

Marsh Bird Population Estimates to Inform Conservation Decisions in the Midwest



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Prepared For:

U.S. Fish and Wildlife Service, Upper Mississippi / Great Lakes Joint Venture

31 January 2020

MNFI Report No 2020-03

Suggested Citation:

Monfils, M. J., D. B. Hayes, M. Al-Saffar, G. J. Soulliere, and R. Pierce. 2020. Marsh bird population estimates to inform conservation decisions in the Midwest. MNFI Report Number 2020-03. Lansing, USA.

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Executive Summary

Several marsh bird species are thought to be in decline but uncertainty regarding population status hinders conservation efforts. Estimation of regional population sizes of secretive marsh birds was identified as a top priority by the Midwest Marsh Bird Working Group; population estimates provide a baseline for trend assessment, inform regulatory decisions, and facilitate the development of regional conservation objectives. With several ongoing state marsh bird surveys in the Midwest, substantial data now exist to estimate spring population abundance of multiple marsh bird species to directly inform regional conservation planning and decisions. We used regional survey data to address three objectives: 1) develop and implement an approach to estimate population abundance for secretive marsh bird species; 2) estimate the detectability of marsh birds; and 3) assess our power to monitor trends in marsh bird populations over time.

We began by estimating the amount of potential marsh bird habitat within the region, according to broad and narrow definitions, using a GIS and National Wetlands Inventory (NWI) data. Marsh bird densities were estimated using distance sampling, N-mixture, and heterogeneity models. Years-combined and annual population estimates were determined by multiplying densities by the broad and narrow habitat areas estimated for the Upper Mississippi / Great Lakes Joint Venture (Joint Venture) region, Bird Conservation Region (BCRs) 12 and 23, and states. We estimated marsh bird occupancy and detection probabilities for the Joint Venture region using single- and multi-season occupancy models. Population parameters (abundance, occupancy) were then used to assess our power to detect change at the regional scale.

We analyzed data from 1,333 unique marsh bird survey points and over 10,000 point counts conducted during 2008-2017 in Michigan, Minnesota, Ohio, and Wisconsin. We estimated approximately 5.8 million ha of potential marsh bird habitat occurs within the Joint Venture region according to our broad definition and 2.8 million ha using our narrow definition. Our analyses indicate regional population sizes for American Bittern, Least Bittern, Pied-billed Grebe, and Wilson's Snipe, both with years combined and annual estimates, are conservatively in the tens of thousands and could be well into the hundreds of thousands depending on the model used. Regional Sora and Virginia Rail estimates were well into the hundreds of thousands, with some years and models suggesting Sora populations over 500,000 individuals and Virginia Rail estimates over 1 million birds. For most species and spatial scales, distance models produced the most conservative estimates, often close to estimates using raw densities for species with high detectability. N-mixture models typically resulted in the greatest population estimates, with heterogeneity models usually having estimates intermediate between distance and N-mixture models. Densities and population sizes of Least Bittern, Pied-billed Grebe, and Sora were greater in the southern part of the Joint Venture region, whereas American Bittern and Wilson's Snipe estimates were greater in the northern portion of the region. Estimates of Virginia Rail densities were generally similar across spatial scales.

We estimated detection probability using both occupancy and distance models and observed considerable differences in estimates. Detection probability from occupancy models varied by species and survey period, ranging from a low of 0.16 (Wilson's Snipe, period 3) to a high of 0.57 (Sora, period 1). On average, detection probabilities were greatest for Sora, American Bittern, Virginia Rail, and Pied-billed Grebe, lowest for Least Bittern, and intermediate for American Coot and Wilson's Snipe. American Bittern, Sora, and Wilson's Snipe exhibited peak detection probabilities during the first period and declining detectability in subsequent periods, whereas the remaining species had relatively consistent detection probabilities across survey

periods. Distance sampling indicated detection probability = 1 for American Bittern, Pied-billed Grebe, and Wilson's Snipe within 100 m, with occupancy modeling producing much lower estimates. Detection probability for Virginia Rail from distance sampling was lower compared to the occupancy model. Effective survey radii for most marsh birds was well below the 100-meter threshold used in our analyses, with 6 of 10 species analyzed having radii less than or equal to 63 m. With all years combined, estimated occupancy was greatest for Sora and Virginia Rail (~0.30) and lowest for Common Gallinule, American Coot, and Least Bittern (<0.10), with the remaining species having intermediate estimates. Annual estimates of occupancy varied substantially across years, with Least Bittern and Wilson's Snipe exhibiting the greatest variation. No discernable trends in occupancy were observed at the regional level for the six species analyzed. We ran multi-season (i.e., multiple year) occupancy models at a subset of points having multiple years of survey data, which indicated stable occupancy for Least Bittern, Pied-billed Grebe, and Virginia Rail, and potentially increasing occupancy for American Bittern, Sora, and Wilson's Snipe. Despite estimates indicating stable to increasing rates of occupancy over time, probabilities of local extinction were greater than probabilities of local colonization for all species examined.

We examined the level of variation observed in our abundance models to assess expected precision in estimates under a range of sample effort. Species with low abundance and frequency of occurrence (e.g., Least Bittern) exhibited greater levels of variation in estimates compared to more common species, resulting in wide confidence intervals even with high sample effort. For species with medium levels of abundance and occurrence (e.g., American Bittern, Pied-billed Grebe), moderate levels of precision were obtained with a sample size of about 300 points for the distance model and 700 points for the N-mixture model. Species with the greatest abundance and occurrence rates (e.g., Virginia Rail, Sora) had relatively high levels of precision even at low levels of sampling effort, suggesting population trends could be assessed even at local scales.

Using recommendations in the literature and our estimates of occupancy and detectability, we expect more than three visits per season would be required to have high levels of confidence that lack of detection equates to true absence for most species. We estimated low power to detect change in occupancy of species with low levels of occupancy and detectability (e.g., Least Bittern), even with high survey effort. For species with medium levels of occupancy and detectability (e.g., American Bittern, Pied-billed Grebe), we found moderate power (≥ 0.60) to detect moderate to high amounts of change in occupancy (e.g., ≥ 0.50 decline, ≥ 0.35 increase) with high sample sizes ($n = 675$ or $1,000$). For species with high levels of occupancy and detectability (e.g., Sora, Virginia Rail), we estimated moderate power (about 0.50) to detect high proportions of occupancy change (e.g., ≥ 0.50 decline, ≥ 0.35 increase) even with a moderate sample size ($n = 225$) and about 0.50 power to detect 0.25 change with high sample sizes.

Prior to our study, the only regional marsh bird population estimates came from an expert-derived process associated with regional conservation planning. Even when considering our most conservative population estimates, our models suggest marsh bird population sizes are likely far greater than previously thought. However, our estimates are based on imprecise habitat areas derived using the NWI, so there is potential for overestimation of population sizes due to the incorporation of unsuitable habitats, such the inclusion of areas mapped as wetlands by the NWI but lacking inundation. Further refinement of marsh bird habitat area estimates could potentially improve the precision of population abundance estimates. This project represented the first effort to produce regional estimates, so we chose to use and compare three commonly used modeling techniques that could be readily replicated. However, more sophisticated approaches (e.g., hierarchical, Bayesian) have been used to estimate wetland bird

densities and hold promise for increasing the precision of estimates with the same survey effort, so additional analyses using more complex modeling approaches could be explored. We suggest future assessments of marsh bird population trends follow the approach used in this study, in which multiple parameters are examined, including raw indices, abundance, and occupancy, to determine if similar patterns emerge. We also recommend focusing on larger spatial scales (e.g., Joint Venture Region, BCRs) and longer time frames (e.g., 5- or 10-year increments) to increase the precision of estimates. Despite the challenge presented by high variation in detecting change over time, our analyses suggest the regional survey effort should be able to detect moderate change in relative abundance or occupancy of American Bittern, Pied-billed Grebe, Sora, and Virginia Rail, possibly even at the BCR or state scale.

Introduction

Concern about declining marsh bird populations has grown in recent years and there is substantial interest in reversing these population trends (Kushlan et al. 2002; Soulliere et al. 2007, 2018; Wires et al. 2010). Unfortunately, conservation efforts have been hindered by the lack of biological and ecological data necessary to support planning and management (Soulliere et al. 2007, 2018). The Midwest Marsh Bird Working Group (MMBWG) and Upper Mississippi / Great Lakes Joint Venture (Joint Venture) have made marsh bird monitoring a priority to address these knowledge gaps (Soulliere et al. 2007, 2012, 2018; Larkin et al. 2013). Among the many information needs, estimating regional population abundance for primary target species was identified as the top priority by the MMBWG. Science-based abundance estimates would provide a baseline for future trend assessment, inform regulatory decisions (e.g., harvest guidelines), facilitate the development of population and habitat objectives in conservation planning, and provide a means for evaluating our power to assess long-term population trends under a regional survey program.

The base of research and monitoring information available for marsh birds has been steadily growing in North America over the last two decades. Although many of these studies included the estimation of population parameters, such as abundance (e.g., density, population size) or occupancy, their utility for large-scale management or conservation planning in the Midwest is limited by project scopes that focused on particular species (Darrah and Kremetz 2009), localities (Harms and Dinsmore 2012; Saunders et al. 2019), and questions regarding management or habitat use (Bolenbaugh et al. 2011; Harms and Dinsmore 2013; Monfils et al. 2014, 2018; Glisson et al. 2015; Tozer et al. 2016, 2018). With the implementation and coordination of several state marsh bird surveys in the Midwest region of the United States, substantial data now exist to estimate population abundance of multiple marsh bird species to directly inform conservation planning and decision making at the regional scale.

Several state-level organizations in the Midwest developed secretive marsh bird surveys using a consistent survey protocol (Conway 2011) and sample design (Johnson et al. 2009); annual surveys have been conducted in Wisconsin since 2008, in Michigan since 2010, in Ohio since 2011, and in Minnesota since 2016. Our project goals were to use these data to produce estimates of breeding population abundance and occupancy (probability a site is occupied by a species) for several secretive marsh bird species in the upper Midwest to inform conservation decisions and to assess the power of the regional survey effort to detect population change. We leveraged data collected from multiple sources to inform decisions regarding marsh bird regulation, conservation planning, and monitoring by addressing three objectives: 1) develop and implement an approach to estimate population abundance for secretive marsh bird species in the upper Midwest; 2) estimate detectability of marsh birds using two modeling techniques; and 3) assess our power to monitor trends in marsh bird populations over time. We hope the results of this project will provide a better understanding of the status of marsh bird populations in the upper Midwest and help guide future monitoring and habitat conservation planning in the region.

Methods

Study Area and Sample Design

Our goal was to estimate marsh bird population sizes for several spatial scales: the Joint Venture region; Bird Conservation Regions (BCRs) 12 and 23; and the four individual states (Michigan, Minnesota, Ohio, and Wisconsin) contributing data to our analyses. The Joint Venture region is largely covered by BCRs 22 (Eastern Tallgrass Prairie), 23 (Prairie Hardwood Transition), and the U.S. portion of BCR 12 (Boreal Hardwood Transition), but small portions of BCR 24 (Central Hardwoods) and BCR 13 (Lower Great Lakes / St. Lawrence Plain) also occur within the Joint Venture boundary (see Soulliere et al. 2018). We chose to estimate population sizes for only BCRs 12 and 23, because limited areas of other BCRs in the Joint Venture region were surveyed and thus had small sample sizes. Although the Minnesota and Ohio state borders extend beyond the Joint Venture boundary, we developed statewide population estimates to coincide with the scale of the marsh bird surveys.

We analyzed marsh bird survey data collected in the upper Midwest from 1,333 unique survey points (Figure 1). These data were obtained from four state-level programs that formed the basis of a coordinated regional marsh bird survey. Each of the four states randomly selected its own set of primary (i.e., cluster or route) and secondary (i.e., individual survey points) sample units following the procedure described by Johnson et al. (2009). Potential survey points were visited in the field to ensure the presence of potential marsh bird habitat and accessibility for volunteers; inaccessible points or those lacking potential habitat were discarded or moved a short distance (≤ 150 m) to a suitable sampling location.

Marsh Bird Surveys

All surveys were conducted according to the North American Marsh Bird Monitoring Protocols (Conway 2011). The Conway (2011) protocol provides substantial flexibility in selecting primary and secondary target species, so each state tailored its methodology to meet its own survey objectives (Wisconsin Department of Natural Resources [DNR] 2009, Ohio DNR 2011, Michigan Bird Conservation Initiative 2015, Audubon Minnesota 2017). There was substantial overlap in the target species selected, with Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Gallinule (*Gallinula galeata*), and American Coot (*Fulica americana*) being surveyed by all four states. In addition, Yellow Rail (*Coturnicops noveboracensis*), King Rail (*Rallus elegans*), and Wilson's Snipe (*Gallinago delicata*) were surveyed by three of the four states according to their breeding distributions.

Wetland Characterization

National Wetlands Inventory (NWI) data were used to describe the potential marsh bird habitat available within the Joint Venture region, portions of BCRs 12 and 23 occurring within the Joint Venture boundary, and individual surveyed states. Wetlands delineated by the NWI in the region were summarized into 33 combinations of system, subsystem, and class (Cowardin et al. 1979, Federal Geographic Data Committee 2013). Of the 33 wetland types observed, we identified 26 of them as potential marsh bird habitat under our broad definition (Appendix A, Table A1). Under our narrow definition of potential marsh bird habitat, we only included palustrine wetlands having the emergent class (6 types total), either alone or in a split-class designation (e.g., palustrine emergent/scrub-shrub). Wetland data analysis and compilation was conducted using ArcMap 10.6 (ESRI, Redlands, CA).

