Gotelli and Entsminger 2006) by using a fixed-row-fixed-column null model and the sequential swap algorithm. This null model maintains the number of times each species occurs and the number of species observed in each site in each of the generated matrices. For each species pair, we calculated the mean and standard deviation (SD) of the dissimilarity matrices of the generated null models. We then computed the standardized effective species (SES) pairwise dissimilarity that occurs beyond random expectation as $Dis_{SES} = (Dis_{Obs} - Dis_{SimMean})/Dis_{SimSD}$ for each year of data. The Dis_{SES} measures the number of SDs that the observed index is above or below the mean index of

Table 1. Number of detections per round of surveys and total for each marsh bird species for the Upper Mississippi River and Great Lakes Joint Venture region in 2008 and 2009.

	Round 1		Round 2		Round 3		Total	
	2008	2009	2008	2009	2008	2009	2008	2009
Pied-billed grebe <i>Podilymbus podiceps</i>	157	113	100	146	86	68	343	327
American bittern <i>Botaurus lentiginosus</i>	60	44	17	32	8	5	85	81
Least bittern <i>Ixobrychus exilis</i>	17	13	15	33	6	17	38	63
Yellow rail <i>Coturnicops noveboracensis</i>	0	0	0	0	0	0	0	0
King rail <i>Rallus elegans</i>	2	1	5	4	1	0	8	5
Virginia rail <i>Rallus limicola</i>	4	48	15	31	18	17	37	96
Sora <i>Porzana carolina</i>	46	99	10	11	6	5	62	115
Common moorhen <i>Gallinula chloropus</i>	61	12	25	36	12	21	98	69
American coot <i>Fulica americana</i>	27	73	3	62	3	33	33	168
Total	374	403	190	355	140	166	704	924

dissimilarity observed in the simulated null models, thereby identifying the degree to which each species pair co-occur more or less often than expected by chance. Because Dis_{SES} is negative for positively associated species and the distance matrix for clustering requires positive values, we rescaled the Dis_{SES} index to values between 0 and 1, with the minimum value set to 0 and the maximum set to 1. Values close to 0 indicate a strong positive association between species and values approaching 1 represent a strong negative association.

The final step was to determine the species groups for each year of data by using hierarchical clustering. For this step, we used Ward's algorithm method (Ward 1963) as implemented in the 'hclust' function in the package 'maptree' version 1.4–6 (White 2010) in program R version 2.12.0 (R Development Core Team 2010). Ward's algorithm method uses an analysis of variance approach that minimizes the sum of squares at each level to create clusters of like objects.

To determine the optimal number of species groups in each of the hierarchical trees generated for the 2 y of data, we used the Kelley–Gardner–Sutcliffe penalty function (Kelley et al. 1996) as implemented in the 'kgs' function in 'maptree.' This method determined the optimal number of species groups by determining the number of species groups that would maximize the differences between groups and cohesiveness within groups.

Relation of groups to habitat variables. To estimate relations among species groups and the landscape and local site characteristics, we used zero-inflated abundance models that accounted for incomplete detection (Wenger and Freeman 2008). Because of the differences in habitat caused by heavy precipitation in 2008, we ran models for 2008 and 2009 separately. These models simultaneously estimate detection (p), occupancy (Ψ), and abundance (λ) probabilities. Poisson models are frequently used in analyses of avian count data; however, the assumption that the mean and variance are equal in Poisson models is often not met due to high variation in the number of birds observed. Negative binomial models allow for higher variance in relation to the mean and hence better fit datasets with over-

dispersion, but these models require the estimation of an additional parameter. Because of this issue, we fit both Poisson and negative binomial distribution models of bird abundance and used Akaike's Information Criterion (AIC) rankings to determine which distribution model better fit the data. Because of small sample sizes for some species (Table 1), we found that the stability of some estimates was poor as evidenced by relatively large standard errors suggesting numerical problems (Hosmer and Lemeshow 2000:138). To address this problem, we chose to reduce uncertainty in our results by excluding those estimates where the standard error exceeded half of the value of the β point estimate. When necessary, explanatory variables were transformed to approximate normality; no variables were transformed for the 2008 dataset, and interspersed and open water were log transformed for the 2009 dataset.

