

2013

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Abstract

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Keywords

bittern, grebe, iowa, marsh bird, occupancy, rail

Disciplines

Behavior and Ethology | Natural Resources Management and Policy | Ornithology | Other Ecology and Evolutionary Biology

Comments

This is a manuscript of an article from *Wetlands* 33 (2013): 561, doi:10.1007/s13157-013-0414-0. Posted with permission. The final publication is available at Springer via <http://dx.doi.org/10.1007/s13157-013-0414-0>.

Habitat associations of secretive marsh birds in Iowa

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Abstract Drastic losses of wetland habitats across North America over the past century have resulted in population declines of many marsh birds therefore emphasizing the need for proper management of remaining wetlands for the conservation of marsh birds. Our objective was to evaluate the probability of site occupancy of secretive marsh birds in Iowa in response to habitat variables at multiple scales. We conducted call-broadcast surveys for eight species of marsh birds at wetlands in Iowa from 16 May – 15 July 2009 and from 20 April – 10 July 2010. We utilized occupancy models in Program MARK to estimate site occupancy probability based on habitat covariates for four species with the most detections (Pied-billed Grebe [*Podilymbus podiceps*], Least Bittern [*Ixobrychus exilis*], Virginia Rail [*Rallus limicola*], and Sora [*Porzana carolina*]). Wetland size had a positive effect on site occupancy for Least Bitterns, water depth positively affected site occupancy for Pied-billed Grebes and Least Bitterns, and percent cover of cattail positively affected site occupancy for Virginia Rails. Knowing habitat associations of secretive marsh birds in Iowa will allow us to provide guidance on wetland restoration and management decisions that will aid the conservation of these birds.

Keywords bittern, grebe, Iowa, marsh bird, occupancy, rail

Introduction

Drastic losses of wetland habitats across North America over the past century have resulted in declines of many populations of marsh birds (Eddleman et al. 1988, Conway et al. 1994, Conway 2008, 2011). Greater than 90% of wetlands were lost across the

United States by the 1970s with the greatest losses occurring in the Midwest and California (Tiner 1984, Dahl 1990). In Iowa, more than 98% of wetlands have been drained for agricultural purposes since settlement, leaving <30,000 acres of the original 7.6 million acres of wetland habitat by 1980 (Bishop 1981). In response to these wetland losses, several species of marsh birds are of heightened conservation concern at the state and regional levels (Lor and Malecki 2002, Conway and Gibbs 2005). The need for proper management of remaining wetlands for the conservation of marsh birds and other wetland-dependent birds is emphasized by this loss of wetland habitats (Lor and Malecki 2006, Rehm and Baldassarre 2007, Darrah and Krementz 2010).

Until recently, little was known about population trends and habitat preferences of secretive marsh birds across the United States and, in Iowa, we know very little about their population status and distribution and life history requirements. Additionally, few studies (Darrah and Krementz 2010, Bolenbaugh et al. 2011) have examined habitat associations of marsh birds in the Great Plains region of the United States, an area likely critical to marsh bird reproduction given species' breeding ranges. Their secretive nature and tendency to occupy habitats with dense emergent vegetation makes monitoring these birds very difficult (Lor and Malecki 2002). The North American Marsh Bird Monitoring Program (see <http://ag.arizona.edu/research/azfwru/NationalMarshBird/>) was developed as a result of the lack of information and lack of effective survey methods. The goal of this program was to develop a standardized set of survey protocols that could be implemented across the U.S. as a long-term monitoring tool to gain more information on secretive marsh birds in the U.S. including status and population trends, habitat

associations, and the effectiveness of targeted survey methodologies (Conway 2008, 2011).

Several studies have examined habitat associations of marsh birds relative to different wetland characteristics. For example, some studies have examined the effects of different landscape-level variables on habitat use such as degree of isolation (Brown and Dinsmore 1986, 1988, Craig and Beal 1992, Fairbairn and Dinsmore 2001), wetland size (Brown and Dinsmore 1986, 1988, Craig and Beal 1992, Craig 2008), and adjacent land use (Smith and Chow-Fraser 2010). Other studies have evaluated the effects of local-scale characteristics such as water-vegetation interspersion (Lor and Malecki 2006, Rehm and Baldassarre 2007), vegetation density and height (Sayre and Rundle 1984, Lor and Malecki 2006, Darrah and Krementz 2010), and water level and fluctuation (Gonzalez-Gajardo et al. 2009). Little research, however, has utilized occupancy models to evaluate how different habitat characteristics affect the probability of marsh birds to occupy particular wetlands across Iowa when detection probability is <1 (Darrah and Krementz 2010, Bolenbaugh et al. 2011). The goal of our study was to evaluate the probability of site occupancy by secretive marsh birds in Iowa in response to habitat variables at multiple spatial scales.

Methods

Study area and site selection

We used the National Wetlands Inventory (NWI; USFWS 2009) as a base from which to select our sites. The NWI classifies wetlands into systems, subsystems, and classes based

on wetland characteristics (USFWS 2009). We considered wetlands from the Aquatic Bed (AB), Emergent (EM), and Unconsolidated Bottom (UB) classes of the Palustrine system (Wilen and Bates 1995). Wetlands within these classes fit one or more of the following general habitat criteria required by one or more of our target species: 1) shallow water (less than 1m deep; Sayre and Rundle 1984, Johnson and Dinsmore 1986), 2) surrounded by few or no trees (Winstead and King 2006, Darrah and Kramentz 2010), and 3) the presence of emergent vegetation (Johnson and Dinsmore 1986, Darrah and Kramentz 2010, Benoît et al. 2011). We considered both natural and constructed wetlands for selection. Most wetlands were permanent or semi-permanent given the higher percentage of this wetland type in Iowa, although some temporary or seasonal wetlands were also represented in our selection (Stewart and Kantrud 1971). Wetlands contained a mix of emergent vegetation that included cattail (*Typha* spp.), sedge (*Carex* spp.), river bulrush (*Scirpus fluviatilis*), soft-stem bulrush (*Schoenoplectus tabernaemontani*), and reed canarygrass (*Phalaris arundinacea*). Mean water depth at survey points within wetlands was 30 cm (\pm 1 cm) ranging from 0 to 115 cm.