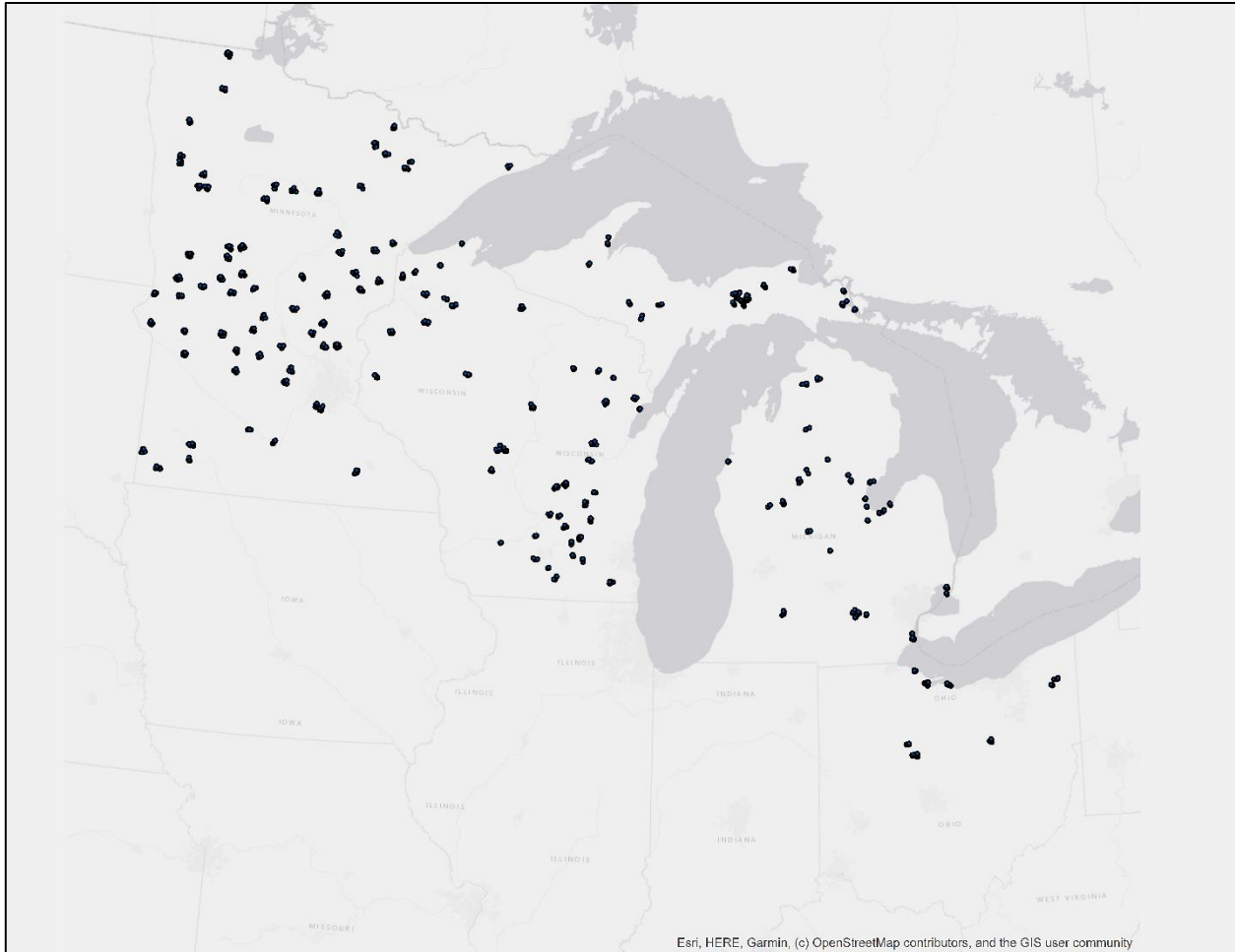


Figure 1. Marsh bird survey point locations used in Michigan, Minnesota, Ohio, and Wisconsin during 2008-2017.

We used NWI data in two ways: 1) as covariate in abundance models; and 2) to estimate marsh bird population sizes based on density estimates. The proportion of the area within 100 m of each survey point consisting of potential marsh bird habitat (broad definition) was used as a covariate in abundance models. We estimated the area of potential marsh bird habitat under both broad and narrow definitions within the following spatial extents (Appendix A, Table A2): 1) Joint Venture boundary; 2) portion of BCRs 12 and 23 falling within the Joint Venture region (i.e., BCR clipped to Joint Venture boundary); and 3) boundaries of each of the four states contributing marsh bird data for our analyses, including portions of the states extending beyond the Joint Venture boundary. Estimates of potential marsh bird habitat area were then used to estimate marsh bird population sizes as described below.

Analysis

Four modeling techniques were employed to estimate marsh bird population parameters. Three models, distance sampling (Buckland et al. 2001), N-mixture (Royle 2004), and heterogeneity (Royle and Nichols 2003), were used to produce abundance estimates (i.e., densities). We used single-season occupancy models to estimate occupancy and detection probabilities. These parameters, along with detection probabilities and effective survey distances obtained from

distance sampling models, were used to help assess the power of the current survey effort to detect changes in marsh bird population parameters over time. Multi-season (i.e., multiple year) occupancy models were developed for species at a subset of more regularly surveyed points.

Abundance

Distance Sampling: Data on the distance at which birds were detected were summarized for the entire dataset (i.e., all four states combined) as the distribution of data was generally sparse for finer subdivisions (e.g., state level). Data for each species were filtered by using the total number of birds detected within 100 m at a point to remove birds detected beyond 100 m. As such, all subsequent analyses were based on treating plots as having a 100-m radius. Estimates of effective detection radius were computed using the `dfuncEstim` function in R (sample R code provided in Appendix B), which implements methods described in Buckland et al. (2001). This function requires the specification of a truncation distance, and preliminary analyses indicated that the final estimate was sensitive to this specification, and further, that setting it to exactly 100 m resulted in estimates inconsistent with the data. Evaluation of various truncation distances indicated that estimates stabilized when truncation distance was set to 125 m.

As the shape of the detection function was unknown, we used a multi-model approach to estimate the final detection radius. In our multi-model evaluation, we considered the uniform, half-normal, negative exponential, hazard rate, and gamma distributions as candidates for the detection function. The likelihood and AIC value associated with each function was computed and graphs depicting the fit of each function to the data were constructed for each species. The weight of evidence associated with each model was computed using methods from Burnham and Anderson (2002), and the final estimate of effective detection radius was the weighted average of the detection radius estimated under each candidate detection function. The model failed to converge for some of the candidate detection functions for some species, particularly rare species with few detections; these detection functions were simply dropped from further calculations.

For each species, the mean count per 100-m radius plot was computed for the level of aggregation desired (e.g., individual BCR). This was then transformed to observed density per hectare by dividing the count by the area of the plot (3.14 hectares). Observed densities were then scaled up to true density by the following formula:

$$\text{True Density} = \text{Observed Density} * \frac{\text{Area of 100-m plot}}{\text{Area of species-specific effective detection radius}}$$

For example, an effective detection radius of 57.74 m would encompass a circle with an area one third as large as a 100-m radius circle, resulting in a multiplier of 3.0.

N-mixture and Heterogeneity Models: We produced N-mixture (Royle 2004) and heterogeneity (Royle and Nichols 2003) models to estimate marsh bird density using the program Presence (Version 2.12.33; Hines [2006]). For each species, we estimated an overall density using the combined dataset containing observations across all years (2008-2017) and annual densities using one-year datasets during 2010-2017. Annual estimates for 2008 and 2009 were not attempted because surveys were only conducted in Wisconsin during those years. A sequential process was used to create candidate models for each species, dataset, and model type. The detection probability parameter was modeled first by comparing two detection models, one assuming constant detection probability across survey periods and the second incorporating variable detection probabilities by survey period. The best-supported configuration of the two

models, as indicated by AIC, was used in subsequent models. We then compared models containing all possible combinations of three covariates that could influence marsh bird detection: time of day (categorical variable of morning [0] or evening [1]); noise level (ranked from 0 [no noise] to 4 [intense noise]); and wind speed (ranked from 0 [no wind] to 6 [strong breeze, 39-49 km/h]). The best-approximating detection model was included in all subsequent occupancy models. We then created occupancy models using covariates to describe the availability of potential marsh bird habitat (using NWI analysis described above), spatial location (latitude and longitude), and BCR. Fifteen occupancy models were developed using all combinations of four covariates: proportion of potential marsh bird habitat within 100 m, latitude, longitude, and BCR.

Population Size Estimation: Marsh bird population sizes were estimated by taking the mean densities from the abundance models for the spatial extent being examined and multiplying them by the estimated total area of potential habitat for that region (Appendix A, Table A2). We estimated population sizes for the entire Joint Venture region, BCR 12 and 23 portions of the Joint Venture region, and the four states. For comparison with model-estimated densities and population sizes, we calculated “raw” densities (i.e., unadjusted detections within 100 m converted to detections per hectare) and converted to population sizes using the broad and narrow marsh bird habitat area estimates.

Occupancy

Single-season Occupancy: We estimated probability of occupancy and detection using the single-season model described by MacKenzie et al. (2002, 2006). Models were developed for all years combined (2008-2017) and for individual years (2010-2017) following the same sequential process described above for N-mixture and heterogeneity models. All occupancy analyses were conducted using the program Presence (Version 2.12.33; Hines [2006]).

Multi-season Occupancy: We estimated annual marsh bird occupancy probabilities at a subset of sites using the single species, multi-season occupancy model presented by MacKenzie et al. (2003, 2006). Use of the multi-season model also provides estimates of probability of colonization (probability an unoccupied site becomes occupied) and extinction (probability an occupied site becomes unoccupied). Only points surveyed during at least two of the eight years were included in the analyses, resulting in 621 of the 1,333 possible points being used. Multi-season occupancy models were produced using Presence (version 2.12.33, Hines [2006]). We began by first comparing the four model parameterizations available for the multi-season model using Akaike’s Information Criterion (AIC). The best-approximating parameterization was used in subsequent models. A tiered approach was used to develop candidate models. Detection probability was modeled first by comparing four models: one assuming constant probability of detection across survey periods and seasons, a second incorporating variable detection probabilities by survey period within seasons, a third with detectability varying by year, and a fourth with detectability varying by year and season. The best-supported configuration of the four models, as indicated by AIC values, was used in subsequent models. We then compared three models each containing one of three detection covariates used in previous models (time of day, noise level, and wind speed). The best-approximating detection model was included in all subsequent occupancy models. Finally, we compared occupancy models containing the following combinations of variables as covariates for the occupancy, colonization, and extinction parameters: proportion of potential marsh bird habitat within 100 m radii; latitude; longitude; latitude and longitude; and BCR. This process resulted in a maximum of 14 candidate models for each species, with the best-approximating model selected using AIC.

Monitoring Design Implications

We used the results from our abundance and occupancy models to assess change in population parameters given various sampling scenarios. To assess our ability to track change in abundance over time at the regional scale, we estimated 95% confidence intervals for two model types and three marsh bird species/groups. We set mean abundance for analyses at 1 and selected standard deviation values that produced coefficients of variation (CVs) consistent with those observed in our models using real data. We conducted analyses using average CVs observed in our distance sampling and N-mixture models, because they represented the range of precision in estimates from low to high, respectively. Confidence intervals were estimated for three marsh bird species/groups representing low (Least Bittern), medium (American Bittern and Pied-billed Grebe), and high (Sora and Virginia Rail) abundance and across a range of sampling effort from 50 to 1,000 points.

We used our occupancy and detection probability estimates to determine the number of surveys recommended by MacKenzie and Royle (2005) for a standard survey design (i.e., all sites surveyed the same number of times). Detection probabilities were used to assess the number of surveys needed to have a selected level of confidence that lack of detection equates to absence according to Reed (1996); this analysis was done for a range of confidence levels (75 – 95%). We also conducted power analyses following Guillera-Arroita and Lahoz-Monfort (2012) using three levels of occupancy and detection probabilities: 1) low (occupancy = 0.10, detectability = 0.20; representative of Least Bittern); 2) medium (occupancy = 0.20, detectability = 0.30; representative of American Bittern and Pied-billed Grebe); and high (occupancy = 0.30, detectability = 0.35; representative of Sora and Virginia Rail). Power analyses were done using two levels of survey visits (3 and 4 visits per season) and four sample sizes. Sample sizes were selected to represent a range of spatial scales and survey effort: 1) annual sampling effort that might be expended at a local scale ($n = 75$); 2) approximate annual survey effort in either the BCR 12 or 23 portion of the Joint Venture region in 2017 ($n = 225$); 3) approximate survey effort within the Joint Venture region in 2017 (i.e., status quo); and 4) approximate annual survey effort within the Joint Venture region if each of the four states were to sample the greatest number of points surveyed in any one year during 2010 – 2017 ($n = 1,000$).

Results

We analyzed data from 1,333 unique marsh bird survey points visited at least once during 2008 through 2017 in Michigan, Minnesota, Ohio, and Wisconsin. Although the overall survey effort in the region has increased since 2016 with the addition of Minnesota and additional routes in Ohio, the number of points visited in Michigan and Wisconsin has declined since survey effort peaked in 2013 and 2010, respectively (Table 1). Survey effort reported for 2016 and 2017 is underestimated because surveys were conducted in Wisconsin during those years but data were not available for analysis. The combined data set analyzed for this project represented over 10,000 point counts conducted during 2008-2017 (i.e., a point count being one survey of an individual point). The bulk of the surveys conducted within the four states examined occurred in BCRs 12 and 23 (Table 1). We estimated 5,762,072 ha of potential marsh bird habitat within the Joint Venture region using our broad definition and 2,792,626 ha under our narrow definition (Appendix A, Table A2). These habitat estimates were used in calculating regional population sizes.

Table 1. Number of points surveyed for marsh birds in the upper Midwest by year and spatial extent.

Spatial Area	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
BCR 11	---	---	---	---	---	---	---	---	101	89
BCR 12	68	75	109	90	151	159	136	145	156	212
BCR 13	---	---	---	35	33	23	26	34	34	34
BCR 22	---	---	---	8	8	18	10	18	36	46
BCR 23	100	181	217	205	167	221	191	136	175	232
Michigan	---	---	57	61	136	221	209	162	77	137
Minnesota	---	---	---	---	---	---	---	---	338	371
Ohio	---	---	---	70	71	71	63	88	87	105
Wisconsin	168	256	269	207	152	129	91	83	---	---
Combined Total	168	256	326	338	359	421	363	333	502	613

Abundance

With all years combined, our marsh bird density and population abundance estimates varied substantially across species, model type, and spatial extent. Distance sampling indicated American Bittern and Pied-billed Grebe detection probability at 100 m was equal to 1, so their densities mirrored raw density and population estimates (Table 2). For all species except Virginia Rail, the greatest densities and population estimates were produced with N-mixture models. Distance sampling estimated the greatest density and population size for Virginia Rail due to its low estimated detection probability and short effective survey radius. Heterogeneity models typically produced densities and population estimates intermediate between distance sampling and N-mixture model estimates (Table 2).

We observed high variation in annual abundance estimates across years and models, especially for Least Bittern, Sora, and Virginia Rail (Figure 2). Although the N-mixture and heterogeneity models indicated potentially increasing American Bittern abundance over time, we did not see discernable patterns in population abundance for other species. Estimates at smaller spatial scales suggest increasing American Bittern abundance may be related to sampling within the BCR 12 portions of Michigan and Minnesota (Appendix D). Our analyses indicate annual population estimates for American and Least Bittern, Pied-billed Grebe, and Wilson's Snipe within the Joint Venture region are conservatively in the tens of thousands and could be well into the hundreds of thousands depending on the model used (Figure 2). For Sora and Virginia Rail, regional estimates were well into the hundreds of thousands, with some years and models suggesting Sora populations over 500,000 individuals and Virginia Rail estimates over 1 million birds.