To account for the possibility that observers differed in their ability to detect secretive marsh birds, we first modeled detection using both observers and a constant rate of detection (null) for each of the species groups. After determining whether detection was best modeled with an observer effect or the null, we then investigated landscape variables because Fairbairn and Dinsmore (2001) found that the total area of all wetland habitat within 3 km explained wetland bird species richness, whereas emergent cover within a wetland explained species densities. Naugle et al. (2001) also found many wetland-dependent birds in the Prairie Pothole Region were directly affected by both local and landscape variables. Thus, we assumed that marsh birds would use landscape variables during migration to decide which wetland to occupy, and then, once at that site, they would use local habitat variables to make decisions about specific areas within the wetland to use; hence, abundance would reflect those decisions. We modeled occupancy using woody wetland area within 5 km and emergent herbaceous wetland area within 5 km (Brown and Dinsmore 1986); only the variable with the lowest AIC ranking was used in subsequent models. Abundance was then modeled using percentage of cover of woody vegetation, short emergent vegetation, tall emergent

vegetation, and open water. In 2009, we also modeled abundance using interspersions. We were unable to assess whether landscape or local variables were better at explaining marsh bird presence and abundance, respectively, than null models because the Wenger and Freeman (2008) program does not allow null models for either occupancy or abundance estimation.

Results

Of the seven species that we surveyed, both the yellow rail (no detections either year) and the king rail (eight detections in 2008, five detections in 2009) were poorly represented (Table 1; also see *Supplemental Material*, Table S1; <http://dx.doi.org/10.3996/012011-JFWM-001.S1>). In 2008, for the remaining species, we detected a low of 33 American coots to a high of 343 pied-billed grebes. In 2009, for the remaining species, we detected from a low of 63 least bitterns to a high of 327 pied-billed grebes.

Because both the yellow rail and king rail made up less than 5% of the marsh bird detections, we could not include them in our classification analysis. We identified two species (least bittern and American bittern) that occurred less frequently with other marsh birds than expected by chance and two species groups—rails (sora and Virginia rail) and open-water birds (pied-billed grebe, common moorhen, and in 2009, American coot)—whose members co-occurred more often than expected by chance. Our species groupings were consistent between the 2 y of study (Figure 2).

We detected one or more marsh bird groups at 156 sites (59%) in 2008 and 185 sites (70%) in 2009. We detected all four marsh bird groups at one site in 2008 and at three sites in 2009. We found fewer sites were occupied by each marsh bird group in 2008 than in 2009 (Figure 3). Overall, the open-water species group occupied the most sites during both years (125 in 2008, 130 in 2009), followed by the rail group (50 in 2008, 93 in 2009), American bittern (44 in 2008, 46 in 2009), and least bittern (25 in 2008, 39 in 2009).

In both years across all sites, emergent herbaceous wetland cover was approximately the same (2008: \bar{x} = 643 ha, range = 17–2039 ha; 2009: \bar{x} = 713 ha, range = 4–3353 ha), whereas woody wetland covered approximately twice the area in 2008 (\bar{x} = 792 ha, range = 0–2798 ha) as in 2009 (\bar{x} = 459 ha, range = 0–2554 ha). Based on the model selection results (Table 2), occupancy was negatively associated with the amount of woody wetland in the landscape for least bitterns in 2008, rails in 2008, and open-water birds in 2008 (Table 3). Least bitterns in 2009 were positively associated with the amount of emergent herbaceous wetland in the landscape. We found no landscape variables that were associated with American bittern occupancy.

