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A Tale of Two Complexes: Secretive Marsh Bird Abundance Differs in the Sandhills and Rainwater Basin, Nebraska

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Abstract
Wetland complexes in the Great Plains are critical for many bird populations. In Nebraska, two large and important wetland complexes are the Rainwater Basin (RWB) and Sandhills. The RWB is a highly altered landscape where most historic playa wetlands have been destroyed and remaining isolated wetlands are altered. The extensive wetlands of the Sandhills are influenced by water table levels and the wetlands and overall landscape are, by comparison, far less altered. Secretive marsh birds (SMBs; bitterns, rails, gallinules and certain species of grebes) are a group of difficult-to-detect species which have received little attention in both complexes. Standardized SMB surveys were conducted in both regions to determine whether (1) conservation actions in the RWB have the potential to benefit breeding SMBs, (2) SMB species assemblages are similar between the two complexes, and (3) whether certain habitat conditions influence SMBs abundance in each complex. Most SMB species, especially Virginia Rail, Least Bittern, Pied-billed Grebe, and American Bittern, were numerous in the Sandhills as expected, but moderate densities of Pied-billed Grebe, Sora and American Bittern were also present in the RWB. While certain SMBs were found in both complexes, overall SMB communities differed between the complexes. Water level and complex were important variables influencing SMB abundance. The purchase, restoration and management of additional wetlands in the RWB, as well as proactively working with private landowners to maintain the Sandhills as a working landscape, will benefit SMBs in Nebraska.

Keywords Secretive marsh birds · Rainwater Basin · Sandhills

Wetlands in the North American Great Plains provide habitat for a variety of species, including birds that use these systems during migration, breeding and winter periods. Palustrine wetlands have basic similarities of possessing shallow water and extensive emergent vegetation (Cowardin 1979). However, different palustrine wetland types also have different characteristics (e.g., hydrology, vegetation, pH, etc.) and these features influence the bird communities that use them. Since settlement by European Americans, wetland ecosystems in the Great Plains and the landscapes in which they are embedded have been altered in various ways, primarily for agriculture. Types, extent and intensity of alterations have been influenced by the inherent characteristics of the wetland and the surrounding landscape (Dahl 1990, Olimb and Robinson 2019), as well as economic factors and government policy (Higgins et al. 2002). Generally, fertile and arable land has been converted to row crops, and wetlands that were easily drained have been lost. Landscapes which are inherently less compatible for row crop agriculture have often been less altered and used for other purposes such as livestock grazing. Wetlands in highly altered landscapes may become less resilient and more vulnerable to further changes, such as sedimentation and colonization by invasive species (Gleason and Euliss 1998, Beas et al. 2013). Understanding how different species use superficially similar wetland types in distinctly different landscapes can be important in developing conservation priorities for declining species.

In Nebraska, two important large wetland complexes for migratory birds are the Sandhills in the north-central part of the state and the Rainwater Basin (RWB) in the south-central (Johnsgard 2018). At their nearest points the two landscapes are separated by < 100 km. The ecosystems and the wetlands within the two regions share basic similarities, but they also have important differences. The Sandhills is a relatively unaltered landscape of grass-stabilized sand dunes. Water

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levels in Sandhills wetlands are influenced by the water table, which moderates water levels in wetlands even during climate extremes (Gosselin et al. 2006). Wetland areas are extensive and cover large areas (LaGrange 2005, Gosselin et al. 2006). Conversely, the RWB is a highly altered landscape composed of wind-blown loess soils that was formerly dominated by prairie. This landscape has been mostly converted to row crop agriculture (Smith 2003, LaGrange 2005). The majority of wetlands have been destroyed and remaining wetlands have reduced function (LaGrange 2005, Tang et al. 2018). Wetlands embedded in this landscape are playas, which are the lowest areas in a closed watershed and water levels are only naturally dictated by precipitation runoff (Smith 2003, LaGrange 2005, Tang et al. 2018). Thus, the landscapes and wetlands within them are different. Sandhills wetlands are extensive and water levels less dynamic over short periods of time compared to highly dynamic and altered wetlands in the RWB which are isolated and exist within a mosaic of row-crop agriculture.