Estimates of densities and population sizes at BCR and state scales followed known patterns in breeding distributions and relative abundance (Appendix D). Densities and population sizes of Least Bittern, Pied-billed Grebe, and Sora were greater in the southern portion of the Joint Venture region (e.g., BCR 23). Conversely, American Bittern and Wilson's Snipe densities and population estimates were greater in the northern portion of the Joint Venture region (e.g., BCR 12). Estimates of Virginia Rail densities were generally similar between BCRs 12 and 23 and among states.

Table 2. Estimated marsh bird densities (detections per ha) and population sizes for all years combined (2008-2017) by species, model type, and potential habitat definition for the Joint Venture region.

Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Density (detections/ha)												
Raw	0.027	---	0.006	---	0.018	---	0.051	---	0.034	---	0.014	---
Distance sampling	0.026	0.002	0.017	0.002	0.019	0.001	0.135	0.007	0.288	0.015	0.032	0.002
N-mixture	0.107	0.012	0.037	0.010	0.092	0.011	0.198	0.017	0.147	0.015	0.086	0.015
Heterogeneity	0.082	0.011	0.033	0.009	0.061	0.009	0.123	0.012	0.103	0.011	0.063	0.012
Mean estimated	0.072	0.008	0.029	0.007	0.058	0.007	0.152	0.012	0.180	0.014	0.061	0.010
Population Size – Broad Habitat Definition												
Raw	153,467	---	34,815	---	106,272	---	295,301	---	196,175	---	78,270	---
Distance sampling	149,814	11,524	97,955	11,524	109,479	5,762	777,880	40,335	1,659,477	86,431	184,386	11,524
N-mixture	616,161	70,935	215,267	57,608	532,649	63,209	1,141,724	97,967	848,666	84,138	497,266	85,949
Heterogeneity	475,208	60,984	191,506	49,193	353,772	50,742	710,818	68,125	596,107	64,904	364,968	67,966
Mean estimated	413,728	47,814	168,243	39,442	331,967	39,904	876,807	68,809	1,034,750	78,491	348,873	55,146
Population Size – Narrow Habitat Definition												
Raw	74,379	---	16,873	---	51,505	---	143,119	---	95,077	---	37,934	---
Distance sampling	72,608	5,585	47,475	5,585	53,060	2,793	377,005	19,548	804,276	41,889	89,364	5,585
N-mixture	298,627	34,379	104,330	27,920	258,152	30,635	553,344	47,480	411,312	40,778	241,003	41,656
Heterogeneity	230,312	29,556	92,815	23,842	171,458	24,592	344,503	33,017	288,907	31,456	176,884	32,940
Mean estimated	200,516	23,174	81,540	19,116	160,890	19,340	424,950	33,349	501,498	38,041	169,084	26,727

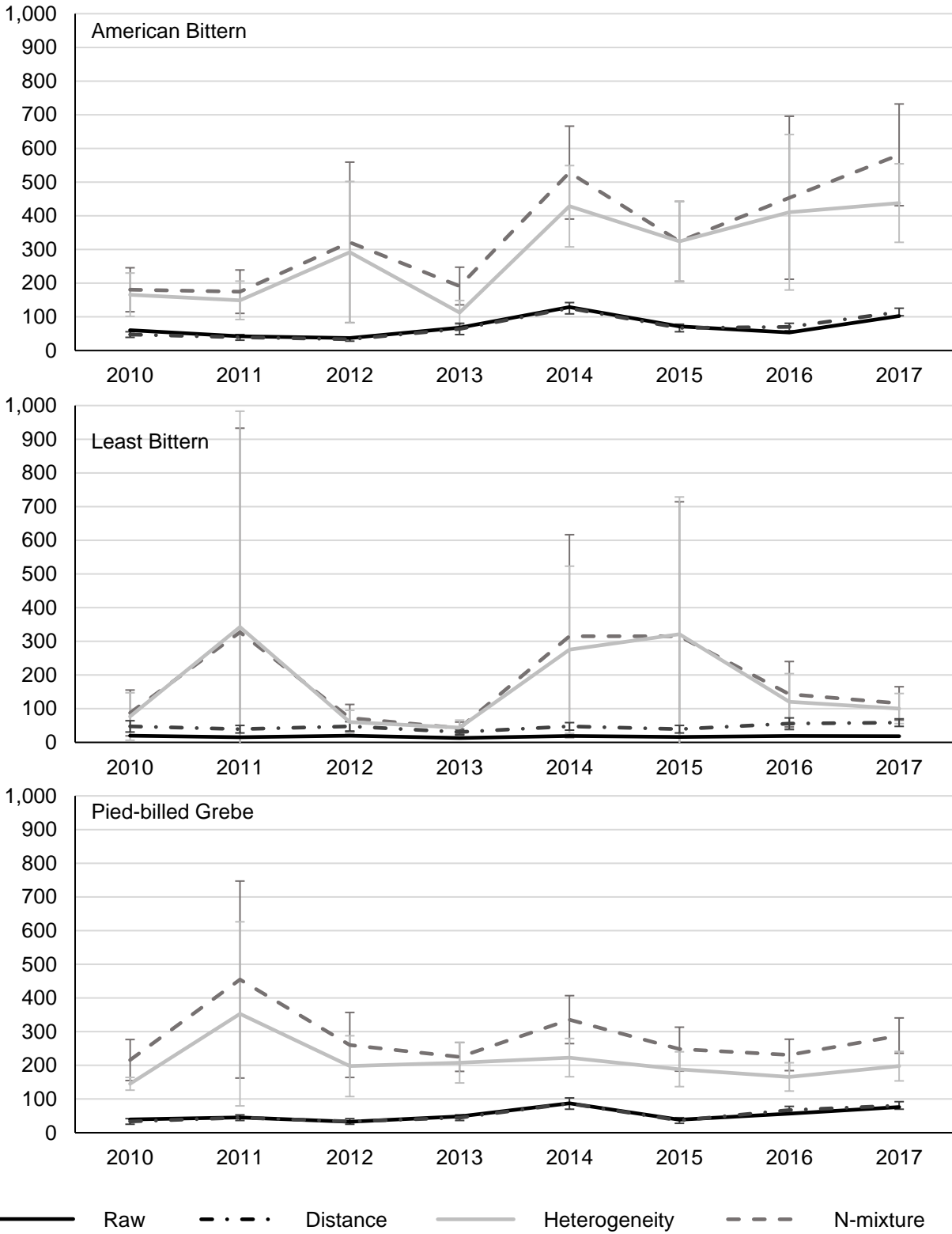
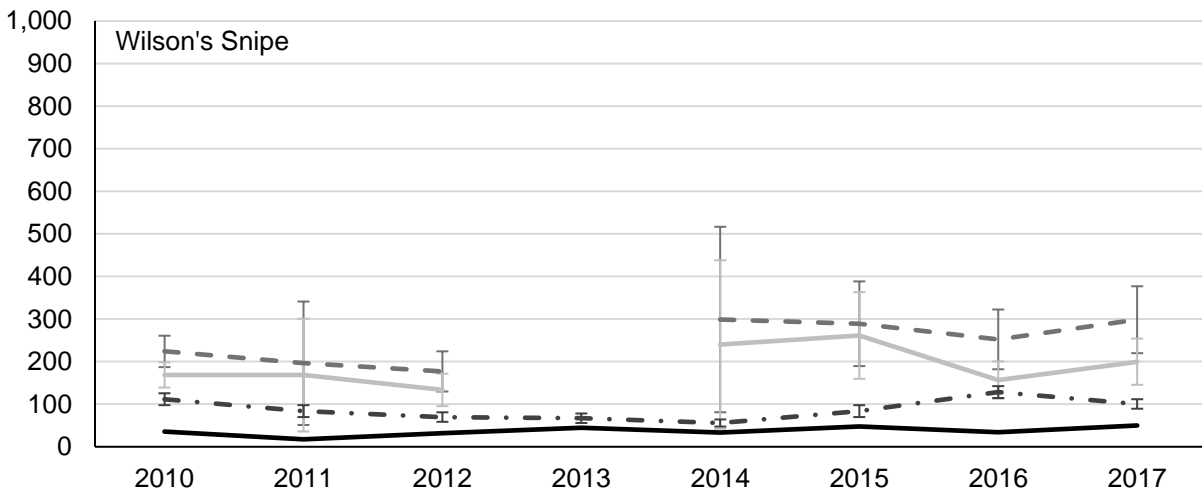
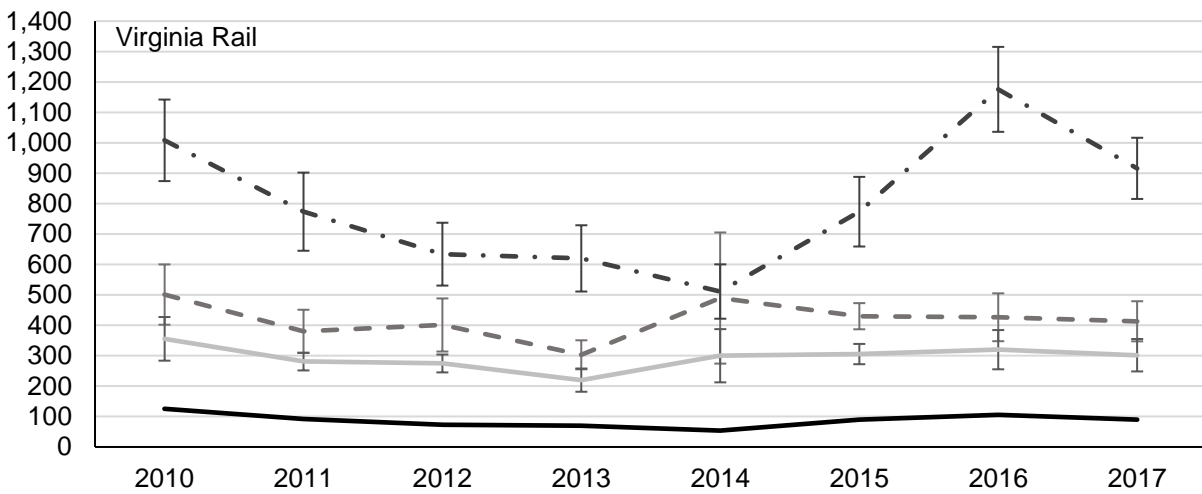
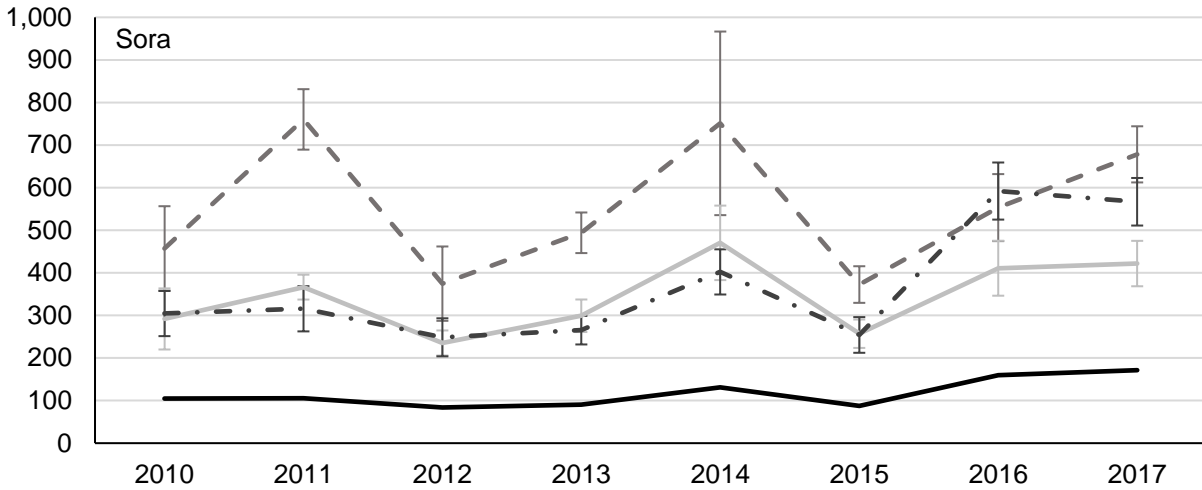


Figure 2. Estimated population size (thousands) using the narrow habitat definition for the Joint Venture region by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.



Raw
 Distance
 Heterogeneity
 N-mixture

Figure 2, continued. Estimated population size (thousands) using the narrow habitat definition for the Joint Venture region by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Detection and Occupancy Probability

To help evaluate survey effectiveness, we estimated probability of detection using both occupancy modeling and distance sampling using detections recorded within 100 m of survey points. When data from all years were combined, naïve occupancy was low for all species examined, with the greatest raw proportion of points occupied being about 0.20 for Sora. Estimated occupancy was greatest for Sora and Virginia Rail (~0.30) and lowest for Common Gallinule, American Coot, and Least Bittern (<0.10), with the remaining species having intermediate occupancy estimates (Table 3).

We observed considerable differences in detection probabilities produced using the two modeling techniques. Detection probability from occupancy models varied by species and survey period, ranging from a low of 0.16 (Wilson's Snipe, period 3) to a high of 0.57 (Sora, period 1). On average, detection probabilities were greatest for Sora, American Bittern, Virginia Rail, and Pied-billed Grebe, lowest for Least Bittern, and intermediate for American Coot and Wilson's Snipe. American Bittern, Sora, and Wilson's Snipe exhibited peak detection probabilities during the first period and declining detectability in subsequent periods, whereas the remaining species had relatively consistent detection probabilities across the three survey periods (Table 3). Distance sampling indicated complete detection of American Bittern, Pied-billed Grebe, and Wilson's Snipe within 100 m (Table 4). Detection probability estimates from distance sampling were much greater for American Bittern, Pied-billed Grebe, Wilson's Snipe, and American Coot compared to occupancy model estimates. Conversely, detection probability for Virginia Rail from distance sampling was lower compared to the occupancy model. Distance sampling indicated that the effective survey radii for most marsh birds was well below the 100-meter threshold used for our analyses, with 6 of 10 species analyzed having radii less than or equal to 63 meters (Table 4).

Annual estimates of occupancy from single-season models varied substantially across years, with Least Bittern and Wilson's Snipe exhibiting the greatest variation (Figure 3). There were no discernable trends in occupancy at the regional level for the six species analyzed (Figure 3). Estimated probability of detection also varied across species and years. Sora had the most consistent seasonal pattern in detection probabilities of the six species analyzed, with the greatest probability being observed in the first period and substantial decline in estimates with each subsequent survey (Figure 4). Conversely, Least Bittern and Virginia Rail had similar detection probabilities across survey periods. The remaining species had variable detection probabilities, with some annual models suggesting greater detectability during the first period, whereas in other years detection probability appeared similar across survey periods (Figure 4).

Table 3. Results of single-season occupancy models for marsh bird species in the upper Midwest with all years (2008-2017) combined ($n = 3,679$). Estimates were obtained from the best-approximating model for each species.