Local habitat variable measurements reflected the effects of flooding in 2008 with open water (2008: \bar{x} = 33%, range = 0–99%; 2009: \bar{x} = 23%, range = 0–82%) and woody cover (2008: \bar{x} = 10%, range = 0–100%; 2009: \bar{x} = 6%, range = 0–97%) being higher in 2008, whereas short emergent cover (2008: \bar{x} = 7%, range =

0–90%; 2009: \bar{x} = 21%, range = 0–97%) and tall emergent cover (2008: \bar{x} = 15%, range = 0–100%; 2009: \bar{x} = 48%, range = 0–100%) were lower in 2008. In 2009, interspersions had a mean of 11% (range = 0–46%; Table 3). Modeling results of the response of group and species abundance to local habitat variables varied by year (Tables 2 and 3). There was strong support for percentage of cover of short emergent vegetation having a negative relationship with American bittern abundance in 2008. For least bitterns as well, the model containing percentage of cover of short emergent vegetation was the best supported model in 2008 with abundance increasing with short emergent vegetation cover, whereas in 2009 the model containing interspersions had the most support with abundance increasing with interspersions. The model containing short emergent vegetation also had support for rails in 2008, with rail abundance decreasing with short emergent vegetation cover but not in 2009, when rail abundance decreased with woody vegetation cover. For the open-water bird group, the model containing open water was the only supported model in 2008, with abundance increasing with open-water coverage, but in 2009 the model containing interspersions had the most support, with abundance increasing with interspersions (note that interspersions was not recorded in 2008).

Discussion

We identified two groups (rails and open-water birds) whose members tended to co-occur more often than expected by random chance and two species (least bittern and American bittern) that tended to co-occur with other marsh bird species less often than expected by random chance. Recently, managers have placed greater emphasis on managing for secretive marsh birds, especially those that are classified as a “Bird of Management Concern” or a “Gamebird below Desired Condition” in the United States by the USFWS (2008, Cooper 2008) and birds that are federally endangered species in Canada (Government of Canada 2010). However, not all secretive marsh birds co-occur, making management of multiple species difficult. By recognizing which sets of species that have similar or distinct response patterns to habitat types (Raphael and Molina 2007; Rodrigues and Brooks 2007), managers can better tailor their management strategies for the conservation of particular species or groups.

The basis for many federal and state land management decisions with respect to animals is commonly determined via indicator species, but there is an ongoing debate regarding the validity of this practice (Lindenmayer and Likens 2011). We recognize the limitations of this approach, which include, among others, poor justification of why a species is an indicator species, and a lack of transferability within groups, between groups, and between locations and over time (Lindenmayer and Likens 2011). In our case, secretive marsh birds are by definition difficult to detect (detection probabilities <0.4%, Darrah and Kremetz 2009) and are often rare (occupancy rates <0.15%, Darrah and Kremetz 2009). Thus, we collected data on the marsh