Even though it is highly altered, the RWB is an internationally-recognized stopover and staging area for migratory waterfowl (USFWS and CWS 1986, Webb et al. 2010), shorebirds (Jorgensen 2004, WHSRN 2021) and the federally endangered Whooping Crane (Richert 1999). However, it is generally not considered a major breeding area for most of these species (LaGrange 2005). In comparison, the Sandhills is considered an important breeding area for waterfowl (Bellrose and Kortright 1976, LaGrange 2005), shorebirds (Sharpe et al. 2001, Gregory et al. 2012) and various waterbirds (Sharpe et al. 2001), but is less often identified as an important stopover region for most species. Considerable efforts to restore and manage wetlands in the RWB have occurred over recent decades and are ongoing (RWBJV 2013a). Fewer wetland conservation actions have occurred in the Sandhills because there is less need, as both individual wetlands and the overall landscape are less altered (LaGrange 2005).

Secretive marsh birds (SMBs; bitterns, rails, gallinules and certain species of grebes) are a group of species that are difficult to detect and which have received limited attention from researchers in the Sandhills and RWB. Generally, SMBs have declined in North America and especially in the Great Plains. Loss and degradation of wetland habitat are considered a primary cause of population declines. Indeed, wetland losses by state in the central United States from the 1780s to the 1980s range from as low as 35% to as high as 89% (Dahl 1990). Wetland loss and conversion have continued in subsequent decades (Dahl 2014). Although marsh bird populations are known to have declined, an important barrier hindering conservation of these species is poor and incomplete information on population sizes and trends. This lack of information, when compared to other species groups, is largely a consequence of the difficulty of detecting SMBs through traditional monitoring programs, such as the Breeding Bird Survey (BBS). SMBs generally stay hidden in dense wetland vegetation and vocalize infrequently. Thus, specialized survey methods are needed to adequately detect the species so that populations can be monitored.

Although information is sparse, several marsh bird species are known to occur in both the Sandhills and RWB. American Bittern (*Botaurus lentiginosus*), Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*) and Pied-billed Grebe (*Podilymbus podiceps*) are known to breed in both regions (Silcock and Jorgensen 2021). Least Bittern (*Ixobrychus exilis*), King Rail (*Rallus elegans*) and Common Gallinule (*Gallinula galeata*) have been reported infrequently in both regions and are known to have bred in the state on occasion (Silcock and Jorgensen 2021). Black Rail (*Laterallus jamaicensis*), which was recently federally-listed as threatened (85 Federal Register 63,764), has only been documented in the state on two occasions (Silcock and Jorgensen 2021). For all of these species, density or abundance has not been estimated and their breeding status is uncertain in one or both regions. This is problematic for conservation. For example, the Rainwater Basin Joint Venture (RWBJV), a partnership among federal, state and local agencies, non-governmental organizations and private landowners, is charged with conserving birds in both the Sandhills and Rainwater Basin. The RWBJV Waterbird Plan (RWBJV 2013b) states there are insufficient data to set valid population objectives for marsh birds in Nebraska and estimating breeding population sizes has been identified as a priority (RWBJV 2015). Previous research on SMBs in other regions of North America have identified multiple wetland characteristics and habitat features that impact marsh bird densities, such as overall wetland site size and water depth (Baschuk et al. 2012, Harms and Dinsmore 2013, Vanausdall and Dinsmore 2019). It is unclear to what extent these same features impact breeding densities within either the Sandhills or Rainwater Basin complexes.

To address important information gaps, we conducted surveys to estimate SMB density and abundance at conservation properties during the breeding season in the RWB and Sandhills. A specific question we sought to address is whether any SMBs occur in sufficient numbers that warrant their consideration in ongoing conservation actions to purchase, restore and/or manage wetlands in the RWB. In other words, can conservation work in the RWB benefit breeding populations of SMBs? Second, we were also interested in whether the SMB species assemblages in both regions were similar and whether certain species should be a higher conservation priority in one region or the other based on our results. Finally, we compared detections and conditions between the two regions to assess the potential influences of the different wetland systems on the marsh bird communities in Nebraska. These results should also clarify the breeding status of SMBs in both regions and inform conservation efforts.