Using the NWI database, we stratified wetlands into six size classes based on area (ha) (\leq 5 ha, >5-10 ha, >10-20 ha, >20-30 ha, >30-40 ha, and >40 ha). We randomly selected wetlands from each size class using Hawth's Analysis Tools for ArcGIS (Beyer 2004). Stratification allowed for an equal representation of both large and small wetlands and ensured that potential area-dependent bird species were sampled (Brown and Dinsmore 1986). To facilitate access for surveys, we only selected wetlands that were on public lands, which accounted for approximately 8% of the total number of wetlands in

the NWI database for Iowa. We randomly assigned a fixed number of survey points 400 m apart to wetlands within each size class to allow for maximum coverage of each wetland and to minimize double-counting birds (Conway 2008, 2011). We assigned 1 point to both the ≤ 5 ha and $>5-10$ ha size classes, 2 points to the $>10-20$ ha size class, 3 points to the $>20-30$ ha size class, 4 points to the $>30-40$ ha size class, and 5 points to the >40 ha size class. The number of survey points placed along the wetland edge compared to those placed in the interior of the wetland depended largely on wetland size. The probability of survey points being randomly placed along the wetland edge was greater in smaller wetlands than in larger wetlands due to the decreased amount of wetland interior in smaller wetlands. In few cases, survey points placed in the interior of the wetland were moved slightly closer to the wetland edge to facilitate access. This random placement of points both along the wetland edge and in the interior of the wetland allowed for an adequate representation of the varying water depths and other habitat characteristics present in the wetland.

Habitat measurements

Prior to conducting surveys, we measured habitat variables at each survey point within each wetland. We conducted measurements at both the survey point and within a 50-m radius of the survey point to assess local habitat characteristics (Conway 2008, 2011). We measured water depth (cm; WATERDEP) and maximum vegetation height (m; VEGSIZE) at the survey point. Vegetation height was measured from the surface (either the ground or surface of the water) and assigned to one of three size classes (1 = 0.0-0.5

m, 2 = 0.5-1.0 m, 3 = >1.0 m). Within a 50-m radius of the survey point, we visually estimated percent coverage of the major types of emergent vegetation (Conway 2008, 2011). These vegetation types included cattail (*Typha* spp.; CATTAIL), bulrush (*Schoenoplectus* spp.; BULRUSH), sedge (*Carex* spp.; SEDGE), reed canarygrass (*Phalaris arundinacea*; REEDCAN), and woody vegetation (WOOD). We took the sum of all vegetation cover estimates to obtain the total percent coverage of emergent vegetation (TOTVEG). We also visually estimated the percent coverage of open water (WATER). Percent coverage was estimated in 5% increments. We assumed that the mean of all local habitat variables measured at survey points within each wetland was representative of habitat characteristics in the entire wetland (Darrah and Krementz 2010).

Using ArcGIS (v. 9.3; ESRI 2009), we measured five landscape-level variables we hypothesized may affect marsh bird occupancy based on a review of the literature and on our prior knowledge of marsh birds in Iowa. We obtained wetland size (ha; WETSIZE) for each surveyed wetland from the NWI database. The NWI database includes size (ha) as a measured characteristic for each wetland polygon in the database. Wetland size was an important variable because studies have shown that larger wetlands host greater avian diversity (Brown and Dinsmore 1986, 1988) and because some of our study species are potentially area-dependent. Those species are Pied-billed Grebe (Brown and Dinsmore 1986, Naugle et al. 1999), American Bittern (Brown and Dinsmore 1986), Least Bittern (Brown and Dinsmore 1986), King Rail (Craig 1990), and Common Moorhen (Chabot 1996). Using ET Geo Wizards extension for ArcGIS

(Tchoukanski 2011), we measured distance to the nearest wetland (m; DIST). We calculated the area of wetland habitat within a 1 km (ONEKM), 3 km (THREEKM), and 5 km (FIVEKM) buffer of the periphery of the surveyed wetland to assess the degree of isolation of the surveyed wetland (Brown and Dinsmore 1986).

Bird surveys

We conducted unlimited-radius point counts in conjunction with call-broadcast surveys from 16 May to 15 July 2009 and from 20 April to 10 July 2010 during the early-morning (one-half hour before sunrise to three hours after sunrise) and late-evening (three hours before sunset to one-half hour after sunset). In accordance with the North American Marsh Bird Monitoring Protocol (Conway 2008, 2011), we conducted surveys for eight species of secretive marsh birds: Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosis*), Least Bittern (*Ixobrychus exilis*), King Rail (*Rallus elegans*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Moorhen (*Gallinula chloropus*), and American Coot (*Fulica americana*). We surveyed 56 wetlands four times during 2010 to create the encounter histories necessary to estimate probability of site occupancy and detection probability (MacKenzie et al. 2002). We also included data from single surveys of 253 wetlands during 2009 and 2010. Therefore, all wetlands were surveyed a minimum of one time, and some were surveyed as many as four times. Using an mP3 player (SanDisk Sansa Clip 1GB, SanDisk Corporation, Milpitas, California, USA) attached to a pair of amplified speakers (Panasonic Model RPSPT70, Panasonic Corporation, Secaucus, New Jersey, USA), we broadcast the call