Species	Occupancy			Detection Probability						
	Naïve	Estimated	SE	Period 1	SE	Period 2	SE	Period 3	SE	Mean
American Bittern	0.123	0.192	0.020	0.452	0.039	0.341	0.034	0.173	0.023	0.322
American Coot	0.037	0.072	0.015	0.296	0.058	0.234	0.048	0.189	0.041	0.240
Common Gallinule	0.024	0.041	0.009	0.311	0.075	0.328	0.075	0.199	0.058	0.279
King Rail	0.008	---	---	---	---	---	---	---	---	---
Least Bittern	0.037	0.091	0.018	0.188	0.033	0.188	0.033	0.188	0.033	0.188
Pied-billed Grebe	0.087	0.156	0.019	0.335	0.035	0.264	0.031	0.247	0.030	0.282
Sora	0.197	0.293	0.023	0.574	0.029	0.288	0.020	0.168	0.016	0.343
Virginia Rail	0.155	0.257	0.024	0.350	0.026	0.303	0.023	0.289	0.024	0.314
Wilson's Snipe	0.071	0.160	0.025	0.280	0.035	0.179	0.025	0.159	0.024	0.206

Table 4. Effective detection radius (meters) from distance sampling models of all marsh bird (2010-2017) according to distribution type and species ($n = 3,240$). Weighted mean detection radius and detection probability are provided for each species.

Species	Effective Detection Radius						Weighted Mean	Detection Probability
	Half-normal	Exponential	Uniform	Hazardrate	Gamma	Weighted Mean		
American Bittern	82	69	100	100	86	100	1.00	
American Coot	66	50	87	86	70	86	0.74	
Common Gallinule	63	45	57	63	64	63	0.40	
King Rail	48	28	---	20	---	24	0.06	
Least Bittern	66	47	53	65	59	62	0.38	
Pied-billed Grebe	85	72	100	100	90	100	1.00	
Sora	63	44	44	60	53	57	0.33	
Virginia Rail	52	33	---	43	---	33	0.11	
Wilson's Snipe	79	66	100	96	85	100	1.00	
Yellow Rail	65	43	---	47	---	49	0.24	

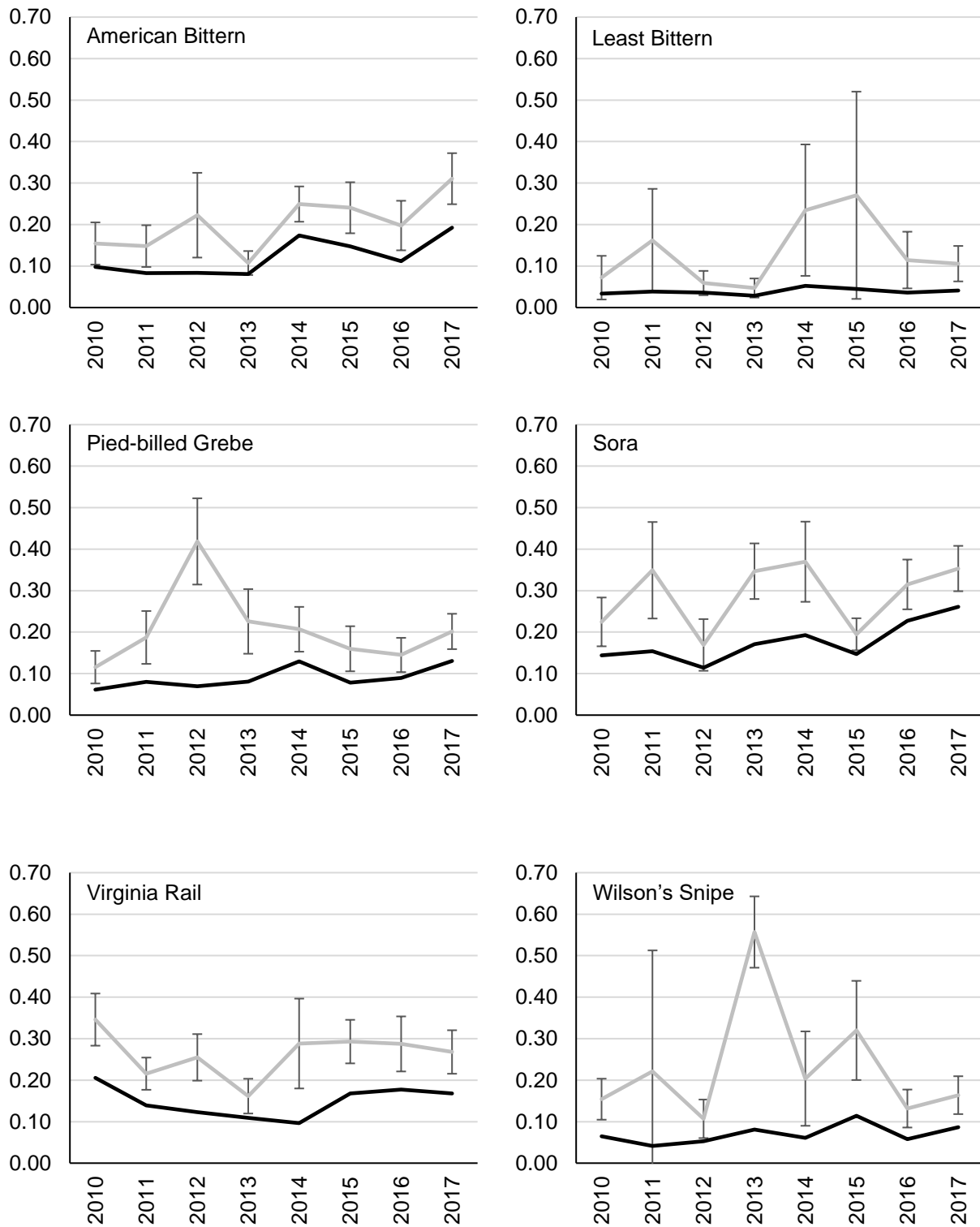


Figure 3. Naïve occupancy (black lines) and estimated annual occupancy (gray lines) from single-season models for six marsh bird species in the upper Midwest during 2010-2017 ($n = 3,679$). Error bars represent estimated occupancy plus/minus the standard error.

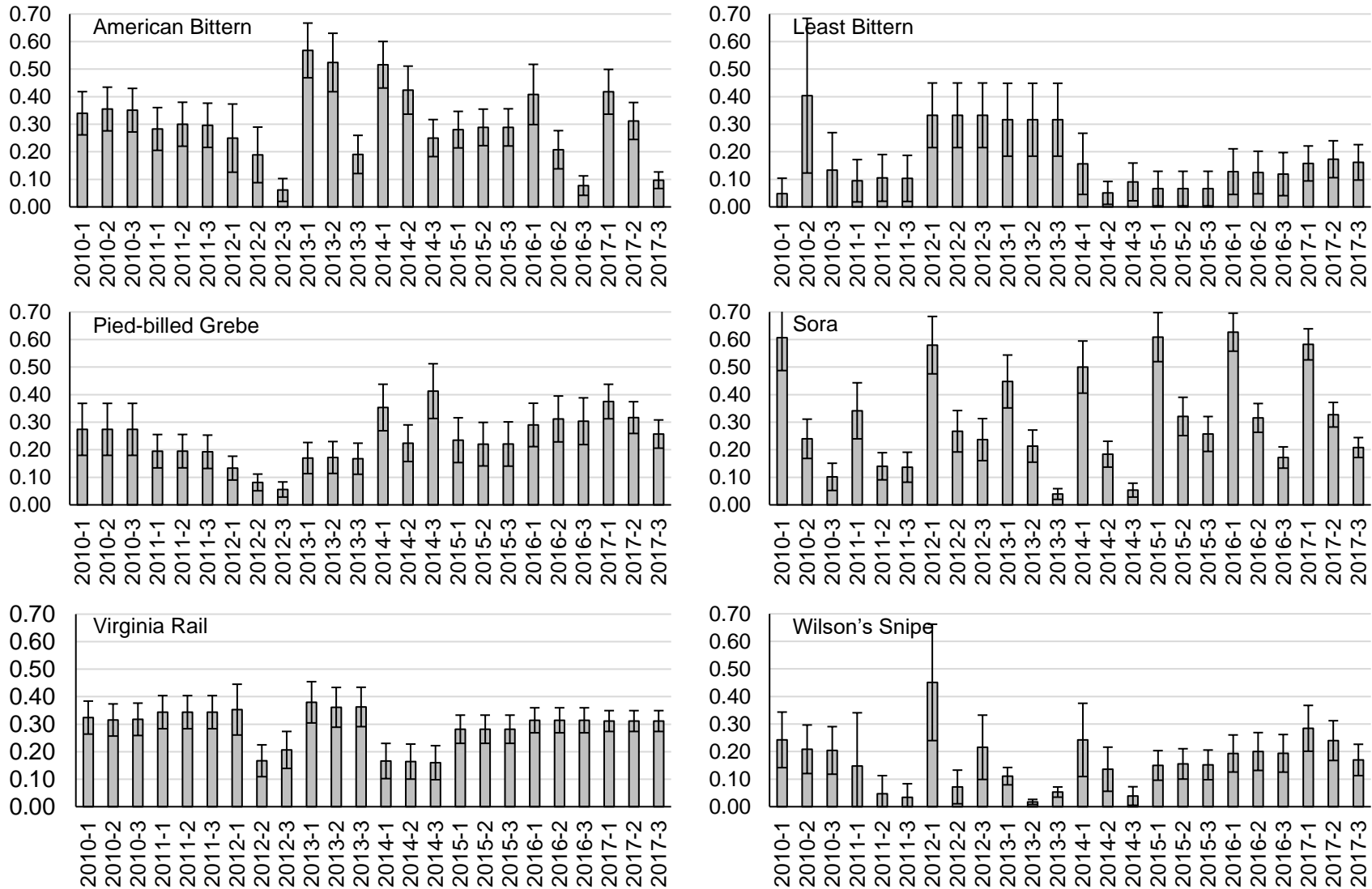


Figure 4. Estimated detection probability by year and survey period (1-3) from single season models for six marsh bird species in the upper Midwest during 2010-2017 ($n = 3,679$). Error bars represent estimated detection probability plus/minus the standard error.

Multi-season models indicated stable occupancy at the subset of points examined for Least Bittern, Pied-billed Grebe, and Virginia Rail, and potentially increasing occupancy for American Bittern, Sora, and Wilson's Snipe (Figure 5). Compared to annual estimates from single-season models, occupancy probabilities from multi-season models tended to be lower for Least Bittern and Sora and similar for the remaining species (Figures 3 and 5). Annual detection probability estimates from multi-season models were consistent with estimates from single-season models, except for Least Bittern and Virginia Rail. Detection probabilities for Least Bittern ($\bar{X} = 0.64$, range 0.56 – 0.78) were much greater than single-season model estimates, whereas Virginia Rail detectability estimates were lower ($\bar{X} = 0.10$, range 0.05 – 0.13) compared to single-season models. The rate of change in occupancy ($\lambda_t = \Psi_{t+1} / \Psi_t$) was > 1 for all species and years except for Virginia Rail, which had λ estimates slightly below 1 following 2012 (0.97 – 0.99). Despite estimates indicating stable to increasing rates of occupancy over time, probabilities of local extinction (i.e., probability an occupied site becomes unoccupied) were greater than probabilities of local colonization (i.e., probability an unoccupied site becomes occupied) for all species examined. This pattern could be related to inconsistent survey effort applied to points over time, resulting in substantial missing data in the analyses. See Appendix E for parameter estimates from the best-approximating model for each species.

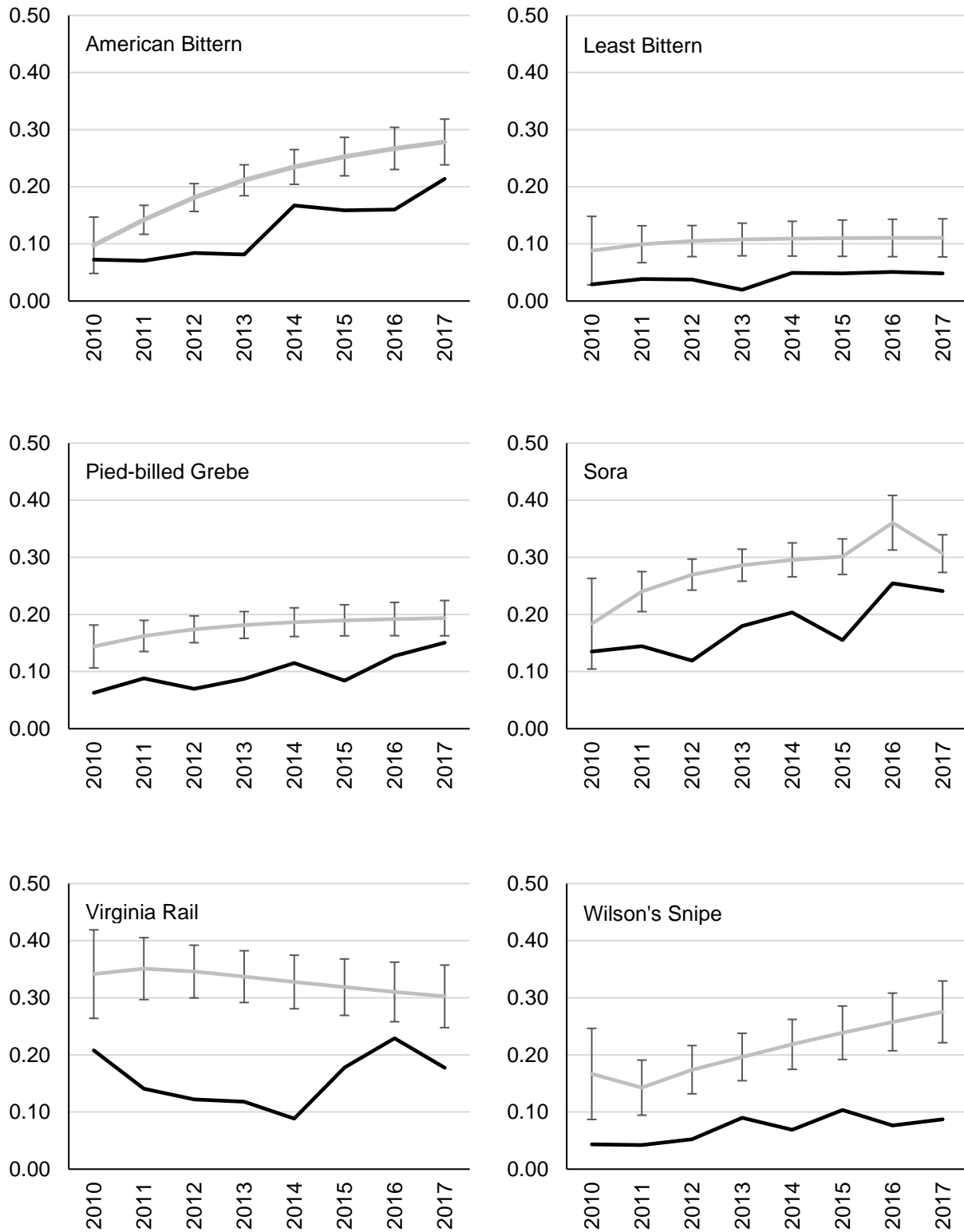


Figure 5. Naïve occupancy (black lines) and estimated annual occupancy (gray lines) from multi-season models for six marsh bird species in the upper Midwest during 2010-2017 ($n = 621$). Error bars represent estimated occupancy plus/minus the standard error.