Methods

Study Area and Site Selection

Our study areas were the RWB and Sandhills (Fig. 1; LaGrange 2005). To simplify access for surveys, only wetlands on publicly owned lands were considered. In the RWB there are 59 federally-managed Waterfowl Production Areas (WPAs), 35 state-managed Wildlife Management Areas and a complex of properties owned by Ducks Unlimited that are open to the public. Public areas range in size from 16 to 807 ha. In the Sandhills there are two large National Wildlife Refuges (NWRs), Crescent Lake (18,541 ha) and Valentine (29,173 ha) that possess multiple wetlands, as well as 15 WMAs that range in size from 65 to 1174 ha. We used ArcGIS (ESRI Inc. 2013, Version 10.2, Redlands, CA, www.esri.com), the National Wetlands Inventory (U.S. Fish and Wildlife Service 2009) and the RWB Wetland Vegetation Map (Nugent et al. 2015) to identify wetland survey sites. Only wetlands defined within the lacustrine system and the aquatic bed (AB), emergent (EM), and unconsolidated bottom (UB) classes of the palustrine system were considered in our survey site selection process (Cowardin 1979) as these wetlands possess habitat characteristics preferred by breeding SMBs (Bolenbaugh et al. 2012).

Survey sites were determined using two methods because of differences in total area between two large NWRs and all other sites. For non-NWR properties, we combined all palustrine polygons within each property and treated the polygon(s) as an individual survey site. For the NWRs, which have many wetlands within the refuge boundary, we considered touching selected palustrine and lacustrine polygons as larger wetland units. Palustrine polygons within each wetland unit were then considered a single survey site. We chose not to combine lacustrine and palustrine areas into single survey sites because wetland areas in the Sandhills are located near or surrounding open shallow lakes lacking emergent vegetation. Thus, these areas do not possess habitat used by SMBs (Bolenbaugh et al. 2012). Polygons < 0.3 ha in size were excluded from all areas. We chose two methods so that wetland area of potential survey sites were comparable between those within the two NWRs (117.6 ± 31.1 ha) and total wetland area at all other sites (123.1 ± 23.2 ha). This approach also ensured survey sites in the Sandhills were distributed across each region and not clustered within one NWR. We also chose to include all polygons at smaller sites to maximize the number of surveys that could be conducted during survey windows. The majority (62.9%, range 1–5) of smaller sites possessed only one wetland polygon.

We determined the number of survey sites selected within each wetland complex based on the total area of public access wetland habitat within each wetland complex. We stratified survey sites into 4 size classes based on area

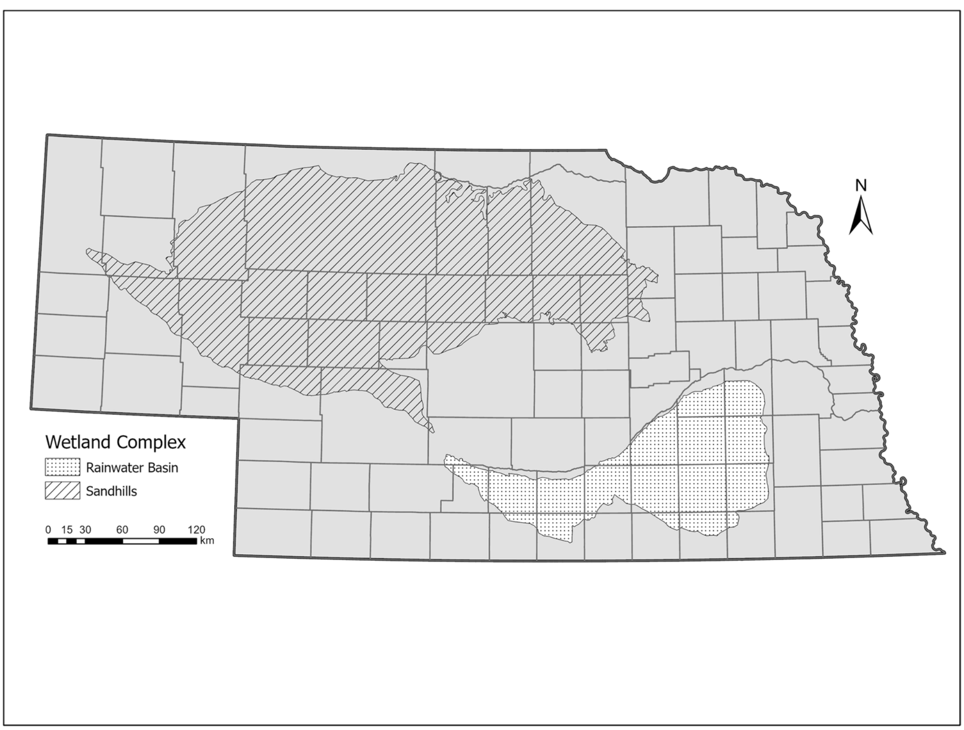

Fig. 1 Location of study areas in Nebraska 2016-17

calculations made using ArcGIS: 1) ≤ 15 ha, 2) 16–60 ha 3) 61–150 ha, and 4) > 150 ha. Survey site size classes were determined by calculating the total area of wetland habitat described above within each survey site. We made every effort to survey an equivalent number of wetlands within each size class. However, small sites are very limited in the RWB as most small wetlands have been destroyed (LaGrange 2005). Survey sites were randomly selected and we surveyed the same sites in 2016 and 2017. We randomly assigned as many survey points as possible, located at least 400 m apart, to each survey site (Conway 2011). We used the area from all polygons in each complex to calculate total wetland area for all sites.