sequence at 90 dB 1 m from the source (Conway 2008, 2011). We placed the speakers 0.5 m from the substrate (ground or water surface) and pointed them towards the interior of the wetland. The call-broadcast sequence was obtained from the North American Marsh Bird Monitoring Program coordinator (Conway 2008, 2011) and consisted of a 5-minute passive listening period followed by 8 minutes of vocalizations. Each minute of the 8-minute call-broadcast period corresponded to one species and consisted of 30 seconds of vocalizations and 30 seconds of silence. Vocalizations were ordered by species dominance so that all species heard their conspecific calls prior to the calls of more dominant coexisting species (Conway 2008, 2011). We recorded all visual and aural detections of all eight target species at each survey point.

Using a Weather Kestrel 4000 (Nielsen Kellerman, Boothwyn, Pennsylvania, USA), we measured wind speed (Beaufort; bft) and temperature ($^{\circ}\text{C}$). We visually estimated the amount of cloud cover and assigned it to one of four categories (0 – few or no clouds, 1 – partly cloudy, 2 – cloudy or overcast, 4 – fog). We refrained from conducting surveys during periods of rain or when wind speeds exceeded 12 km/hr. Most survey points were accessed by foot, although we used a canoe to reach points on some larger wetlands.

Occupancy models

We used the site occupancy model (MacKenzie et al. 2002) in Program MARK (White and Burnham 1999) to evaluate the effects of habitat variables on site occupancy of marsh birds. Parameters generated by this model include the probability that marsh birds

occupy a particular wetland (ψ) and the probability of detecting marsh birds given that they are present (p). We modeled site occupancy for three species that had the greatest number of detections. Those species were Pied-billed Grebe, Least Bittern, and Virginia Rail. We were unable to model site occupancy for Soras because they are migrants in Iowa and were assumed to violate the closure assumption of occupancy modeling. The site occupancy model in Program MARK estimates the above mentioned parameters from encounter histories generated from repeated surveys of sites (MacKenzie et al. 2002, White and Burnham 1999). Because Least Bitterns do not arrive in Iowa until mid-May, we truncated the data for this species to 15 May for both years. We assumed that each wetland was independent and was closed to changes in occupancy state by marsh birds throughout the survey season. The assumption of closure was reasonable in our study because our surveys were restricted to a portion of the marsh bird nesting season, a time when each focal species was unlikely to be immigrating or emigrating from a wetland (Darrah and Kremenz 2010). Pied-billed Grebes arrive in mid-March and initiate nesting in late April (Kent and Dinsmore 1996). Least Bitterns don't arrive in Iowa until mid-May and initiate nesting in late May or early June (Kent and Dinsmore 1996). Virginia Rails arrive in Iowa in late April and initiate nesting in early May (Kent and Dinsmore 1996). We may have detected some migrant Virginia Rails in late April, but most birds were likely establishing breeding territories at this time. Soras arrive in Iowa in late April but migrants are still observed through mid-May with nests initiated in late May or early June.

Based on an extensive literature review and our own observations pertaining to habitat associations of secretive marsh birds, we developed species-specific predictions about the effects of different habitat variables on site occupancy probability (ψ). We also considered the life history characteristics of each species when developing hypotheses. Predicted effects of habitat variables on site occupancy probability are listed in Table 3.

We included variables wind speed (WIND), temperature (TEMP), cloud cover (CLOUD), and observer (OBS) as factors affecting detection probability. We modeled detection probability as a time-varying parameter by day to account for seasonal differences in vocalization frequencies of the target species (T.M. Harms, pers. obs.). Observers ($n = 4$) were familiar with vocalizations of target species and highly trained at detecting birds at varying distances. Training included repeated exposure to all calls of each species, then placing the call-broadcast system in wetlands and blindly positioning observers at distances varying from 10-500 m. Training was conducted for each species at wetlands with different vegetative conditions (vegetation density and height) and during various weather conditions.

We utilized a two-step modeling process by which covariates on p were modeled first while keeping ψ constant; the top model for p was then included in the models for ψ (Olsen et al. 2005, Kroll et al. 2010). When modeling ψ , we envisioned a hierarchical model selection framework similar to that described by Johnson (1980) in which birds are first selecting for broad-scale, landscape variables to establish home ranges and then select for microhabitat variables to establish feeding and nesting sites. When building

models, we first included landscape-level variables (WETSIZE, DIST, ONEKM, THREEKM, FIVEKM) and then added local-level habitat variables. We modeled all landscape-level variables individually and then modeled combinations of landscape-level variables that received the most support in the single-variable models to determine the best-supported combination. Next, we added local-level habitat variables singly to the best-supported model of landscape-level variables. Based on our review of the literature and prior knowledge of marsh birds, we added those local-level habitat variables we hypothesized would affect site occupancy of a particular species. Local-level habitat variables included WATERDEP and VEGSIZE, as well as percent cover of each individual vegetation type (CATTAIL, BULRUSH, SEDGE, REEDCAN, WOOD), percent cover of open water (WATER), and total percent cover all vegetation combined (TOTVEG). Lastly, we modeled the best-supported combination of landscape-level variables and the best-supported combination of local-level variables to obtain the overall best-supported, biologically-relevant model. Therefore, the overall best-supported model could include one to many landscape-level variables and one to many local-level variables depending model selection results. A similar approach was used by Cunningham and Johnson (2006) when evaluating distributions of grassland birds at multiple spatial scales. We compared models using Akaike's Information Criterion (AIC) adjusted for small sample sizes (AIC_c) and considered models with $\Delta AIC_c \leq 2$ to have strong support (Burnham and Anderson 2002). There is currently no test for overdispersion in these data because the occupancy model in Program MARK does not currently have a goodness-of-fit test. We assessed correlation among the site-specific

covariates by constructing a correlation matrix. Variables with $r \geq 0.80$ were considered highly correlated (Lor and Malecki 2006). Pairs of highly correlated variables included TOTVEG and WATER ($r = -0.98$), ONEKM and THREEKM ($r = 0.85$), and THREEKM and FIVEKM ($r = 0.96$). Therefore, we did not include these pairs of variables as additive effects in the models.