Monitoring Design Implications

Species with low abundance and frequency of occurrence, such as Least Bittern, exhibited higher levels of variation in estimates compared to more common species, resulting in wide confidence intervals even with high sample effort (Figure 6). A moderate level of precision (i.e., $CI \approx \pm 50\%$ of mean) could only be achieved for Least Bittern under the distance sampling model with a sample size of about 700 points, which is slightly greater than the number of points (613) analyzed for the Joint Venture region in 2017. American Bittern and Pied-billed Grebe represent marsh bird species with moderate levels of abundance and occurrence. Moderate levels of precision were achieved for these species with a sample size of about 300 points (representative of sampling at the BCR scale) for the distance model and 700 points (i.e., Joint Venture region scale) for the N-mixture model (Figure 6). Sora and Virginia Rail were the most common marsh bird species observed, both in abundance and frequency of occurrence. Our analyses suggest we could achieve relatively high levels of precision for these species even at low levels of sampling effort (Figure 6), indicating monitoring of population trends may be possible at state-level and potentially smaller scales.

We used estimates of occupancy and detection probabilities from our models and recommendations from the literature to help inform marsh bird survey design. MacKenzie and Royle (2005) provided guidance for the number of surveys to conduct per season based on occupancy and detection probabilities for standard designs (Table 5). According to the range of estimates observed in our models, three surveys is likely only sufficient for the most common and highly detectable species, such as Sora and American Bittern. For the remaining species, at least 4 or 5 surveys would be optimum according to MacKenzie and Royle (2005) to minimize total survey effort and occupancy variance. Reed (1996) provided a method to estimate the number of surveys needed to achieve a minimum level of confidence based on estimated detection probabilities. Using our range of detection probabilities, it appears that three visits per season is potentially enough to have moderate to high levels of confidence that lack of detection equates to absence for American Bittern, Sora, and Virginia Rail (Table 5). The other species would require at least 4 – 6 surveys to have a moderate level of confidence that lack of detection means the species is not present.

We used our occupancy and detection values to estimate the power to detect change in occupancy according to Guillera-Arroita and Lahoz-Monfort (2012). Our analyses indicate that we have low power to detect change in occupancy of species with low levels of occupancy and detectability, such as Least Bittern, even with high survey effort, such as that expended at the Joint Venture region scale (Figure 7). The addition of another visit per season (i.e., from 3 to 4 surveys per season) increased the power to moderate levels (e.g., 0.50) with high sample effort and high proportions of change (> 0.50 decline in occupancy). For species with medium levels of occupancy and detectability, such as American Bittern and Pied-billed Grebe, we observed moderate power (≥ 0.60) to detect moderate to high proportions of occupancy change (e.g., ≥ 0.50 decline, ≥ 0.35 increase) with high sample sizes ($n = 675$ or $1,000$) and three visits per season (Figure 7). For species with high levels of occupancy and detection probability (e.g., Sora and Virginia Rail), we estimated there would be moderate power (about 0.50) to detect high proportions of occupancy change (e.g., ≥ 0.50 decline, ≥ 0.35 increase) even with a moderate sample size ($n = 225$) and three visits per season (Figure 7). With higher sample sizes, we estimated about 0.50 power to detect 0.25 change (decrease or increase). The addition of a fourth survey resulted in modest increases in power for species with medium and high levels of occupancy and detectability (Figure 8).

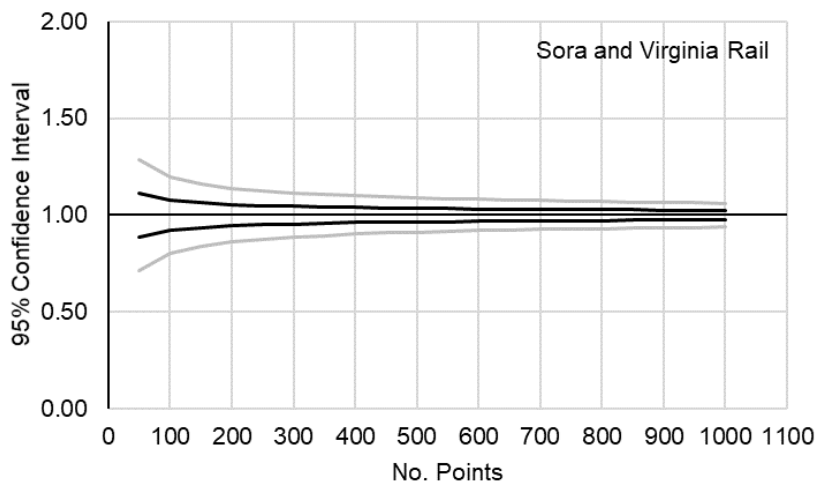
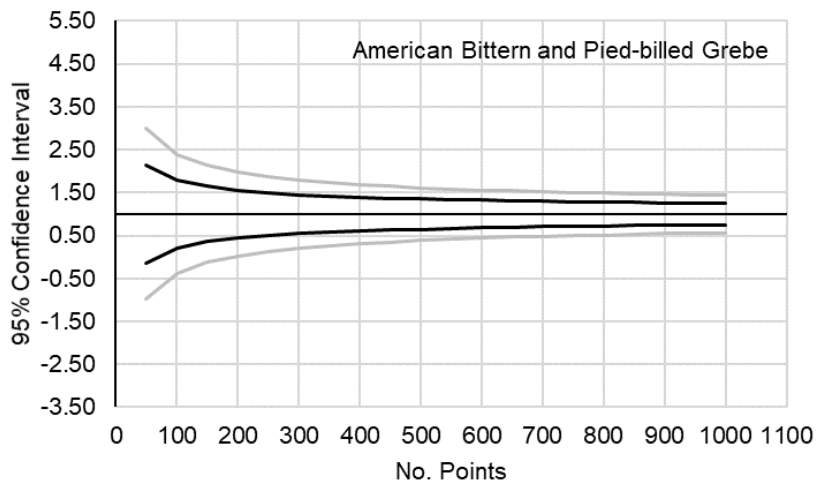
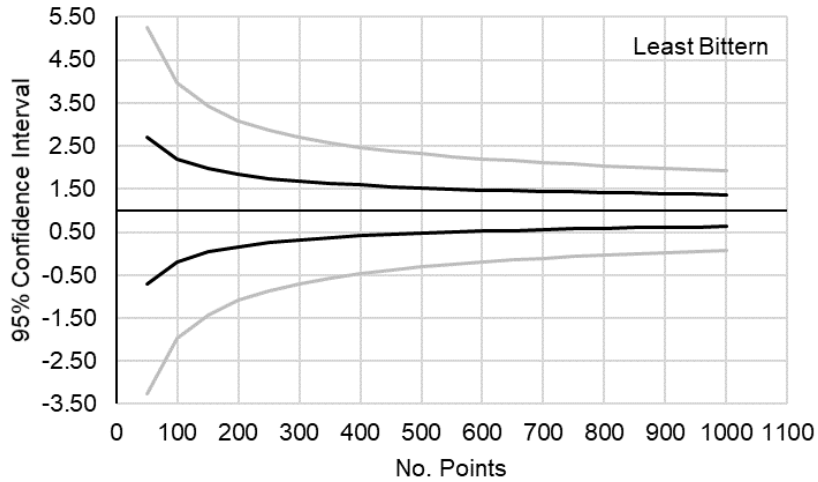


Figure 6. Estimated 95% confidence intervals for three marsh bird species/groups across a range of sampling effort. Confidence intervals were generated using means set at 1 and standard deviations that produced coefficients of variation consistent with those observed in our distance sampling (black lines) and N-mixture (gray lines) models.

Table 5. Recommended number of surveys per season using standard design and to ensure lack of detection equates to true absence based on observed marsh bird occupancy and detection probabilities.

Species	Occupancy Probability	Detection Probability	No. Surveys (std. design) ¹	No. Surveys Needed to be Certain of Absence at Given Confidence Level				
				95%	90%	85%	80%	75%
American Bittern	0.20	0.20 – 0.50	3 – 7	4 - 13	3 – 10	3 – 9	2 – 7	2 – 6
American Coot	0.10	0.20 – 0.30	5 – 7	8 - 13	6 – 10	5 – 9	5 – 7	4 – 6
Common Gallinule	0.04	0.20 – 0.30	> 5 – 7	8 - 13	6 – 10	5 – 9	5 – 7	4 – 6
Least Bittern	0.10	0.20	7	13	10	9	7	6
Pied-billed Grebe	0.20	0.20 – 0.30	5 – 7	8 - 13	6 – 10	5 – 9	5 – 7	4 – 6
Sora	0.30	0.20 – 0.60	2 – 8	3 – 13	3 – 10	2 – 9	2 – 7	2 – 6
Virginia Rail	0.30	0.30 – 0.40	4 – 5	6 – 8	5 – 6	4 – 5	3 – 5	3 – 4
Wilson's Snipe	0.20	0.20 – 0.30	5 – 7	8 - 13	6 – 10	5 – 9	5 – 7	4 – 6

¹From MacKenzie and Royle (2005).

²From Reed (1996).

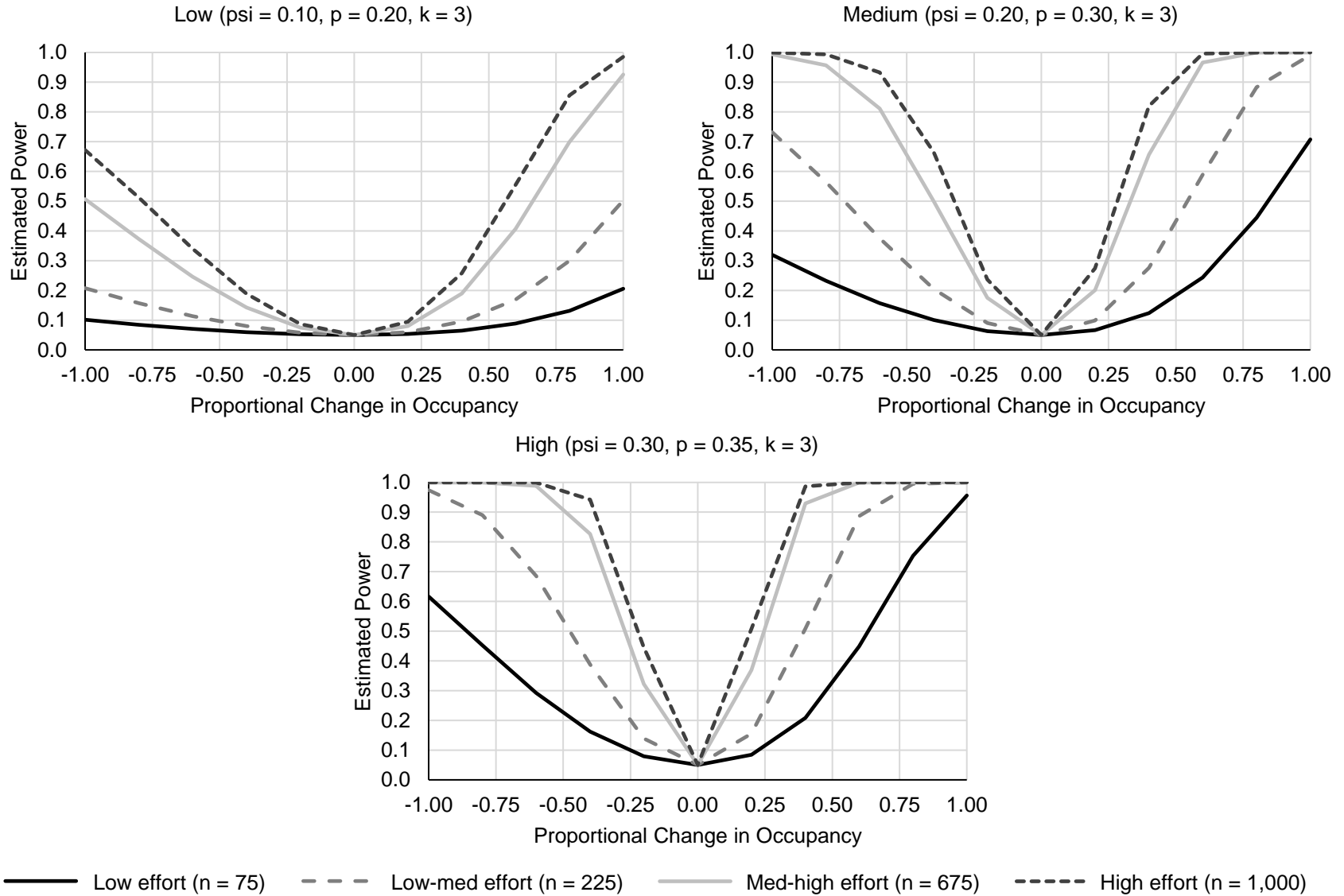


Figure 7. Estimated power to detect change in occupancy from year 1 to year 2 based on three levels of occupancy (psi) and detection (p) probabilities, four levels of survey effort, and three surveys per season (k = 3).