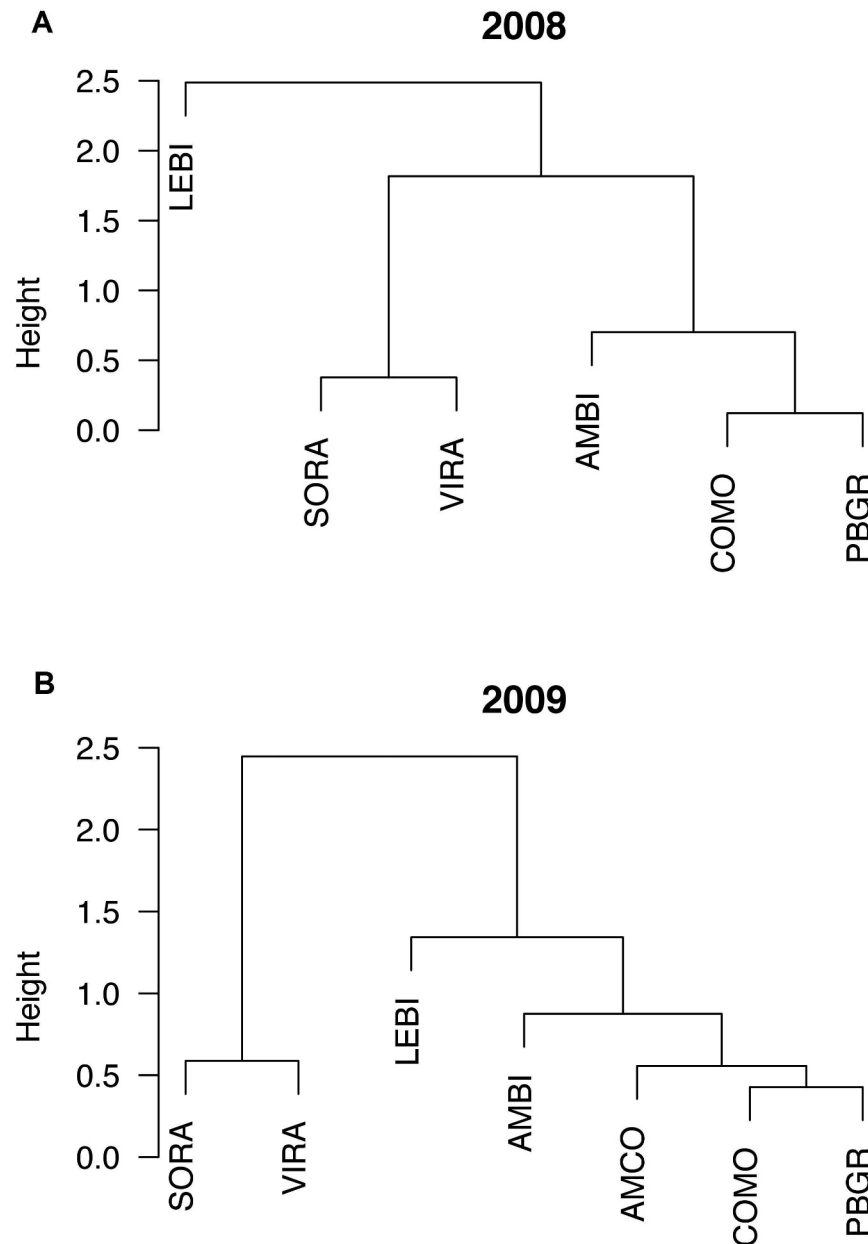


Figure 2. Dendrograms showing species groups as classified by co-occurrence based on hierarchical clustering and Ward's agglomeration algorithm for marsh birds surveyed during summers of 2008 (**A**) and 2009 (**B**) across the Upper Mississippi River and Great Lakes Joint Venture region. AMBI = American bittern *Botaurus lentiginosus*, AMCO = American coot *Fulica americana*, COMO = common moorhen *Gallinula chloropus*, LEBI = least bittern *Ixobrychus exilis*, PBGR = pied-billed grebe *Podilymbus podiceps*, SORA = sora *Porzana carolina*, and VIRA = Virginia rail *Rallus limicola*. American coots were only included in surveys during 2009.

bird community in the event that if our detections of certain species were inadequate to determine individual species-habitat relations, we could turn to the surrogate approach. We felt that using surrogates allowed us to offer managers some alternative management practices that are of value to the more common marsh birds in the hopes that there will be additional, positive effects for the rarer marsh birds. If managers want to manage wetlands for secretive marsh birds, we see the surrogate approach as a valid approach at this time.

To our knowledge, we are the first to estimate co-occurrences of marsh birds by using a formal analytical

approach. However, naturalists have produced similar marsh bird groupings based on field observations. Weller (1999) summed up his field observations of marsh birds of robust or persistent herbaceous emergent wetlands into several groups, including 1) walking rails (Virginia rail, sora, and king rail) that prefer shallow water to almost dry ground for both nest sites and feeding locations (Weller and Spatcher 1965), 2) bitterns that nest among the top of robust emergents and also feed there during nesting, and 3) swimming rails (American coots and common moorhens) that use deeper to shallow water where they nest in emergents but feed in open