We obtained model-based predictions of site occupancy probability by utilizing the user-specified covariate values option in Program MARK. We used the best model for each species and specified a range of values for the covariate of interest while setting values for all other covariates in the model to the mean, therefore allowing us to obtain a set of occupancy predictions for species based on a range of values for biologically-relevant covariates. For Pied-billed Grebes and Least Bitterns, we predicted site occupancy at wetlands with varying water depths (10 -100 cm) because this covariate was included in the best-supported model for both species. We also predicted site occupancy for Virginia Rails at wetlands with percent cover of cattail ranging from 10-90% because this species typically avoids complete stands of emergent vegetation (Johnson and Dinsmore 1986) and prefers wetlands with a moderate cover/open water ratio (Conway 1995).

Occupancy models estimate detection probability for a species based upon repeated visits to sites assuming that once a site is occupied, it is closed to changes in occupancy during the survey season (MacKenzie et al. 2002). We included 56 sites in our occupancy models that received four visits during the survey season and 253 sites

that received one visit during the survey season. Because detection probability is estimated only for those 56 sites that received repeated visits, we wanted to determine if this affected estimates of site occupancy probability and the effects of covariates on those 253 sites that only received a single visit. Therefore, we conducted an occupancy analysis on the 56 sites that received repeated visits and a logistic regression analysis on the 253 sites that received single visits to see if the effects of covariates differed. We conducted these analyses on each of the three species mentioned above. Logistic regressions were conducted using Program R (R Development Core Team 2011). For each species, model sets were the same for both analysis methods and we compared results based upon the direction and magnitude of covariate effects. Results of the occupancy analysis on the 56 wetlands that received repeated visits and logistic regression analysis on the 253 wetlands that received single visits were different in some cases and not in others. For example, the effect of WATERDEP on site occupancy of Pied-billed Grebe was not significant in the occupancy analysis, but was highly significant and positive in the logistic regression analysis. When comparing the top models of both analysis methods for all species, we found only six differences in the magnitude and direction of the covariate effects (Table 1). The use of logistic regression for secretive marsh birds is problematic because detection probability is assumed to equal 1. Several studies have estimated detection probability to be less than 1 for marsh birds (Darrah and Krementz 2010, Bolenbaugh et al. 2011, Harms and Dinsmore 2011). Occupancy models estimate detection probability and are arguably a more rigorous approach for evaluating habitat associations, particularly for secretive species. Although

occupancy models are using only those 56 wetlands that received repeated visits to estimate detection probability, the 253 wetlands that received a single visit are still contributing information to the estimation of site occupancy probability. Therefore, below we present results from our first occupancy analysis using all 309 sites.

Results

Pied-billed Grebe

We detected Pied-billed Grebes at 127 sites during both years of surveys with the greatest percentage of sites occupied occurring in the >30-40 ha size class (77.2%; Table 2). The best-supported model for Pied-billed Grebe included the covariate WETSIZE on detection probability and the covariates WETSIZE, WATER, WOOD, and WATERDEP on site occupancy probability (Table 4). Competitive models ($\Delta AIC_c \leq 2.0$) also included the covariate TOTVEG on site occupancy probability in addition to those covariates included in the top model (Table 4). Detection probability was not affected by WETSIZE ($\beta = 0.008$, 95% CI = -0.002-0.018) because the 95% confidence interval included zero. Site occupancy probability was not affected by WETSIZE ($\beta = 0.02$, 95% CI = -0.005-0.039) and WATER ($\beta = 0.02$, 95% CI = -0.003-0.052). Site occupancy probability was positively affected by WATERDEP ($\beta = 0.07$, 95% CI = 0.028-0.109) and negatively affected by WOOD ($\beta = -0.06$, 95% CI = -0.101--0.027). TOTVEG did not have an effect on site occupancy probability because the 95% confidence interval included zero ($\beta = -0.01$, 95% CI = -0.046-0.006).

Least Bittern

We detected Least Bitterns at 60 sites during both years of surveys with the greatest percentage of sites occupied occurring in the >30-40 ha size class (36.3%; Table 2). The best-supported model for Least Bitterns included the covariate CLOUD on detection probability and the covariates WETSIZE, VEGSIZE, and WATERDEP on site occupancy probability (Table 4). The single competitive model ($\Delta AIC_c = 0.79$) included the covariate CLOUD on detection probability and the covariates WATERDEP and WETSIZE on site occupancy probability. Detection probability was not affected by CLOUD ($\beta = -0.520$, 95% CI = -1.08-0.052) because the 95% confidence interval included zero. Site occupancy probability was positively affected by WETSIZE ($\beta = 0.041$, 95% CI = 0.002-0.080) and WATERDEP ($\beta = 0.070$, 95% CI = 0.032-0.101). Site occupancy probability was not affected by VEGSIZE ($\beta = 0.862$, 95% CI = -0.183-1.910).