Survey Methods

Surveys were conducted following methods outlined by Conway (2011) and modified by Harms and Dinsmore (2012, 2013, and 2014). We divided the study period into two survey windows, 15 May – 13 June and 14 June – 10 July, and planned to survey each selected site once during each survey window each year (Harms and Dinsmore 2014). In both 2016 and 2017, the first and second surveys at each site were separated by approximately 30 days. There were a small number of sites that were only surveyed once in a given year and a few sites that were only surveyed in 2016, and not surveyed in 2017, due to unforeseen circumstances (e.g., severe weather). All surveys were conducted either in the morning, 30 min before sunrise to three hours after sunrise, or in the evening, three hours before sunset to 30 min after sunset (Harms and Dinsmore 2012, 2013, 2014). As recommended by Conway (2011), we did not conduct surveys during periods of sustained rain, heavy fog, or when wind speed was greater than 20 kph. For consistency, surveys were conducted by the same two individuals within each year. Both years of surveys were not considered periods of climatic extremes (sustained drought or extreme flooding) in the region (U.S. Drought Monitor 2021).

The call broadcast point counts focused on eight species: Virginia Rail, King Rail, Black Rail, Sora, American Bittern, Least Bittern, Common Gallinule, and Pied-billed Grebe. At each site, surveyors navigated to points using a handheld Global Positioning System (GPS) unit (Garmin Geko 201, Garmin LTD., Olathe, KS, USA) and conducted a 13-minute call broadcast sequence provided by the North American Marsh Bird Monitoring Program coordinator (Conway 2011). The call broadcast sequence consisted of a 5-minute silent listening period followed by 30 s of calls and 30 s of silence for each of the eight focal SMB. Calls of focal SMBs were sequenced in the following order: Black Rail, Least Bittern, Sora, Virginia Rail, King Rail, American Bittern, Common Gallinule and Pied-billed Grebe. Playbacks were broadcast using a portable speaker (JBL Flip 4) set at maximum volume. The five-minute period of silence was divided into one-minute intervals. We recorded all species detected (visually and aurally) during each one-minute interval throughout the entire 13-minute survey sequence. We used a laser rangefinder (Nikon Prostaff 3, Nikon Corporation, Tokyo, Japan) to measure the distance from the survey point to each bird detected. Distances to birds only detected aurally were estimated. We also collected measurements of water depth (cm) using a 1 m ruler at each point during each visit.

Analysis

We used Program Distance (version 7.3; Thomas et al. 2010) to model detection probability and obtain density estimates for SMBs for which we had sufficient detections. We used conventional distance sampling and pooled data from both years because of the limited number of detections of all species. We conducted separate analyses for the RWB and Sandhills. We used the four models suggested by Buckland et al. (2001) in our analysis. These models were (1) uniform key function with a cosine expansion, (2) uniform key function with a simple polynomial expansion, (3) half-normal key function with a Hermite polynomial expansion, and (4) hazard-rate key function with a cosine expansion. We truncated 10% of the detections observed at the farthest distances to eliminate outliers (Buckland et al. 2001). We compared models using Akaike's Information Criterion and considered models within two units to have strong support (Burnham and Anderson 2002). We calculated abundance of each species using the density estimate from the best supported model and multiplied that by the total area of wetlands in our study areas. We only included total wetland area in public lands because that is what we sampled.