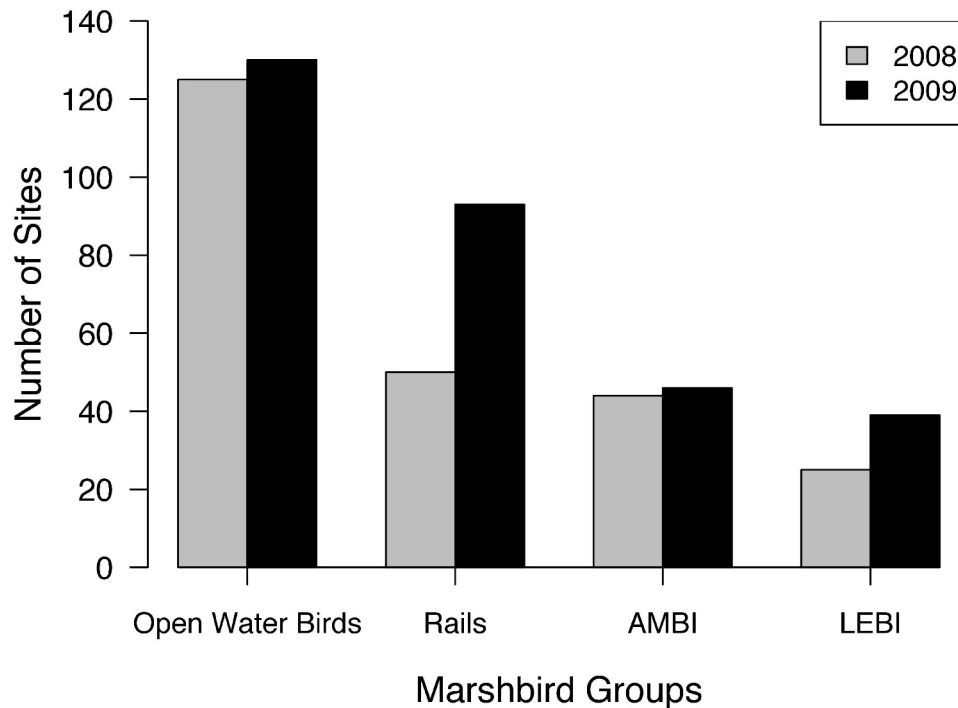


Figure 3. Total number of sites ($n = 264$ each year) each species (AMBI = American bittern *Botaurus lentiginosus*, LEBI = least bittern *Ixobrychus exilis*) and marsh bird group (Rails [Rallidae], Open Water Birds [Podicipedidae, Rallidae]) occupied during the 2008 and 2009 breeding seasons across the Upper Mississippi River and Great Lakes Joint Venture region.

water. Our marsh bird associations were similar to those of Weller (1999), with the exception that our approach separated the bitterns. In both of our annual assessments, the American bittern was more closely grouped to the open-water birds than was the least bittern. We speculate that American bitterns grouped with the open-water birds because they tended to occupy sites that were adjacent to open water. In the flood-prone year of 2008, least bitterns were more closely grouped with rails than with American bitterns.

The only marsh bird group associated with emergent herbaceous wetlands in an area at the landscape level was for least bitterns in 2009, whereas in 2008, the proportion of woody wetlands in an area was negatively associated with least bitterns, rails, and open-water birds. The only marsh bird group not related to either landscape measurement was the American bittern. We were surprised that American bittern occupancy was not related in a positive way to emergent herbaceous wetlands because in a review of American bittern habitat use during the breeding season, Gibbs et al. (1992) stated that tall emergent vegetation is typically used by American bitterns, and Hay (2006) reported that American bitterns were associated with increased proportions of marsh area within 5 km. Three marsh bird groups were negatively associated with woody wetlands in the landscape during 2008. This annual effect was, in part, a consequence of the much greater coverage of woody wetlands in 2008 ($\bar{x} = 791$ ha) compared with in 2009 ($\bar{x} = 458$ ha), resulting in less coverage of emergent herbaceous wetlands in 2008.

In contrast to landscape habitat associations, only a single local habitat association was consistent across groups within a year: least bitterns and open-water birds were positively associated with interspersed. The importance of a heterogeneous habitat for these species has been found in other studies. Weller and Spatcher (1965) noted that American coot, common moorhen, and pied-billed grebe all were more abundant at sites with dense emergents that were well interspersed with open pools. Lor and Malecki (2006) found least bitterns and pied-billed grebes were more likely to nest in wetlands that closely approximated a 50:50 cover-to-water ratio compared with the American bittern, Virginia rail, and sora that were found more often in wetlands that were highly vegetated (70–100%). Brackney and Bookhout (1982) found common moorhen densities were greatest in wetlands with approximately 50% open water interspersed with emergent vegetation. In New York, relative abundance of least bitterns was positively related to increasing amounts of interspersed (Rehm and Baldassarre 2007).