Virginia Rail

We detected Virginia Rails at 123 sites during both years with the greatest percentage of sites occupied occurring in the >40 ha size class (56.4%; Table 2). The best-supported model for Virginia Rails included the covariate WETSIZE on detection probability and the covariates CATTAIL, WETSIZE, REEDCAN, and VEGSIZE on site occupancy probability (Table 4). Competitive models ($\Delta AIC_c \leq 2$) also included the covariates WATERDEP and DIST on site occupancy probability in addition to those covariates included in the top model. Detection probability was positively affected by WETSIZE ($\beta = 0.02$, 95% CI = 0.010-0.028). Site occupancy probability was positively affected by

CATTAIL ($\beta = 0.16$, 95% CI = 0.051-0.268) and REEDCAN ($\beta = 0.03$, 95% CI = 0.001-0.067). All other covariates mentioned above had little or no effect on site occupancy probability because the 95% confidence intervals included zero.

Sora

We detected Soras at 98 sites during both years of surveys with the greatest percentage of sites occupied occurring in both the >30-40 ha and >40 ha size classes (50.0% in each; Table 2). Soras are abundant in Iowa during migration and are a rare breeder (Kent and Dinsmore 1996). We presumed that this violated the closure assumption because individuals were not available for detection throughout the duration of the survey season (MacKenzie et al. 2002). To satisfy this assumption, we truncated detections to the breeding season only (1– 30 June) and eliminated the possibility of migrants through late May (Melvin and Gibbs 1996). Truncation of the data in this manner resulted in too few detections ($n = 48$) to model site occupancy for this species.

Parameter estimates and model predictions

The probability of occupancy for Least Bitterns was lower than the probability of occupancy for both Pied-billed Grebes and Virginia Rails.

We used the best model for each species to make predictions about site occupancy as a function of important covariates. Site occupancy for Pied-billed Grebes ranged from 0.49 (SE = 0.06) at 10-cm depths to >0.99 (SE = 0.01) at 90-cm depths (Figure 1). For Least Bitterns, site occupancy was 0.25 (SE = 0.02) at 10-cm depths and 0.98 (SE = 0.02)

at 90-cm depths (Figure 1). Site occupancy for Virginia Rails across varying percent cover of cattail ranged from 0.51 – >0.99 (SE = 0.12 and <0.01, respectively; Figure 2).

Discussion

Wetland size had a positive effect on site occupancy probability for Least Bitterns and had a positive effect on detection probability for Virginia Rails. Several studies have shown that larger wetlands support the greatest avian species diversity (Brown and Dinsmore 1986, Craig and Beal 1992, Fairbairn and Dinsmore 2001, Craig 2008). Studies have found evidence of area-dependency in Least Bitterns (Brown and Dinsmore 1986, Moore et al. 2009). Least Bitterns are believed to occupy larger wetlands to increase distance (>123 m) between breeding territories and avoid aggressive interactions between conspecifics (Bogner and Baldassarre 2002) and prefer larger wetlands for nesting (Lor and Malecki 2006). Virginia Rails have been found to occupy wetlands of various sizes (Brown and Dinsmore 1986). However, detection probability can be affected by wetland size because larger wetlands presumably support more nesting pairs than smaller wetlands. Virginia Rails breed in densities of approximately 1.4 pairs/ha (Johnson and Dinsmore 1986). Therefore, larger wetlands with suitable habitat will support more breeding pairs of Virginia Rails, thus increasing the probability of detecting a Virginia Rail at the respective wetland.

Water depth positively affected site occupancy probability for Pied-billed Grebes and Least Bitterns. Published literature suggests that Pied-billed Grebes prefer wetlands with deeper water (Lor and Malecki 2006). Pied-billed Grebes forage by diving and

studies have shown that other diving species (e.g., diving ducks) occupy wetlands with deeper water (Murkin et al. 1997, Webb et al. 2010). This could be because wetlands with deeper water possess larger invertebrates, such as salamanders and small fish, which are preferred prey items of Pied-billed Grebes (Muller and Storer 1999, Osnas 2003). In addition, Pied-billed Grebes build nests over deeper water (Lor and Malecki 2006) and have higher reproductive success in deep wetlands (Osnas 2003). Deep water may result in increased foraging efficiency and may eliminate access to nests by potential mammalian predators. Several studies have also found Least Bitterns to be associated with relatively deep water (Bogner and Baldassarre 2002, Lor and Malecki 2006, Poole et al. 2009). Least Bitterns utilize tall emergent vegetation for a variety of purposes including nesting (Bogner and Baldassarre 2002, Lor and Malecki 2006, Poole et al. 2009) and foraging (Poole et al. 2009). Kantrud and Stewart (1984) found that deeper water increases water permanence in wetlands, thus allowing establishment of robust emergent vegetation communities. Water depth and vegetation height were not highly correlated in our study ($r = 0.26$), therefore the effect of water depth on site occupancy of Least Bitterns is not likely a result of the relationship between water depth and vegetation height.

Site occupancy probability for Pied-billed Grebes was negatively affected by percent cover of woody vegetation, which is consistent with the species' preference for areas of open water interspersed with emergent vegetation (Muller and Storer 1999). Darrah and Krementz (2010) also found that site occupancy decreased with increased cover of woody vegetation. Woody plants are not common in prairie pothole wetlands

(Galatowitsch and Van Der Valk 1996) and are frequently found in wetlands with little or no emergent vegetation and deeper water (pers. obs.). Pied-billed Grebes require some component of emergent vegetation for nesting (Muller and Storer 1999, Osnas 2003), which may explain why site occupancy decreased at wetlands with increased cover of woody vegetation and decreased cover of emergent vegetation. Darrah and Krementz (2010) also suggest the Pied-billed Grebes may avoid wetlands with increased woody vegetation to avoid risk of predation by hawks and mammals.