We used generalized linear mixed-effects models (GLMMs) to determine the effect of wetland complex, water level, and site on the number of detections for each marsh bird species of interest. While estimating densities of these species in the two major wetland complexes was our main goal, we also wanted to compare detections between the two regions broadly to determine if there were any inherent differences between them. We modeled number of detections at each survey point and fit models using a mixed Poisson regression. We included survey point nested within survey site as a random effect, and examined wetland complex (RWB vs. Sandhills), water level, and site size as fixed effects. Water levels during the breeding season could impact multiple breeding SMBs (Baschuk et al. 2012) and site size can also influence breeding SMB dynamics and detections (Harms and Dinsmore 2013, Vanausdall and Dinsmore 2019). Previous work on SMBs in nearby states found a significant impact on the time of season for most species, noting more vocalizations (and thus detections) early in the survey period (15 May – 13 June) compared to later (14 June – 10 July; Harms and Dinsmore 2014). We chose not to include this variable in our models because (a) we were most concerned with potential differences between the two major wetland complexes related to habitat and not methodology or seasonal differences, (b) assumed time of season would similarly impact both complexes given our even study design and the previous research on the subject, and (c) wanted to limit the number of terms in our analysis to avoid over-fitting our models.

There were enough detections for American Bittern, Pied-billed Grebe, Sora, and Virginia Rail to model potential environmental effects for each species. We initially fit or attempted to fit a global model (all fixed and random effects) for detections for each species, and then fit models with individual fixed effects or combinations of effects. We eliminated models that failed to converge and then compared viable models using AIC criteria (Burnham and Anderson 2002). We assessed model fit for the top 3 scoring (lowest AIC) models using simulated datasets from the models for each species to test for over-dispersion and zero-inflation (Harrison et al. 2018). We simulated 10,000 datasets from our top performing models to compare the proportion of zeros in our real data compared to expected and generated 5,000 iterations of simulated data to assess if the sum of squared Pearson residuals for the real data falls within the expected values from simulation (Harrison et al. 2018). We found no evidence of zero-inflation in our data or over-dispersion in any of the top models for each of our four species (Bolker et al. 2009, Harrison 2014; Supplemental Fig. 1). We used Program R (R Core Team 2021) for model comparison and simulations and the *lme4* package (Bates et al. 2015) for creating mixed effect models.

Results

We conducted 663 call broadcast point counts at 225 survey points in 46 wetland survey sites during the combined 2016–2017 field seasons. In 2016, we conducted a total of 341 call broadcast surveys at 202 points at 46 sites. Out of this total, 181 call broadcast point counts were conducted at 107 points at 22 sites in the RWB and 160 call broadcast surveys were conducted at 95 points at 24 sites in the Sandhills (Table 1). In 2017, we conducted 322 call broadcast surveys at 188 points at 44 sites. Out of this total, 143 call broadcast surveys were conducted at 90 points at 20 sites in the RWB and 179 call broadcast surveys were completed at 98 points at 24 wetlands in the Sandhills. All Sandhills wetlands and 20 of the 22 RWB wetlands were surveyed both years. In 2016, 37 out of 46 (80.4%) sites were surveyed twice. In 2017, 39 out of 44 (88.6%) sites were surveyed twice. We detected seven of the eight focal species included in our surveys (Table 2), but only six in each region. We detected more American Bitterns (360) than any other species, followed by Pied-billed Grebe (246), Virginia Rail (267), Sora (218), Least Bittern (70), King Rail (1) and Black Rail (1).

Table 1 Summary of number of wetland sites, mean number of surveys per site and mean wetland area by four different size classes for each region that were surveyed for secretive marsh birds in Nebraska 2016-17

Size class	# of sites	Mean (range) # of survey points	Mean (SE) wetland area
Rainwater Basin			
< 15 ha	1	2 (2)	14.0 (±0)
16–60 ha	9	2.4 (2–3)	36.1 (±4.0)
61–150 ha	7	4.9 (3–7)	100.4 (±10.8)
> 150 ha	5	12.4 (8–15)	275.6 (±38.7)
Total	22	5.5 (1–15)	110.0 (±22.4)
Sandhills			
< 15 ha	6	1 (1)	4.3 (±2.2)
16–60 ha	5	2.8 (1–4)	46.2 (±3.8)
61–150 ha	6	3.8 (1–5)	89.9 (±13.5)
> 150 ha	7	11.3 (4–23)	310.2 (±41.1)
Total	24	5.1 (1–23)	123.6 (±28.3)

The top models for our distance analysis varied by species and region (Table 3). For most analyses, estimates and coefficients of variation were similar among top models or those within 2 AIC units of the top model. Virginia Rail mean density (0.352 birds/ha) in the Sandhills was the highest among all our analyses and Sora mean density (0.027 birds/ha) in the Sandhills was the lowest (Fig. 2). Total wetland area from public sites which we randomly sampled totaled 7,406 ha in the RWB and 8,006 ha in the Sandhills. We used these values of area and estimates of density to estimate abundance (Table 3; Fig. 2). In the RWB, the most abundant species according to the estimate was Sora (348 individuals), Pied-billed Grebe (348 individuals) and American Bittern (259 individuals; Table 3). In the Sandhills, the most abundant species according to the estimate was Virginia Rail (2818 individuals), followed by Pied-billed Grebe (568 individuals), Least Bittern (528 individuals), American Bittern (416 individuals), and Sora (216 individuals; Table 3).