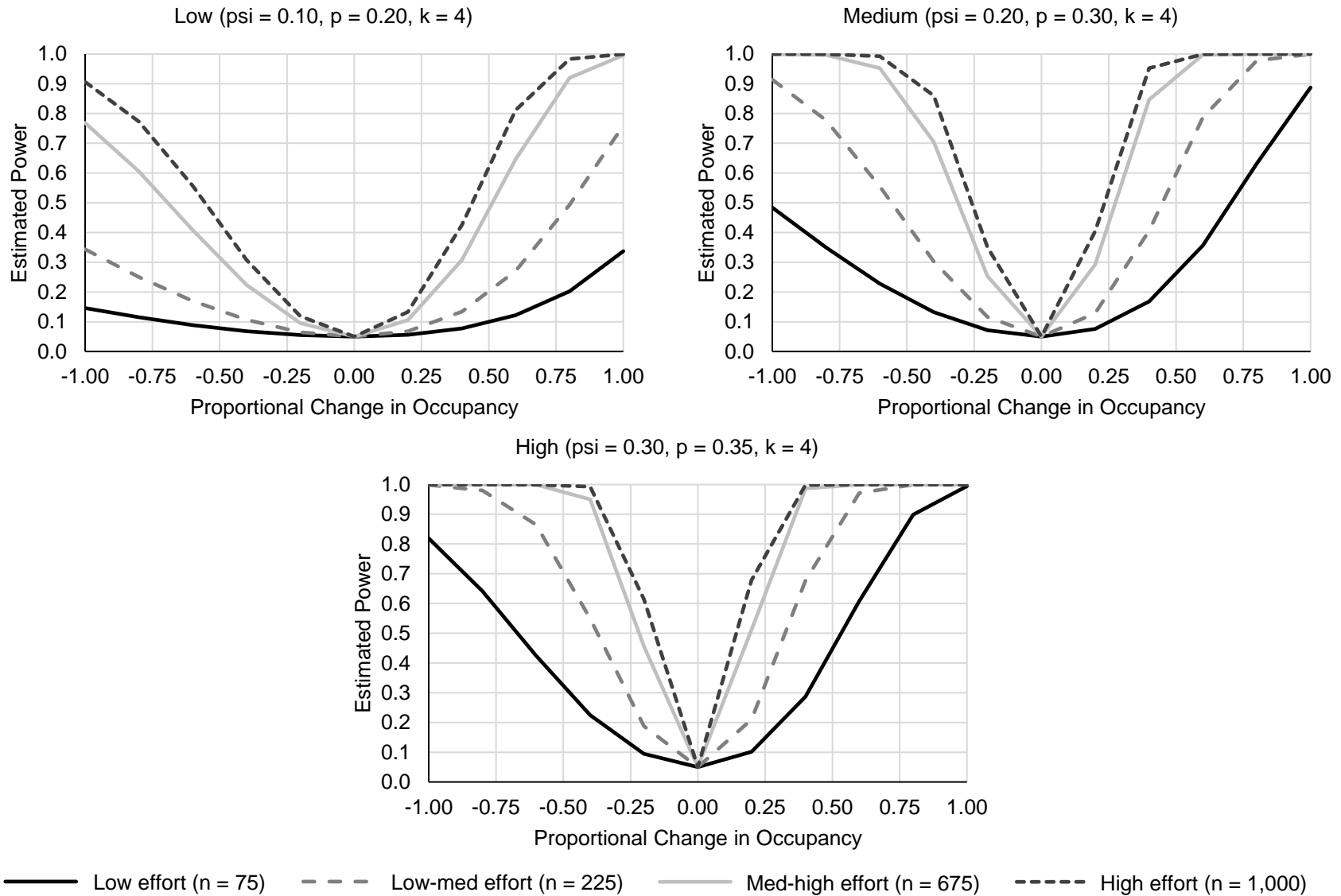


Figure 8. Estimated power to detect change in occupancy from year 1 to year 2 based on three levels of occupancy (ψ) and detection (p) probabilities, four levels of survey effort, and four surveys per season ($k = 4$).

Discussion

Population Size Estimates

Some researchers have estimated marsh bird population parameters, such as density and population size, at regional, state, or local scales (Harms and Dinsmore 2012, Saunders et al. 2019, Tolliver et al. 2019, Wiest et al. 2019), but we are aware of no studies attempting to estimate population sizes for marsh birds in the upper Midwest. We used data collected via coordinated regional surveys to estimate marsh bird population sizes for Joint Venture region, as well as smaller spatial scales (BCRs and states). Because this project represented the first effort to produce regional estimates, we chose to use and compare three modeling techniques that are commonly applied to bird data, intuitive, and could be readily replicated. More sophisticated techniques, such as hierarchical models and Bayesian approaches (e.g., Glisson et al. 2015, Wiest et al. 2019), have been employed to estimate wetland bird densities and hold promise for increasing the precision of estimates with the same survey effort. We suggest additional analyses using more complex modeling approaches be explored.

Prior to our study, Midwest regional-scale population abundance estimates for marsh birds were based largely on an expert-derived process associated with the Upper Mississippi Valley/Great Lakes Region Waterbird Conservation Plan (including BCRs 12, 13, 22, 23, and 24; Wires et al. 2010). The regional population of Pied-billed Grebe was estimated at approximately 5,000 individuals (Wires et al. 2010), whereas our estimates using all data combined and the narrow habitat definition ranged from 53,060 – 258,152 individuals (mean for 3 models = 160,890), which is greater than the North American estimate of 100,000 – 150,000 (Wetlands International 2012). Wires et al. (2010) did not estimate population sizes for American Bittern and Least Bittern. Wetlands International (2012) estimated the American Bittern population size for North America at 2.98 million individuals. Our American Bittern population estimates for the Joint Venture region ranged from 72,608 – 298,627 (mean for 3 models = 200,516) with all years combined and using the narrow habitat definition. Kushlan et al. (2002) estimated the North American Least Bittern population at 128,000 individuals. When using all data and the narrow habitat definition, our estimates for the Joint Venture regional population ranged from 47,475 – 104,330 individuals (mean for 3 models = 81,540). Based on the Sora breeding pair estimates listed by BCR in Wires et al. (2010), the population size for the region was estimated at a minimum range of 20,530 – 42,790 individuals. The number of breeding pairs estimated for Virginia Rail similarly translate to a population size of at least 43,180 – 88,940 individuals. The region used for the Upper Mississippi Valley/Great Lakes Region plan is much larger the Joint Venture region, because it includes the entirety of BCRs 12, 13, 22, 23, and 24. Despite this difference in area, our population estimates for Sora and Virginia Rail ranged from 344,503 – 553,344 (mean for 3 models = 424,950) and 288,907 – 804,276 (mean for 3 models = 501,498), respectively, using models with all years combined and our narrow habitat definition.

Even when considering our most conservative population estimates, our models suggest the population sizes for the marsh bird species analyzed are likely far larger than previously thought. However, our estimates are based on imprecise estimates of wetlands from the NWI, so there is potential for overestimation of population sizes due to the incorporation of unsuitable habitats. Further refinement of marsh bird habitat estimates, perhaps at the species level, could potentially improve the accuracy of population estimates. For example, habitat area could be estimated using thresholds for minimum wetland size based on breeding territory size.

We compared our density estimates to those produced in state-level studies completed in Iowa (Harms and Dinsmore 2012) and Minnesota (Saunders et al. 2019). Harms and Dinsmore (2012) estimated densities of Pied-billed Grebe, Least Bittern, Virginia Rail, and Sora for three regions of Iowa. Pied-billed Grebe densities in Iowa ranged from 0.04 – 0.16 birds/ha, which were greater than our regional distance sampling estimate (0.02) and estimates at BCR and state levels (Appendix C). Our regional Least Bittern distance sampling density of 0.02 detections/ha was similar to those from Iowa (range <0.01 – 0.03). We estimated regional Sora density at 0.14 with distance sampling, which was within the range of densities (0.04 – 0.16) estimated by Harms and Dinsmore (2012) for spring migrant Soras in Iowa. Our regional Virginia Rail density (0.29) was greater than those for Iowa (0.01 – 0.10). Estimates may have differed because of how distances were integrated into models, with our distances truncated at 100 m and Harms and Dinsmore (2012) having an unlimited survey distance, or differences in landscape cover and average wetland sizes.

Saunders et al. (2019) produced abundance estimates for 200-m radius areas surrounding survey points using N-mixture models for Pied-billed Grebe, American Bittern, and Sora using the same data from Minnesota included in our study. We converted their mean abundances to densities (birds/ha), resulting in an average of 0.01 for Pied-billed Grebe, 0.04 for American Bittern, and 0.04 for Sora. Density estimates from our N-mixture models were greater for all three species for both the region (Pied-billed Grebe = 0.09; Am. Bittern = 0.10; Sora = 0.20) and Minnesota (Pied-billed Grebe = 0.08; Am. Bittern = 0.10; Sora = 0.27). Our greater estimates were likely due to use of a different truncation distance of 100 m compared to 200 m by Saunders et al. (2019). We also estimated densities at smaller spatial scales (i.e., Minnesota) by averaging point estimates from the regional model, rather than producing models specific to the smaller areas (BCRs, states).

An important assumption in developing our marsh bird population estimates was that the densities estimated from surveys in the four Great Lakes states are representative of densities throughout the Joint Venture region. Because these four states occur at the northern edge of the breeding range of some species and the southern edge of others, it is possible our population estimates are biased high or low depending on the species and its distribution within the region. Estimates could be improved if additional data sets in the southern portion of the region were incorporated into the models. In recent years, Audubon Great Lakes has been coordinating surveys in Indiana and Illinois using similar survey techniques. Although the survey methods differ from those in other states (Molano-Flores 2002), the Illinois Critical Trends Assessment Program has also been gathering data since 1997 and includes surveys for wetland birds when habitat is present. We recommend working with the coordinators of these surveys to assess the potential for incorporating additional data sets into the population modeling effort.

Occupancy and Detectability

The growing use of occupancy modeling provides opportunities to compare our results with other marsh bird studies. Our estimates of occupancy and detection probabilities were generally consistent with estimates produced in other studies from the Midwest or Great Lakes region. With all years combined, we estimated regional Pied-billed Grebe occupancy at 0.16, which consistent with estimates from Minnesota (0.16; Saunders et al. 2019), undiked Michigan coastal wetlands (0.18; Monfils et al. 2014), and southern Ontario (0.15 and 0.22; Tozer et al. 2018), but lower than probabilities from diked coastal wetlands (0.43; Monfils et al. 2014) and Great Lakes states (0.20 and 0.26; Monfils et al. 2018). Our American Bittern occupancy probability of 0.19 was lower than estimates for Minnesota (0.30; Saunders et al. 2019) and Michigan coastal wetlands (0.37 and 0.69; Monfils et al. 2014), and similar to probabilities from

southern Ontario (0.07 and 0.23; Tozer et al. 2018), Wisconsin (0.10 and 0.23; Glisson et al. 2015), and Great Lakes states (0.13 and 0.19; Monfils et al. 2018). We estimated regional Least Bittern occupancy at 0.09, which is similar to estimates from Great Lakes states (0.11 and 0.15; Monfils et al. 2018) and unmanaged wetlands in Ontario (0.10; Tozer et al. 2018), but lower than occupancy in managed Ontario wetlands (0.47; Tozer et al. 2018). Our Virginia Rail occupancy (0.26) was consistent with estimates from Minnesota (0.24; Saunders et al. 2019), southern Ontario (0.21 and 0.29; Tozer et al. 2018), and three Great Lakes states (0.15 and 0.41; Monfils et al. 2018), but lower than occupancy estimates for wetlands in Michigan (0.55 and 0.68; Monfils et al. 2014) and Wisconsin (0.56 and 0.62; Glisson et al. 2015). Our Sora occupancy probability (0.29) was lower than estimates from Minnesota (0.39; Saunders et al. 2019) and Wisconsin natural wetlands (0.51; Glisson et al. 2015) and similar to estimates for restored Wisconsin wetlands (0.30; Glisson et al. 2015) and three Great Lakes states (0.22 and 0.30; Monfils et al. 2018), but greater than estimates from Michigan coastal wetlands (0.18; Monfils et al. 2014) and southern Ontario (0.07 and 0.17; Tozer et al. 2018). Our regional American Coot occupancy estimate of 0.07 was similar to those from southern Ontario (0.07 and 0.17; Tozer et al. 2018) and three Great Lakes states (0.10 and 0.13) but lower than diked (0.31) and undiked (0.22) Michigan coastal wetlands (Monfils et al. 2014). Common Gallinule occupancy estimates from unmanaged and managed wetlands in southern Ontario (0.06 and 0.21; Tozer et al. 2018) and Michigan (0.08 and 0.12; Monfils et al. 2014) were greater than our 0.04 estimate for the Joint Venture region. We estimated a lower regional Wilson's Snipe occupancy (0.16) compared to the Saunders et al. (2019) estimate of 0.27 for Minnesota. Detection probabilities from our study for Pied-billed Grebe (0.25 – 0.34), American Bittern (0.17 – 0.45), Least Bittern (0.19), Virginia Rail (0.29 – 0.35), and Sora (0.17 – 0.57) were consistent with estimates from other projects in the region (Monfils et al. 2014, 2018; Tozer et al. 2018). Our detectability estimates for American Coot (0.19 – 0.30) and Common Gallinule (0.20 – 0.33) were lower than probabilities from Michigan coastal wetlands (Monfils et al. 2014) and southern Ontario (Tozer et al. 2018).

Although occupancy modeling can be a valuable tool in assessing population status and trends, we caution against using it as the only state variable in regional marsh bird monitoring because of potential bias in parameter estimates due to the likely violation of the closure assumption (Rota et al. 2009, Hayes and Monfils 2015). Similar problems have been raised with the violation of assumptions underlying the distance sampling model (Hutto 2016). We suggest the assessment of marsh bird population trends follow an approach similar to this study – one in which multiple population parameters are examined, including raw indices, abundance, and occupancy, to determine if similar patterns emerge. Steenweg et al. (2017) provided a conceptual framework for understanding how sampling scales affect the definition of occupancy for mobile organisms and described how spatial and temporal sampling scales and the choice of sampling unit affect occupancy-abundance relationships. Those leading regional marsh bird survey efforts could benefit from consideration of these concepts as they plan future analyses and assess the potential effects of violating underlying assumptions.

Marsh Bird Monitoring

We observed high variation in annual population estimates (both abundance and occupancy), which is likely due to a variety of factors, including population fluctuations, dynamic hydrologic conditions, and sampling variation (e.g., changes in observers, survey sites, and sample size). Despite the challenge presented by high variation in detecting change over time, our analyses suggest the regional survey effort should be able to detect moderate change in relative abundance of American Bittern, Pied-billed Grebe, Sora, and Virginia Rail, possibly even at the BCR or state scale. Detecting high levels change in population parameters for species with lower occurrence and abundance levels, such as Least Bittern, American Coot, and Common

Gallinule, may be possible at the regional scale and over longer time frames. Assuming detecting population changes over time remains an objective of the regional marsh bird survey effort, we recommend focusing on larger spatial scales, such as the Joint Venture region or BCRs, and longer time frames (e.g., 5-year or 10-year intervals) to increase the precision of estimates. Furthermore, increasing the number of points surveyed in Michigan and Wisconsin (primary breeding range for many marsh birds) back to peak levels of previous years, as well as improving the consistency of the survey effort over time, could reduce variation in estimates and increase the power to detect population changes.

Several changes to the regional survey's sample frame and survey methods have potential to increase precision of population parameters and improve our ability to detect population change over short- and long-term periods. Following are relevant options that should be considered by those involved with coordinated regional marsh bird surveys: 1) stratify the sample frame to increase efficiency and reduce variation, such as reducing sampling at marginal sites and increasing survey effort at locations more likely to support target species; 2) refine estimates of marsh bird habitat area based on past surveys results, sample frame stratification, and/or species requirements (e.g., minimum wetland area required or home range size); 3) increase the number of surveys conducted per season to four visits (though this is likely unfeasible given the current reliance on volunteers and the increase in precision may not be worth the increased resources required); and 4) shift the current three visits to earlier in the season (e.g., May) when detection probabilities tend to be greater for most species. Changes to the sample frame, such as reducing survey effort in marginal habitats, could increase precision of density, occupancy, and detectability estimates, thus improving population size estimates and our ability to detect change over time. However, estimates of available marsh bird habitat within the region would need to be revised to follow any changes in the sample frame. Deciding upon the most accurate mechanisms to estimate marsh bird habitat area is perhaps the most important way to increase the reliability of estimates without the need for additional or modified field methodologies.