For all other local habitat associations, there were no consistent patterns across species within a year or between years, possibly due to the extensive flooding in 2008. During surveys in 2008, many wetlands were flooded into the adjacent uplands, and the marsh birds were forced into suboptimal habitats at those times. This was reflected in our difficulty in replacing both moderate- and high-scored wetlands with similar wetlands nearby. Only low-scoring wetlands were available to substitute for better sites that year. Still, in 2009, when water levels were normal, other than the consistent

Table 2. Habitat relation model results ($<\Delta AIC_c = 10$; change in Akaike's Information Criterion adjusted for small sample size) by species, group, and year (2008, 2009) for the Upper Mississippi River and Great Lakes Joint Venture region, where ψ = occupancy, λ = abundance, p = detection, K = number of parameters, EHW = emergent herbaceous wetland area within 5 km, WW = woody wetland area within 5 km, SE = short emergent vegetation, TE = tall emergent vegetation, WV = woody vegetation, OW = open water, INT = interspersed (2009 only), and OBS = observers.

Group	Year	Model	AIC _c	ΔAIC_c	K
American bittern <i>Botaurus lentiginos</i>	2008	ψ (EHW) λ (SE) $p(\cdot)$	501.62	0.00	5
		ψ (EHW) λ (SE+SE ²) $p(\cdot)$	508.47	6.85	6
		ψ (EHW) λ (TE) $p(\cdot)$	511.15	9.53	5
	2009	ψ (WW) λ (TE) $p(\cdot)$	507.72	0.00	5
		ψ (WW) λ (TE+TE ²) $p(\cdot)$	509.26	1.54	6
		ψ (WW) λ (WV) $p(\cdot)$	509.53	1.81	5
		ψ (WW) λ (SE) $p(\cdot)$	509.72	2.00	5
		ψ (WW) λ (OW) $p(\cdot)$	510.09	2.37	5
		ψ (WW) λ (INT) $p(\cdot)$	510.13	2.41	5
		ψ (WW) λ (WV+WV ²) $p(\cdot)$	511.00	3.28	6
		ψ (WW) λ (INT+INT ²) $p(\cdot)$	511.54	3.82	6
		ψ (WW) λ (SE+SE ²) $p(\cdot)$	511.69	3.97	6
		ψ (WW) λ (OW+OW ²) $p(\cdot)$	512.11	4.39	6
		Least bittern <i>Ixobrychus exilis</i>	2008	ψ (WW) λ (SE) $p(\cdot)$	1,546.09
ψ (WW) λ (OW) $p(\cdot)$	1,553.30			7.21	5
ψ (WW) λ (OW+OW ²) $p(\cdot)$	1,553.37			7.28	6
2009	ψ (EHW) λ (INT) p (OBS)		419.66	0.00	9
	ψ (EHW) λ (INT+INT ²) p (OBS)		420.50	0.84	8
	ψ (EHW) λ (TE) p (OBS)		423.66	4.00	8
	ψ (EHW) λ (WV) p (OBS)		423.83	4.17	8
	ψ (EHW) λ (OW) p (OBS)		423.85	4.19	8
	ψ (EHW) λ (SE) p (OBS)		423.91	4.25	8
	ψ (EHW) λ (WV+WV ²) p (OBS)		424.88	5.22	9
	ψ (EHW) λ (SE+SE ²) p (OBS)		425.44	5.78	9
	ψ (EHW) λ (TE+TE ²) p (OBS)		425.80	6.14	9
	ψ (EHW) λ (OW+OW ²) p (OBS)		425.97	6.31	9
	Rails (Rallidae)		2008 ^a	ψ (WW) λ (SE) $p(\cdot)$	1,502.53
2009 ^a		ψ (EHW) λ (WV) p (OBS)	1,039.79	0.00	10
		ψ (EHW) λ (TE) p (OBS)	1,043.62	3.83	9
		ψ (EHW) λ (TE+TE ²) p (OBS)	1,044.33	4.54	10
		ψ (EHW) λ (INT) p (OBS)	1,048.43	8.64	9
		ψ (EHW) λ (OW) p (OBS)	1,048.55	8.76	9
		ψ (EHW) λ (INT+INT ²) p (OBS)	1,049.71	9.92	10
Open-water birds (Podicipedidae, Rallidae)	2008 ^a	ψ (WW) λ (OW) $p(\cdot)$	1,482.32	0.00	6
		ψ (WW) λ (OW+OW ²) $p(\cdot)$	1,483.90	1.58	7
	2009 ^a	ψ (WW) λ (INT) $p(\cdot)$	1,629.88	0.00	6
		ψ (WW) λ (INT+INT ²) $p(\cdot)$	1,631.61	1.73	7
		ψ (WW) λ (OW) $p(\cdot)$	1,635.20	5.32	6
		ψ (WW) λ (OW+OW ²) $p(\cdot)$	1,637.11	7.23	7
	ψ (WW) λ (WV) $p(\cdot)$	1,639.20	9.32	6	