Our top-performing models of environmental effects on SMB detections included water depth and wetland complex in all five species. We found wetland complex had a significant effect on Least Bittern, Virginia Rail and Sora detections, and water level had a significant effect only on American Bittern detections (Table 4).

Table 2 Number of detections of Pied-billed Grebe (PBGR), King Rail (KIRA), Virginia Rail (VIRA), Sora (SORA), Common Gallinule (COGA), Black Rail (BLRA), American Bittern (AMBI) and Least Bittern (LEBI) by region in Nebraska during secretive marsh bird surveys conducted 2016-17

Region	PBGR	KIRA	VIRA	SORA	COGA	BLRA	AMBI	LEBI	Total
Rainwater Basin	105	0	12	171	0	1	171	5	465
Sandhills	141	1	255	47	0	0	189	65	698
Total	246	1	267	218	0	1	360	70	1163

Table 3 Model selection results and respective density estimates (with 95% confidence intervals) of species of secretive marsh bird in the Rainwater Basin and Sandhills, Nebraska

Species/model	K	Δ AIC	Density (birds/ha)	CV	Abundance
Rainwater Basin					
Pied-billed Grebe					
Uniform + cosine	2	-	0.035 (0.024–0.050)	19.0	259 (178–370)
Half normal + hermite polynomial	2	0.83	0.032 (0.018–0.058)	30.4	237 (133–429)
Uniform + simple polynomial	2	1.03	0.034 (0.024–0.048)	17.5	251 (177–355)
Sora					
Uniform + cosine	1	-	0.047 (0.036–0.060)	12.8	348 (266–444)
Half normal + hermite polynomial	1	0.27	0.047 (0.034–0.065)	16.2	348 (251–481)
Uniform + simple polynomial	2	1.75	0.044 (0.033–0.059)	15.1	325 (244–437)
Hazard Rate + Cosine	2	1.83	0.040 (0.027–0.058)	19.6	296 (199–430)
American Bittern					
Hazard Rate + Cosine	2	-	0.035 (0.025–0.048)	16.5	259 (185–355)
Uniform + cosine	1	1.36	0.037 (0.031–0.045)	9.9	274 (230–333)
Sandhills					
Pied-billed Grebe					
Uniform + cosine	3	-	0.071 (0.051–0.098)	16.7	568 (408–784)
Hazard Rate + Cosine	3	2.31	0.067 (0.048–0.094)	17.4	536 (384–752)
Virginia Rail					
Uniform + simple polynomial	3	-	0.352 (0.245–0.507)	18.7	2818 (1961–4059)
Uniform + cosine	2	1.24	0.361 (0.242–0.539)	20.6	2890 (1937–4315)
Sora					
Half normal + hermite polynomial	1	-	0.027 (0.018–0.042)	21.4	216 (144–336)
Hazard Rate + Cosine	1	0.12	0.034 (0.017–0.068)	36.1	272 (136–544)
American Bittern					
Hazard Rate + Cosine	2	-	0.052 (0.038–0.071)	15.6	416 (304–568)
Uniform + cosine	2	2.42	0.057 (0.046–0.071)	11.1	456 (368–568)
Least Bittern					
Uniform + cosine	2	-	0.066 (0.036–0.123)	31.7	528 (288–984)
Hazard Rate + Cosine	2	329.98	0.042 (0.025–0.070)	26.4	336 (200–560)

Density estimates are reported as birds/ha and by region. K is the number of parameters estimated by the model, ΔAIC is the difference in AIC units from the top model, and CV is the percent coefficient of variation

Discussion

Our study is the first to focus on SMBs in Nebraska's major wetland complexes and provide important baseline estimates of density and abundance for several species. Our results reinforce the importance of the Sandhills wetlands for most breeding SMB species, especially for Virginia Rail, Least Bittern, Pied-billed Grebe, and American Bittern. This was expected as this region is relatively unaltered, features high wetland connectivity and had relatively high and stable water levels both within and between seasons during this study period. However, our results also show that moderate numbers of Pied-billed Grebe, Sora and American Bittern summer and presumably breed in the RWB. This is