Site occupancy of Virginia Rails was positively affected by percent cover of cattail and percent cover of reed canarygrass. Virginia Rails typically prefer wetlands with tall, robust stands of emergent vegetation during the breeding season (Johnson and Dinsmore 1986, Lor and Malecki 2006), thus explaining the effect of cattail on site occupancy probability of this species. Our results also suggest that Virginia Rails will inhabit wetlands with 100% cattail cover in Iowa, which is contradictory to another finding that this species tends to avoid complete stands of emergent vegetation (Johnson and Dinsmore 1986). Non-native cattail species (e.g., *Typha angustifolia*, *Typha X glauca*) have been increasing on the landscape since the early 1900s and continue to spread in prairie pothole wetlands due to their ability to tolerate a wide variety of water regimes and growing conditions (Galatowitsch et al. 1999). This increase of cattail cover in Iowa wetlands and other wetlands throughout the Midwest may be the reason for an increased use of cattail-dominated wetlands (>90% coverage) by Virginia Rails. Reed canarygrass is an invasive species and is commonly found along the perimeter of wetlands throughout Iowa (T.M. Harms, personal observation). Although this plant

species is not preferred in wetlands, studies have shown that it does not have a negative effect on bird communities (McMillan and Cook 2008, Spyreas et al. 2010). Rundle and Fredrickson (1981) suggested the Virginia Rails select sites based on water conditions and vegetative structure regardless of species composition. Therefore, reed canarygrass may provide the robust vegetation structure that this species prefers for nesting sites.

We found no effect of degree of wetland isolation on site occupancy probability for any species which was a surprising result because other studies have shown that marsh birds prefer wetlands within a complex rather than isolated wetlands (Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001, Smith and Chow-Fraser 2010). Iowa has lost nearly 90% of its original wetland habitat since the development of agriculture and European settlement (Dahl 1990) and the remaining wetlands are isolated on the landscape (Brown and Dinsmore 1986). Birds may be occupying isolated wetlands because they still produce habitat characteristics preferred for nesting and foraging. If few wetland complexes are available on the landscape, birds may focus their selection on alternative habitats (e.g., isolated wetlands) that they can still use and are more readily available on the landscape (Johnson 1980).

Although some habitat characteristics will be suitable for all species, managers should consider species-specific habitat needs for effective conservation. In Iowa, Pied-billed Grebes occupied wetlands with little surrounding woody cover and deeper water for foraging and nesting (Muller and Storer 1999, Darrah and Krementz 2010). Least Bitterns occupied larger wetlands to avoid interactions with conspecifics and wetlands

with deeper water (>20 cm) because these wetlands support emergent vegetation communities needed for building nests and perching while foraging (Bogner and Baldassarre 2002, Lor and Malecki 2006, Poole et al. 2009). Virginia Rails occupied wetlands with greater cover of cattail for placement and construction of nests, cover from predators, and foraging habitats (Sayre and Rundle 1984, Johnson and Dinsmore 1986, Conway 1995, Lor and Malecki 2006). We suggest that land managers in the Midwest focus efforts on restoring and managing wetlands for a variety of water depths and tall emergent vegetation communities. Also, managers should attempt to acquire larger wetlands, although most species will use smaller wetlands when available. Knowing habitat associations of secretive marsh birds relative to wetland characteristics in Iowa will help land managers to make informed decisions when managing and restoring wetlands for multiple species of marsh birds.

Acknowledgments

This project was funded by the Iowa Department of Natural Resources State Wildlife Grant through the U.S. Fish and Wildlife Service Wildlife and Sport Fish Restoration Program (#T-1-R-20) and an Iowa Department of Natural Resources Wildlife Diversity Program Research Grant. A special thanks to field technicians H. Wilkens, E. Spinney, and J. Lautenbach for assistance in data collection. Staff with the Iowa Department of Natural Resources and U.S. Fish and Wildlife Service provided logistical support. Thanks also to T. Hanson for ArcGIS support and to D.L. Otis for statistical and

modeling advice. This manuscript benefitted from careful edits by R.R. Koford and D.M. Debinski.

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Figure Captions

Fig. 1 Predicted probability of site occupancy ($\pm 95\%$ confidence limits) for Pied-billed Grebe and Least Bittern at wetlands with water depths ranging from 10 to 90 cm in Iowa, 2009-2010.

Fig. 2 Predicted probability of site occupancy ($\pm 95\%$ confidence limits) for Virginia Rail at wetlands with 10 to 90 percent cattail cover in Iowa, 2009-2010.

Table 1 Differences in covariate effects between an occupancy analysis conducted using 56 wetlands that received repeated visits (MARK) and a logistic regression analysis conducted using 253 wetlands that received single visits (LR). All wetlands were surveyed in Iowa, 2009-2010. VEGSIZE is height of vegetation (m; categorical as 1, 2, or 3), WATERDEP is water depth (cm), WETSIZE is wetland size (ha), CATTAIL is percent cover of cattail (*Typha* spp.), WATER is percent cover of open water, WOOD is percent cover of woody vegetation, and REEDCAN is percent cover of reed canarygrass (*Phalaris arundinacea*). “N.S.” denotes not significant, “*” denotes weakly significant ($0.03 \leq P \leq 0.05$), “**” denotes moderately significant ($0.01 \leq P < 0.03$), and “***” denotes highly significant ($P < 0.01$). For MARK models, this represents the degree to which the 95% confidence interval for that effect differs from zero.