Acknowledgements

Funding for this project was provided by the U.S. Fish and Wildlife Service (USFWS), Upper Mississippi / Great Lakes Joint Venture. Several individuals assisted in transferring marsh bird data to us for our analysis: Ryan Brady (Wisconsin DNR), Kristin Hall (Minnesota Audubon/Minnesota DNR), Laura Kearns (Ohio DNR), Katie Koch (USFWS), Leo Salas (Point Blue), Sarah Saunders (Audubon Great Lakes). Members of the Data Analysis Team of the Midwest Marsh Bird Working Group provided valuable feedback on analyses and monitoring recommendations: Laura Kearns, Brendan Shirkey (Winous Point Marsh Conservancy), and Sara Saunders. We thank Anna Sidie-Slettedahl (USFWS) for her cooperation and administrative support. Administrative support was provided by Brian Klatt, Ashley Atkinson, and Nancy Toben (MNFI). We appreciate the many volunteers throughout the Midwest who conducted marsh bird surveys.

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Appendix A. Potential marsh bird habitat definitions and area estimates.

Table A1. National Wetlands Inventory wetland categories used in estimating the availability of marsh bird habitat within the Midwest region for use in developing abundance and occupancy models and estimating population sizes.		
Wetland Type ^{1,2}	Potential Marsh Bird Habitat Definition ³	
	Broad	Narrow
L1UB	X	
L2AB	X	
L2EM	X	
L2EM/AB	X	
L2EM/UB (combined with L2UB/EM)	X	
L2UB	X	
L2US	X	
PAB	X	
PAB/EM (combined with PEM/AB)	X	X
PAB/FO	X	
PAB/UB (combined with PUB/AB)	X	
PEM	X	X
PEM/FO (combined with PFO/EM)	X	X
PEM/SS (combined with PSS/EM)	X	X
PEM/UB (combined with PUB/EM)	X	X
PEM/US	X	X
P		
PFO		
PFO/SS (combined with PSS/FO)		
PFO/UB (combined with PUB/FO)	X	
PSS		
PSS/AB	X	
PSS/UB (combined with PUB/SS)	X	
PUB	X	
PUS	X	
R2AB	X	
R2EM	X	
R2EM/UB	X	
R2UB	X	
R2US	X	
R3UB		
R4SB		
R5UB		

¹System and subsystem codes: L = Lacustrine (1 = limnetic, 2 = littoral); P = Palustrine (no subsystem); and R = Riverine (2 = lower perennial; 3 = upper perennial; 4 = intermittent; and 5 = unknown perennial).

²Class codes: AB = aquatic bed; EM = emergent; FO = forested; SS = scrub shrub; UB = unconsolidated bottom; and US = unconsolidated shore.

³Marsh bird habitat definitions: Broad = wetland types with EM, AB, UB, and US classes, except for upper perennial and intermittent subsystems; Moderate = wetland types with EM and AB classes; and Narrow = wetland types with the EM class.

Appendix A. Potential marsh bird habitat definitions and area estimates.

Table A2. Estimated area of potential marsh bird habitat according to broad and narrow definitions by spatial extent.		
Spatial Extent	Potential Marsh Bird Habitat Area (hectares)	
	Broad Definition	Narrow Definition
Joint Venture Boundary	5,762,072	2,792,626
Bird Conservation Regions (BCR) within Joint Venture Boundary		
BCR 11	9,487	8,863
BCR 12	2,750,807	1,331,474
BCR 13	70,911	29,228
BCR 22	1,116,431	309,987
BCR 23	1,814,436	1,113,075
State Boundaries		
Michigan	1,012,929	526,671
Minnesota	3,237,412	1,836,624
Ohio	259,706	73,385
Wisconsin	1,331,738	811,795

Appendix B. Example R code for distance sampling analysis of American Bittern detections.

```
library(Rdistance)
require(Rdistance)

AMBI=read.csv(file="C:/Users/Dan/OneDrive - Michigan State
University/data/projects/Marsh_Birds/2019/d_AMBI.csv",head=TRUE,sep=",")
AMBI_hn <- dfuncEstim(formula=dist~1, detectionData=AMBI, likelihood ="halfnorm", w.hi=125,
pointSurvey=TRUE)
AMBI_ex <- dfuncEstim(formula=dist~1, detectionData=AMBI, likelihood ="negexp", w.hi=125,
pointSurvey=TRUE)
AMBI_un <- dfuncEstim(formula=dist~1, detectionData=AMBI, likelihood ="uniform", w.hi=125,
pointSurvey=TRUE)
AMBI_ha <- dfuncEstim(formula=dist~1, detectionData=AMBI, likelihood ="hazrate", w.hi=125,
pointSurvey=TRUE)
AMBI_ga <- dfuncEstim(formula=dist~1, detectionData=AMBI, likelihood ="Gamma", w.hi=125,
pointSurvey=TRUE)
```

First lines of data set as example of data structure:

siteID	groupsize	dist
1	1	90
1	1	50
1	1	80
1	1	75
1	1	75
1	1	60
1	1	50

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Estimated marsh bird densities (detections per ha) and population sizes for all years combined (2008-2017) by species, model type, and potential habitat definition for the BCR 12 and 23 portions of the Joint Venture region and states (including areas outside of the Joint Venture boundary).

Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
BCR 12												
Density (detections/ha)												
Raw	0.035	---	0.004	---	0.006	---	0.029	---	0.028	---	0.023	---
Distance sampling	0.039	0.003	0.011	0.002	0.006	0.001	0.095	0.009	0.260	0.025	0.029	0.003
N-mixture	0.140	0.015	0.025	0.007	0.031	0.005	0.114	0.011	0.119	0.012	0.145	0.023
Heterogeneity	0.116	0.014	0.023	0.006	0.020	0.004	0.077	0.008	0.085	0.010	0.104	0.018
Mean estimated	0.098	0.010	0.020	0.005	0.019	0.003	0.095	0.009	0.155	0.016	0.093	0.015
Population Size – Broad Habitat Definition												
Raw	96,804	---	10,656	---	17,050	---	80,539	---	77,061	---	62,479	---
Distance sampling	107,281	8,252	30,259	5,502	16,505	2,751	261,327	24,757	715,210	68,770	79,773	8,252
N-mixture	385,904	40,857	68,045	19,030	84,840	13,559	312,894	30,245	328,378	33,942	400,147	64,468
Heterogeneity	318,432	37,472	62,666	16,959	54,030	10,267	212,178	22,222	234,971	26,569	286,621	49,687
Mean estimated	270,539	28,861	53,657	13,830	51,792	8,859	262,133	25,741	426,186	43,094	255,514	40,803
Population Size – Narrow Habitat Definition												
Raw	46,856	---	5,158	---	8,253	---	38,983	---	37,300	---	30,242	---
Distance sampling	51,927	3,994	14,646	2,663	7,989	1,331	126,490	11,983	346,183	33,287	38,613	3,994
N-mixture	186,789	19,776	32,936	9,211	41,065	6,563	151,450	14,639	158,945	16,429	193,683	31,205
Heterogeneity	154,131	18,138	30,332	8,209	26,152	4,970	102,701	10,756	113,733	12,860	138,733	24,050
Mean estimated	130,949	13,969	25,971	6,694	25,069	4,288	126,880	12,460	206,287	20,859	123,677	19,750

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Continued.												
Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
BCR 23												
Density (detections/ha)												
Raw	0.026	---	0.007	---	0.022	---	0.064	---	0.037	---	0.010	---
Distance sampling	0.021	0.002	0.020	0.003	0.024	0.002	0.146	0.010	0.280	0.021	0.031	0.002
N-mixture	0.105	0.012	0.048	0.012	0.114	0.012	0.248	0.019	0.160	0.014	0.063	0.011
Heterogeneity	0.076	0.010	0.042	0.010	0.074	0.009	0.147	0.012	0.108	0.011	0.049	0.009
Mean estimated	0.067	0.008	0.037	0.008	0.071	0.008	0.180	0.014	0.183	0.015	0.048	0.007
Population Size – Broad Habitat Definition												
Raw	47,417	---	13,608	---	40,824	---	116,882	---	67,513	---	18,302	---
Distance sampling	38,103	3,629	36,289	5,443	43,546	3,629	264,908	18,144	508,042	38,103	56,248	3,629
N-mixture	189,876	21,370	86,673	21,577	206,371	21,853	450,484	34,257	291,177	25,948	115,111	20,253
Heterogeneity	137,423	17,367	76,482	18,147	134,498	16,983	265,822	22,431	196,249	19,106	88,459	16,624
Mean estimated	121,801	14,122	66,481	15,056	128,139	14,155	327,071	24,944	331,823	27,719	86,606	13,502
Population Size – Narrow Habitat Definition												
Raw	29,088	---	8,348	---	25,044	---	71,702	---	41,416	---	11,228	---
Distance sampling	23,375	2,226	22,261	3,339	26,714	2,226	162,509	11,131	311,661	23,375	34,505	2,226
N-mixture	116,480	13,109	53,170	13,237	126,599	13,406	276,352	21,015	178,624	15,918	70,615	12,425
Heterogeneity	84,303	10,654	46,918	11,133	82,509	10,418	163,070	13,760	120,390	11,721	54,266	10,198
Mean estimated	74,719	8,663	40,783	9,236	78,607	8,683	200,643	15,302	203,558	17,005	53,129	8,283

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Continued.												
Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
MICHIGAN												
Density (detections/ha)												
Raw	0.042	---	0.007	---	0.014	---	0.032	---	0.027	---	0.016	---
Distance sampling	0.042	0.003	0.020	0.003	0.014	0.002	0.099	0.010	0.248	0.024	0.027	0.003
N-mixture	0.167	0.017	0.049	0.013	0.070	0.009	0.144	0.013	0.144	0.014	0.114	0.019
Heterogeneity	0.133	0.015	0.042	0.010	0.047	0.007	0.089	0.009	0.101	0.011	0.084	0.015
Mean estimated	0.114	0.012	0.037	0.009	0.043	0.006	0.110	0.010	0.164	0.016	0.075	0.012
Population Size – Broad Habitat Definition												
Raw	42,736	---	7,554	---	14,195	---	32,749	---	27,731	---	16,375	---
Distance sampling	42,543	3,039	20,259	3,039	14,181	2,026	100,280	10,129	251,206	24,310	27,349	3,039
N-mixture	169,047	17,540	49,392	12,675	70,422	8,651	145,440	12,998	146,062	14,225	115,546	18,747
Heterogeneity	134,505	15,531	42,261	10,514	47,395	6,741	89,652	8,659	102,506	10,912	85,265	14,884
Mean estimated	115,365	12,036	37,304	8,743	43,999	5,806	111,791	10,595	166,591	16,482	76,053	12,223
Population Size – Narrow Habitat Definition												
Raw	22,221	---	3,928	---	7,381	---	17,028	---	14,418	---	8,514	---
Distance sampling	22,120	1,580	10,533	1,580	7,373	1,053	52,140	5,267	130,614	12,640	14,220	1,580
N-mixture	87,896	9,120	25,681	6,590	36,616	4,498	75,621	6,758	75,945	7,396	60,078	9,748
Heterogeneity	69,936	8,075	21,974	5,467	24,643	3,505	46,615	4,502	53,298	5,674	44,333	7,739
Mean estimated	59,984	6,258	19,396	4,546	22,877	3,019	58,126	5,509	86,619	8,570	39,544	6,356

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Continued.												
Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
MINNESOTA												
Density (detections/ha)												
Raw	0.021	---	0.005	---	0.018	---	0.064	---	0.034	---	0.013	---
Distance sampling	0.026	0.003	0.015	0.005	0.021	0.004	0.246	0.022	0.398	0.043	0.044	0.005
N-mixture	0.099	0.014	0.017	0.006	0.082	0.011	0.273	0.026	0.156	0.017	0.111	0.022
Heterogeneity	0.079	0.013	0.013	0.004	0.044	0.008	0.168	0.018	0.109	0.013	0.076	0.016
Mean estimated	0.068	0.010	0.015	0.005	0.049	0.008	0.229	0.022	0.221	0.024	0.077	0.014
Population Size – Broad Habitat Definition												
Raw	66,617	---	15,019	---	57,654	---	208,570	---	110,220	---	41,423	---
Distance sampling	84,173	9,712	48,561	16,187	67,986	12,950	796,403	71,223	1,288,490	139,209	142,446	16,187
N-mixture	321,062	46,301	56,463	19,403	266,344	34,321	884,148	82,858	503,447	55,239	360,827	70,301
Heterogeneity	256,996	41,231	43,543	14,210	141,769	26,595	544,844	58,077	352,865	43,214	246,519	52,536
Mean estimated	220,743	32,415	49,522	16,600	158,700	24,622	741,798	70,720	714,934	79,221	249,931	46,341
Population Size – Narrow Habitat Definition												
Raw	37,792	---	8,520	---	32,708	---	118,325	---	62,529	---	23,500	---
Distance sampling	47,752	5,510	27,549	9,183	38,569	7,346	451,810	40,406	730,976	78,975	80,811	9,183
N-mixture	182,142	26,267	32,032	11,008	151,100	19,471	501,588	47,006	285,612	31,338	204,701	39,883
Heterogeneity	145,797	23,391	24,703	8,061	80,428	15,088	309,097	32,948	200,185	24,516	139,854	29,804
Mean estimated	125,231	18,389	28,095	9,417	90,032	13,968	420,832	40,120	405,591	44,943	141,789	26,290

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Continued.												
Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
OHIO												
Density (detections/ha)												
Raw	0.001	---	0.008	---	0.044	---	0.034	---	0.024	---	0.000	---
Distance sampling	0.001	0.000	0.021	0.004	0.043	0.004	0.106	0.012	0.215	0.024	0.024	0.003
N-mixture	0.032	0.005	0.053	0.015	0.168	0.020	0.166	0.016	0.151	0.017	0.014	0.003
Heterogeneity	0.022	0.004	0.052	0.014	0.131	0.018	0.113	0.012	0.114	0.014	0.012	0.003
Mean estimated	0.018	0.003	0.042	0.011	0.114	0.014	0.128	0.013	0.160	0.018	0.017	0.003
Population Size – Broad Habitat Definition												
Raw	199	---	2,085	---	11,345	---	8,937	---	6,132	---	0	---
Distance sampling	260	0	5,454	1,039	11,167	1,039	27,529	3,116	55,837	6,233	6,233	779
N-mixture	8,369	1,337	13,743	3,777	43,614	5,161	43,205	4,053	39,278	4,404	3,618	902
Heterogeneity	5,621	1,027	13,452	3,587	34,025	4,749	29,270	3,115	29,487	3,564	3,235	870
Mean estimated	4,750	788	10,883	2,801	29,602	3,650	33,335	3,428	41,534	4,734	4,362	850
Population Size – Narrow Habitat Definition												
Raw	56	---	589	---	3,206	---	2,525	---	1,733	---	0	---
Distance sampling	73	0	1,541	294	3,156	294	7,779	881	15,778	1,761	1,761	220
N-mixture	2,365	378	3,883	1,067	12,324	1,458	12,208	1,145	11,099	1,245	1,022	255
Heterogeneity	1,588	290	3,801	1,014	9,614	1,342	8,271	880	8,332	1,007	914	246
Mean estimated	1,342	223	3,075	791	8,365	1,031	9,419	969	11,736	1,338	1,233	240

Appendix C. Marsh bird density and population estimates for all years combined at BCR and state scales.