^a Negative binomial used.

importance of interspersed, we found no habitat associations that were consistent among groups.

Increased amounts of woody wetlands on a landscape scale and woody vegetation on a local scale decrease the amount of available emergent herbaceous wetland habitat vital for breeding marsh birds; woody vegetation

also may act as a pathway, corridor, or perch site for predators and thereby increase nest predation and reduce reproductive success (Naugle et al. 1999; DeLuca et al. 2004). When secretive marsh birds are the management goal driving wetland restoration, conservation, or mitigation projects, our data suggest conserving areas

Table 3. Untransformed parameter estimates ($\hat{\beta} \pm SE$) for the top selected models comparing landscape variable to species occupancy and local habitat variables to species abundance in 2008 and 2009 for marsh birds surveyed in the Upper Mississippi River and Great Lakes Joint Venture region. The mean amount of woody and emergent herbaceous wetlands within 5 km of survey sites, and the percent of coverage of local habitat variables at each survey point are listed for each year.

Landscape Level Variables	Mean	Species		
		American bittern <i>Botaurus lentiginos</i>	Least bittern <i>Ixobrychus exilis</i>	Rails (Rallidae)
Emergent herbaceous wetlands (ha)				
2008	643.3			
2009	713.4		0.93 (0.39)	
Woody wetlands (ha)				
2008	791.8		-0.41 (0.20)	-0.48 (0.14)
2009	458.5			-0.88 (0.33)
Local habitat variables				
Short emergents (%)				
2008	7.4	-0.91 (0.30)	0.64 (0.27)	-0.59 (0.26)
2009	20.7			
Tall emergents (%)				
2008	14.8			
2009	47.9			
Interspersion (%) ^a				
2009	0.11		9.17 (4.57)	15.15 (3.67)
Woody vegetation (%)				
2008	9.8			
2009	5.6			-0.56 (0.19)
Open water (%)				
08	32.9			0.82 (0.19)
09	22.8			

^a Interspersion given as proportion of gridded squares containing a water-vegetation edge. No interspersion data were collected in 2008.

with a large amount of emergent herbaceous wetlands and a low amount of woody wetlands within the landscape and managing for high amounts of water-vegetation interspersion within the wetland.

Supplemental Material

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Table S1. Local: habitat measurements in a 30-m (2008) and 50-m (2009) radius circle centered at the surveyor. Open.water = percentage of open water; short.emergent = percentage of short emergent vegetation (<1 m tall, e.g., smartweeds, spikerushes, and arrowleaf); tall.emergent = percentage of tall emergent vegetation (>1 m tall, e.g., cattails and bulrushes); woody.veg = percentage of woody vegetation (e.g., buttonbushes, willows, and privets); interspersion = the number of squares containing a water-vegetation edge in a grid covering each 50-m plot (2009 only). Landscape: total area (hectares) within a 5-km buffer centered at the

midpoint of all survey sites within a given survey area (e.g., refuge and conservation area). Emergent.herb.wetland = emergent herbaceous wetlands (includes both palustrine emergent wetlands and palustrine aquatic bed wetlands); woody.wetland = woody wetlands (includes both palustrine-forested wetlands and palustrine scrub-shrub wetlands).

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