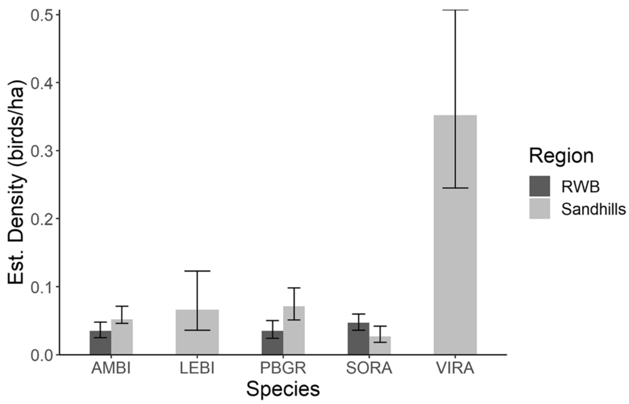

Fig. 2 Estimated density (birds per hectare) of secretive marsh bird species based on top distance models from call-playback surveys in the Rainwater Basin (RWB) and Sandhills in Nebraska, 2016–2017. Error bars represent 95% confidence intervals. There were insufficient detections of Least Bittern (LEBI) and Virginia Rail (VIRA) in the Rainwater Basin to estimate density

Table 4 Total detections model estimates (with 95% confidence interval) for fixed effects by species following marsh bird surveys in Nebraska from 2016–2017

Species	Water Depth	Wetland Complex
American Bittern (AMBI)	0.26 (0.06, 0.46)*	0.06 (-0.66, 0.78)
Least Bittern (LEBI)	0.02 (-0.48, 0.52)	1.55 (0.23, 2.87)*
Pied-billed Grebe (PBGR)	0.11 (-0.28, 0.50)	0.32 (-0.66, 1.30)
Sora (SORA)	0.003 (-0.38, 0.39)	-0.85 (-0.34, -1.35)*
Virginia Rail (VIRA)	-0.25 (-0.06, 0.56)	3.37 (2.47, 4.27)*

Significant effects ($p<0.05$) are denoted with *. Wetland Complex is reported below as the effect of the Sandhills compared to the Rainwater Basin

despite overall wetland numbers being reduced since settlement by European Americans, remaining wetlands are altered and have reduced function and water levels are naturally highly variable. Thus, conservation entities working in the RWB have the opportunity to benefit breeding SMBs by maintaining suitable habitat and therefore SMBs should be considered in conservation planning.

Our study also shows that species densities have important similarities and differences between the two regions. We found similar densities of Pied-billed Grebe and American Bittern between the RWB and Sandhills. Virginia Rail in the Sandhills had the highest density by far of any species in any region, but it was largely absent in the RWB. Also noteworthy was the similar density estimate of Sora in the RWB when compared to the Sandhills. The latter region had previously been considered the more important breeding area for this species (Sharpe et al. 2001). Equally noteworthy is the higher density estimate of Least Bittern in the Sandhills, when it has been considered a species that inhabits eastern Nebraska (Sharpe et al. 2001). Based on our models, water level alone does not explain these differences in species densities (except potentially for American Bittern, see below), even though the points we sampled in the Sandhills had higher average water levels (80.2 cm ± 3.0) than the points we sampled in the RWB (9.0 cm ± 2.6).

For Virginia Rail, detections and estimated density were higher in the Sandhills when compared with Sora, but the cause is unclear. Water level did not explain the difference. Other studies on SMBs also noted water depth does not significantly influence Virginia Rail and Sora densities (Baschuk et al. 2012) and nesting sites were favored for both species at similarly low water depths (Lor and Malecki 2006). Site size is also unlikely to be a major factor impacting density in Nebraska complexes. Even though we did not include any models with site size as an effect, previous research on Sora and Virginia Rail found these species to be area-independent (Brown and Dinsmore 1986, Harms and Dinsmore 2014). Thus, our study is consistent with previous research.