Species	Effect													
	VEG SIZE		WATER DEP		WET SIZE		CATTAIL		WATER		WOOD		REED CAN	
	MARK	LR	MARK	LR	MARK	LR	MARK	LR	MARK	LR	MARK	LR	MARK	LR
PBGR			N.S.	***	N.S.	*			N.S.	N.S.	N.S.	N.S.		
LEBI	**	*	N.S.	**	***	N.S.	*	N.S.						
VIRA					***	**	**	**					*	N.S.

Table 2 Number of wetlands surveyed in each size class in Iowa, 2009-2010, and the percent of wetlands in which each species was detected.

Species	Wetland size (ha)					
	≥5	>5-10	>10-20	>20-30	>30-40	>40
Number	n =52	n =54	n =70	n =49	n =22	n =62
Pied-billed Grebe	31	31	37	33	77	56
American Bittern	4	0	1	2	5	10
Least Bittern	12	11	10	29	36	31
King Rail	0	0	0	0	14	2
Virginia Rail	37	19	36	45	55	56
Sora	21	13	33	31	50	50
Common Moorhen	2	0	3	2	18	3
American Coot	25	11	19	31	64	45

Table 3 Predicted effects of habitat variables on site occupancy probability (ψ) for Pied-billed Grebe, Least Bittern, and Virginia Rail in Iowa, 2009-2010. Predicted effects are based on review of the literature. WATER is percent cover of open water, BULRUSH is percent cover of bulrush (*Schoenoplectus* spp.), CATTAIL is percent cover of cattail (*Typha* spp.), SEDGE is percent cover of sedge (*Carex* spp.), REEDCAN is percent cover of reed canarygrass (*Phalaris arundinacea*), WOOD is percent cover of woody vegetation, TOTVEG is total percent cover of all types of emergent vegetation, WATERDEP is water depth (cm), VEGSIZE is height of vegetation (m; categorical as 1, 2, or 3), WETSIZE is wetland size (ha), DIST is distance to the nearest wetland (m), ONEKM, THREEKM, and FIVEKM is the area of wetland habitat within a 1 km, 3 km, and 5 km radius of the periphery of each survey wetland, respectively. “+” represents a positive effect, “-” represents a negative effect, and “0” represents no effect.

Habitat variables	Species		
	Pied-billed Grebe	Least Bittern	Virginia Rail
WATER	+	+	0
BULRUSH	0	+	0
CATTAIL	0	+	+
SEDGE	0	0	+
REEDCAN	0	0	0
WOOD	-	-	-
TOTVEG	+	0	0
WATERDEP	+	0	-
VEGSIZE	0	+	-
WETSIZE	+	+	0
DIST	-	-	-
ONEKM	+	0	0
THREEKM	+	0	0
FIVEKM	+	0	0

Table 4 Model selection results for site occupancy (ψ) and detection probability (p) of three species of marsh birds in Iowa, 2009-2010. Table displays top models as well as other candidate models considered for ψ as well as top and candidate models for p for each species. ΔAIC_c is the difference in Akaike's Information Criterion relative the smallest value, K is the number of parameters in the model, w_i is the AIC_c weight, and Dev is the model deviance. The single time-varying covariate on detection probability was WETSIZE, which is wetland size (ha). Site-specific covariates on site occupancy probability (ψ) are as follows: WETSIZE is wetland size (ha), WATER is percent cover of open water, WOOD is percent cover of woody vegetation, WATERDEP is water depth (cm), TOTVEG is percent cover of all emergent vegetation, VEGSIZE is the height of vegetation, CATTAIL is the percent cover of cattail (*Typha* spp.), BULRUSH is the percent cover of bulrush (*Schoenoplectus* spp.), REEDCAN is the percent cover of reed canarygrass (*Phalaris arundinacea*), ONEKM is the amount of wetland habitat (ha) within a 1-km radius of the surveyed wetland, THREEKM is the amount of wetland habitat (ha) within a 3-km radius of the surveyed wetland, and DIST is the distance to the nearest wetland (m).

Model	ΔAIC_c	K	w_i	Dev
<i>Pied-billed Grebe</i>				
ψ				
p(WETSIZE) ψ (WETSIZE+WATER+WOOD+WATERDEP)	0.00 ^a	7	0.32	531.69
p(WETSIZE) ψ (WATERDEP+WOOD)	0.15	5	0.30	536.01
p(WETSIZE) ψ (WETSIZE+TOTVEG+WOOD+WATERDEP)	0.94	7	0.20	532.63
p(WETSIZE) ψ (WATERDEP+WOOD+WETSIZE)	1.11	6	0.18	534.89
p(WETSIZE) ψ (WATERDEP)	11.12	4	0.00	549.04

p(WETSIZE) ψ (WATERDEP+WATER+WETSIZE)	12.31	6	0.00	546.09
p(WETSIZE) ψ (WATERDEP+CATTAIL)	13.01	5	0.00	548.87
p(WETSIZE) ψ (WATERDEP+WETSIZE)	13.17	5	0.00	549.03
p(WETSIZE) ψ (WOOD)	15.35	4	0.00	553.28
p(WETSIZE) ψ (WETSIZE+WOOD)	17.41	5	0.00	553.27
p(WETSIZE) ψ (WATER)	22.34	4	0.00	560.27
p(WETSIZE) ψ (CATTAIL)	28.18	4	0.00	566.11
p(WETSIZE) ψ (WETSIZE)	29.52	4	0.00	567.44

p

p(WETSIZE) ψ (.)	0.00 ^b	3	1.00	567.44
p(CLOUD) ψ (.)	14.81	3	0.00	582.26
p(OBS) ψ (.)	17.53	3	0.00	584.98
p(WIND) ψ (.)	18.97	3	0.00	586.42
p(TEMP) ψ (.)	20.65	3	0.00	588.10