Differences in vegetation diversity or structure between the two complexes could explain the high numbers of Virginia Rail in the Sandhills compared to the RWB. However, Johnson and Dinsmore (1986) noted only minor differences by plant species diversity and negligible differences in vegetation structure between breeding Sora and Virginia Rail territories. Estimates of nest success were similar for both two species within study regions in both the southwest (0.53 and 0.53; Conway et al. 1994) and Great Lakes (0.38 and 0.43; Lor and Malecki 2006), further indicating similar microhabitat requirements between species. Given similar habitat needs of the two species, differences in dominant vegetation or wetland structure may not explain the higher number of Sora detections in the RWB and near complete lack of Virginia Rail in the RWB (Table 1). However, differing wetland hydrology between the two complexes may play a role. Soras and Virginia Rails have different diets, likely based on bill morphology, with much higher seed consumption by Soras compared to an insect-dominated diet of Virginia Rails (Horak 1970). Seeds from annual plants such as smartweeds (*Polygonum* spp.) may be more plentiful in the RWB compared to the Sandhills because of the dynamic wetland conditions and moist soil management practices specifically intended to increase seed food resources for migratory waterfowl (RWBJV 2013b). Alternatively or in addition, RWB wetlands likely possess higher levels of chemicals used in agriculture, including Neonicotinoids, which negatively impact invertebrates (Schepker et al. 2020). Ultimately, the configuration of wetlands, grasslands, agricultural land and other contextual differences between the Sandhills and RWB on the landscape scale could be influencing Virginia Rail and Sora abundances more than any site-level factors.

American Bittern was the only species in which detections were associated with water level. American Bittern detections in our system increased with increasing water depth, and previous studies in the Great Lakes region also showed positive associations with water depth and American Bittern nest site locations (Lor and Malecki 2006). Other research in Manitoba wetlands also noted increased densities of American Bitterns as water depth increased, but this effect was relatively small and may have been related to temporary increases in forage (Baschuk et al. 2012). Our results agree with previous assessments of American Bittern numbers and water level, and importantly both the Sandhills and RWB complexes contain at least some wetlands that provide adequate water levels for this species to breed in similar densities in average or wet years. However, the potential for RWB wetlands to be mostly or entirely dry in some years means that this species is likely absent some years.

The near lack of detections of King and Black rails indicate that both species are exceedingly rare in Nebraska. In fact, the detection of the Black Rail during our study is only the second documented record for the state (McGregor et al. 2016, Silcock and Jorgensen 2021). Thus, our study provides no compelling evidence that this species regularly occurs or breeds in Nebraska. However, Nebraska is north and west of the known regular range of that species so this result is not surprising. By contrast, King Rail previously occurred more frequently in the state, especially in eastern Nebraska, and there are several records of or which are suggestive of breeding. However, King Rails have declined dramatically in the Midwest (Bolenbaugh et al. 2012) and wetlands in eastern Nebraska have been especially reduced. Thus, it seems plausible that the King Rail may be mostly extirpated as a breeding species. Our study clarifies the summer and breeding status of Sora and American Bittern in the RWB, which was previously poorly defined (Jorgensen 2012). Nests of both species were found in the RWB during the study.

We conservatively limited our abundance estimates to the public lands that we included in our sampling universe. However, the proportion of all wetland area in which we sampled is different between the two complexes. In the Sandhills, the public sites we sampled represent only 5% of the 149,574 ha of wetlands in this region. In the RWB, the public sites we sampled represent 54% of the 13,801 ha of wetlands in that region. This means that overall estimates of SMBs may be 20x higher in the Sandhills and nearly twice as high in the RWB when we also consider private lands. However, grazing and management regimes can vary between private and public lands. Therefore, an important priority of future research is to determine whether SMBs densities are different between public and private lands. This recognition also reinforces the concept that conservation will be advanced differently in the two regions. Working proactively with private landowners, such as through partnerships including the Sandhills Task Force, to maintain the Sandhills as an ecologically vibrant working landscape and working with conservation entities to purchase, restore and manage wetlands in the RWB are pathways that will benefit SMBs in Nebraska.

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Author contributions Joel G. Jorgensen, Lauren Greenwalt and Mary Bomberger Brown (deceased) contributed to the study conception and design, material preparation and data collection. Analysis were performed by Joel G. Jorgensen and Stephen J. Brenner. The first draft of the manuscript was written by Joel G. Jorgensen and Stephen J. Brenner and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability Data are available by contacting the lead author at Nebraska Game and Parks Commission, 2200 N. 33rd, Lincoln, NE 68,503 at either joel.jorgensen@nebraska.gov or 402-471-5440.

Declarations

The authors have no relevant financial or non-financial interests to disclose.

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