Least Bittern

ψ

p(CLOUD) ψ (VEGSIZE+WETSIZE+WATERDEP)	0.00 ^c	6	0.39	353.93
p(CLOUD) ψ (WETSIZE+WATERDEP)	0.79	5	0.26	356.82
p(CLOUD) ψ (VEGSIZE+CATTAIL+WETSIZE+WATERDEP)	2.12	7	0.14	353.93
p(WETSIZE) ψ (VEGSIZE+WETSIZE+WATERDEP)	3.05	6	0.45	356.98
p(WETSIZE) ψ (WETSIZE+WATERDEP)	3.66	5	0.33	359.70
p(WETSIZE) ψ (VEGSIZE+CATTAIL+WETSIZE+WATERDEP)	5.16	7	0.16	356.98
p(CLOUD) ψ (VEGSIZE+WATERDEP)	6.74	5	0.01	362.78
p(CLOUD) ψ (VEGSIZE+CATTAIL+WATERDEP)	8.10	6	0.01	362.03
p(WETSIZE) ψ (VEGSIZE+WATERDEP)	8.12	5	0.04	364.15
p(WETSIZE) ψ (VEGSIZE+CATTAIL+WATERDEP)	9.54	6	0.02	363.47
p(WETSIZE) ψ (WATERDEP)	12.59	4	0.00	370.71
p(WETSIZE) ψ (WETSIZE)	23.74	4	0.00	381.86
p(WETSIZE) ψ (VEGSIZE)	30.22	4	0.00	388.34

p(WETSIZE) ψ (CATTAIL)	31.80	4	0.00	389.92
p(WETSIZE) ψ (WOOD)	37.79	4	0.00	395.91
p(WETSIZE) ψ (DIST)	38.59	4	0.00	396.70
p(WETSIZE) ψ (WATER)	40.40	4	0.00	398.52
p(WETSIZE) ψ (ONEKMM)	40.56	4	0.00	398.68
p(WETSIZE) ψ (THREEKMM)	40.62	4	0.00	398.74
p(WETSIZE) ψ (FIVEKMM)	41.23	4	0.00	399.34
p(WETSIZE) ψ (BULRUSH)	41.53	4	0.00	399.65

p

p(WETSIZE) ψ (.)	0.00 ^d	3	0.51	400.33
p(CLOUD) ψ (.)	1.32	3	0.26	401.65
p(OBS) ψ (.)	2.64	3	0.14	402.97
p(WIND) ψ (.)	4.82	3	0.05	405.15
p(TEMP) ψ (.)	4.85	3	0.05	405.18

Virginia Rail

Ψ

p(WETSIZE) ψ (CATTAIL+WETSIZE+REEDCAN+VEGSIZE)	0.00 ^e	7	0.19	533.34
p(WETSIZE) ψ (CATTAIL+WATERDEP)	0.49	5	0.15	538.01
p(WETSIZE) ψ (CATTAIL+WETSIZE+WATERDEP+REEDCAN)	0.81	7	0.13	534.15
p(WETSIZE) ψ (CATTAIL+VEGSIZE)	1.41	5	0.10	538.93
p(WETSIZE) ψ (CATTAIL+WATERDEP+VEGSIZE)	1.57	6	0.09	537.01
p(WETSIZE) ψ (CATTAIL+WETSIZE+DIST)	1.96	6	0.07	537.40
p(WETSIZE) ψ (CATTAIL+REEDCAN)	2.10	5	0.07	539.62
p(WETSIZE) ψ (CATTAIL+WETSIZE+WATERDEP)	2.53	6	0.05	537.96
p(WETSIZE) ψ (CATTAIL+WETSIZE+REEDCAN)	2.70	6	0.05	538.13
p(WETSIZE) ψ (CATTAIL+WETSIZE+VEGSIZE)	3.06	6	0.04	538.50
p(WETSIZE) ψ (CATTAIL)	3.27	4	0.04	542.85
p(WETSIZE) ψ (CATTAIL+WETSIZE)	5.08	5	0.02	542.60
p(WETSIZE) ψ (WATERDEP)	24.12	4	0.00	563.70

p(WETSIZE) ψ (WATERDEP+WETSIZE+REEDCAN)	27.35	6	0.00	562.78
p(WETSIZE) ψ (WETSIZE)	34.31	4	0.00	573.89
p(WETSIZE) ψ (REEDCAN)	35.74	4	0.00	575.32
p(WETSIZE) ψ (DIST)	39.51	4	0.00	579.09
p(WETSIZE) ψ (ONEKM)	39.54	4	0.00	579.11
p				
p(WETSIZE) ψ (.)	0.00 ^f	3	1.00	579.39
p(CLOUD) ψ (.)	14.23	3	0.00	593.62
p(TEMP) ψ (.)	19.30	3	0.00	598.69
p(WIND) ψ (.)	19.81	3	0.00	599.20
p(OBS) ψ (.)	19.82	3	0.00	599.21

^aAIC_c value for top ψ model for Pied-billed Grebe is 546.06

^bAIC_c value for top p model for Pied-billed Grebe is 573.52

^cAIC_c value for top ψ model for Least Bittern is 366.28

^dAIC_c value for top p model for Least Bittern is 406.43

^eAIC_c value for top ψ model for Virginia Rail is 547.71

^fAIC_c value for top p model for Virginia Rail is 585.47