Table C1. Continued.												
Variable and Model	American Bittern		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
WISCONSIN												
Density (detections/ha)												
Raw	0.028	---	0.028	---	0.028	---	0.028	---	0.028	---	0.028	---
Distance sampling	0.022	0.003	0.022	0.003	0.022	0.003	0.022	0.003	0.022	0.003	0.022	0.003
N-mixture	0.095	0.010	0.095	0.010	0.095	0.010	0.095	0.010	0.095	0.010	0.095	0.010
Heterogeneity	0.070	0.008	0.070	0.008	0.070	0.008	0.070	0.008	0.070	0.008	0.070	0.008
Mean estimated	0.062	0.007	0.062	0.007	0.062	0.007	0.062	0.007	0.062	0.007	0.062	0.007
Population Size – Broad Habitat Definition												
Raw	37,593	---	37,593	---	37,593	---	37,593	---	37,593	---	37,593	---
Distance sampling	29,298	3,995	29,298	3,995	29,298	3,995	29,298	3,995	29,298	3,995	29,298	3,995
N-mixture	126,106	13,699	126,106	13,699	126,106	13,699	126,106	13,699	126,106	13,699	126,106	13,699
Heterogeneity	92,742	11,264	92,742	11,264	92,742	11,264	92,742	11,264	92,742	11,264	92,742	11,264
Mean estimated	82,715	9,653	82,715	9,653	82,715	9,653	82,715	9,653	82,715	9,653	82,715	9,653
Population Size – Narrow Habitat Definition												
Raw	22,916	---	22,916	---	22,916	---	22,916	---	22,916	---	22,916	---
Distance sampling	17,859	2,435	17,859	2,435	17,859	2,435	17,859	2,435	17,859	2,435	17,859	2,435
N-mixture	76,871	8,351	76,871	8,351	76,871	8,351	76,871	8,351	76,871	8,351	76,871	8,351
Heterogeneity	56,533	6,867	23,824	5,769	43,448	5,613	106,735	9,023	79,708	7,753	49,665	8,660
Mean estimated	50,421	5,884	19,980	4,971	40,668	4,960	129,645	10,406	150,172	13,621	47,688	7,280

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

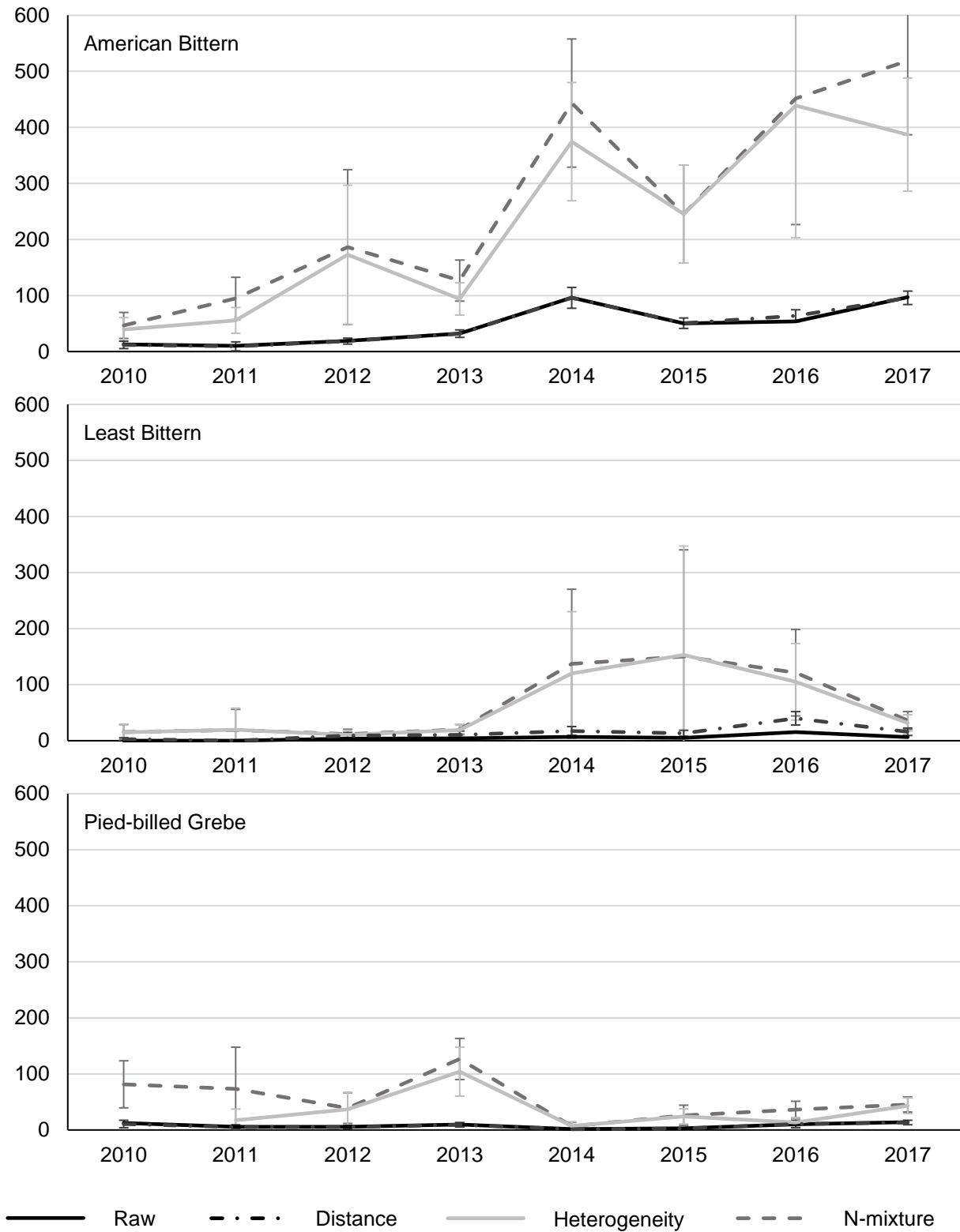


Figure D1. Estimated population size (thousands) using the narrow habitat definition for BCR 12 by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

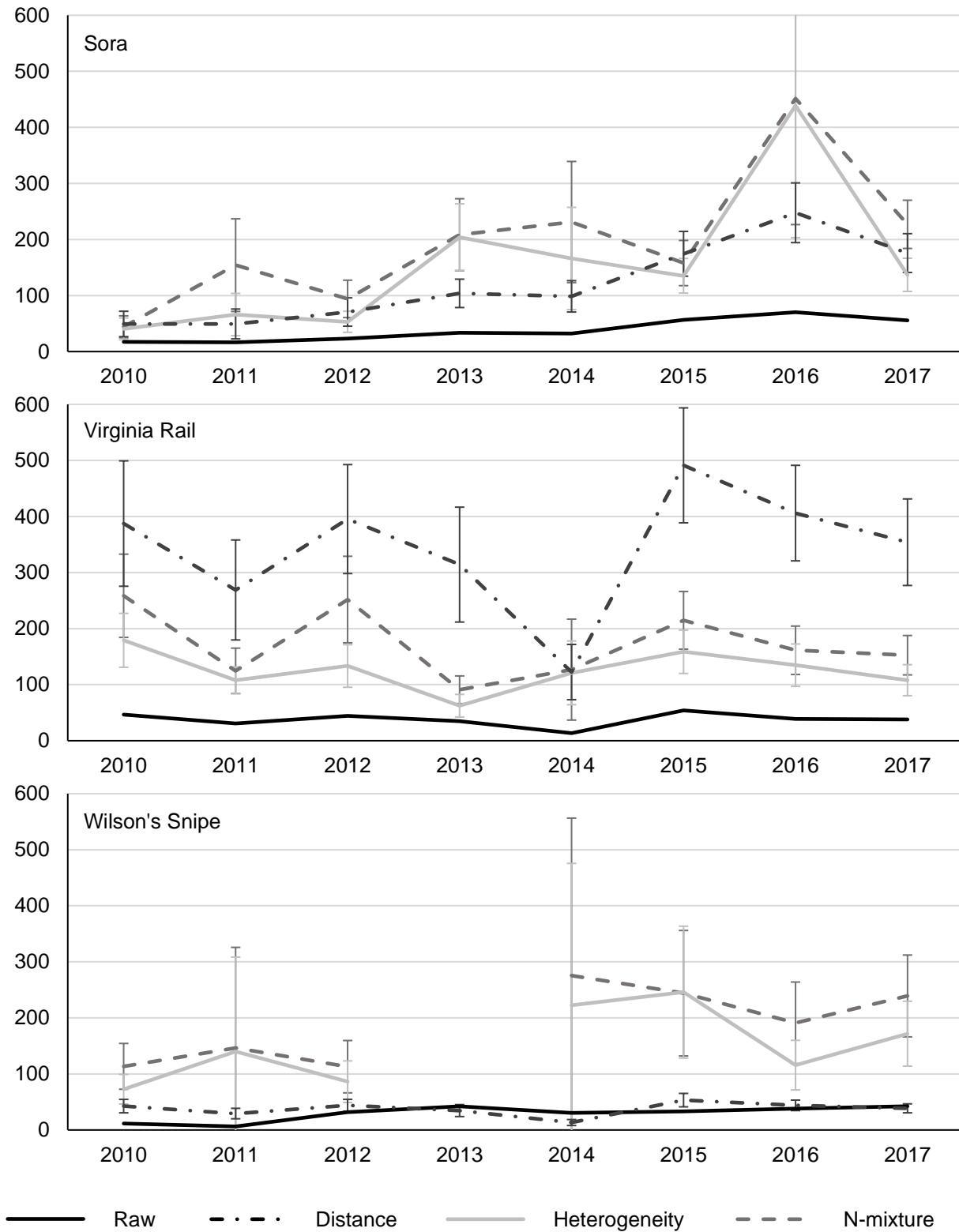


Figure D1, continued. Estimated population size (thousands) using the narrow habitat definition for BCR 12 by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

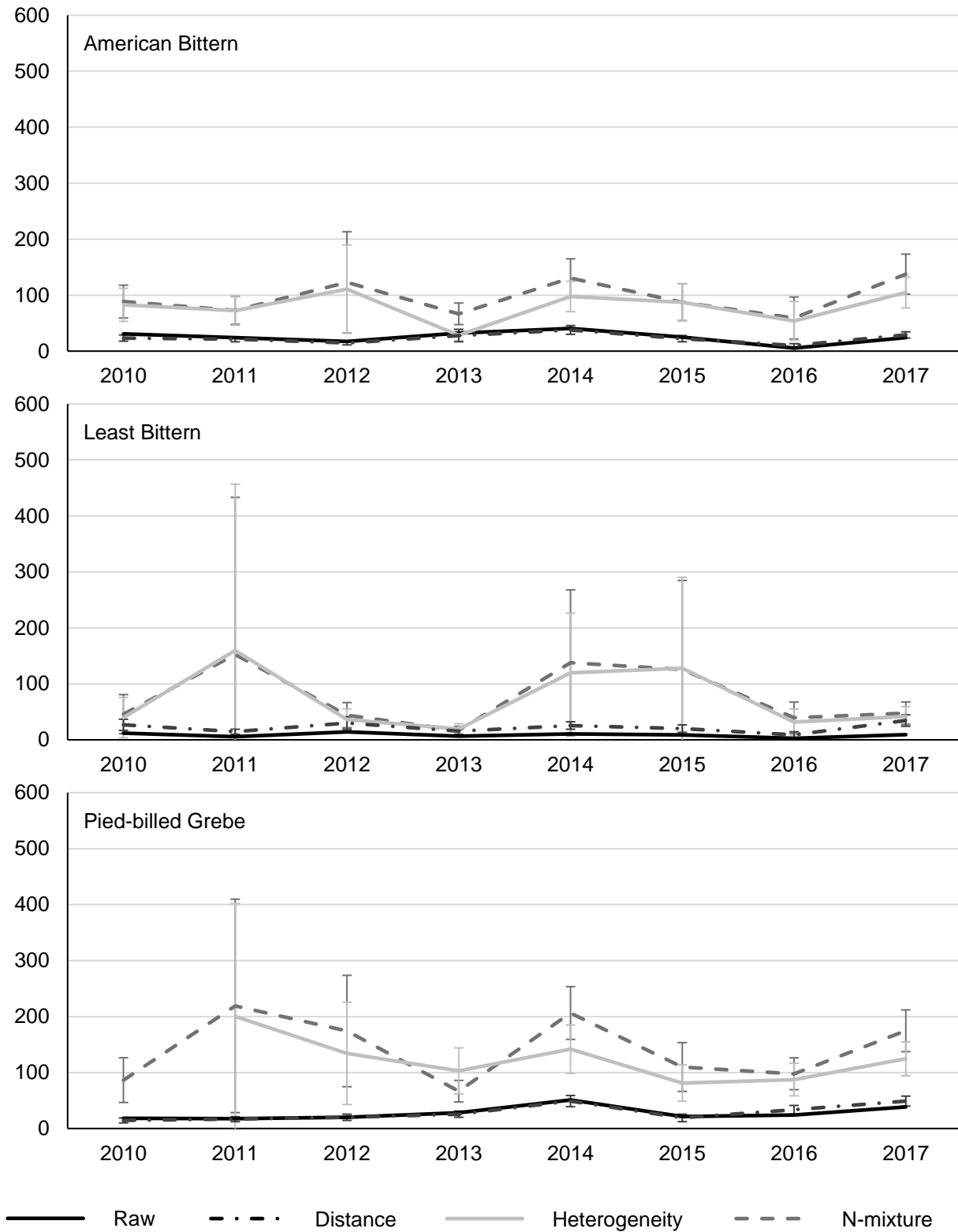


Figure D2. Estimated population size (thousands) using the narrow habitat definition for BCR 23 by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

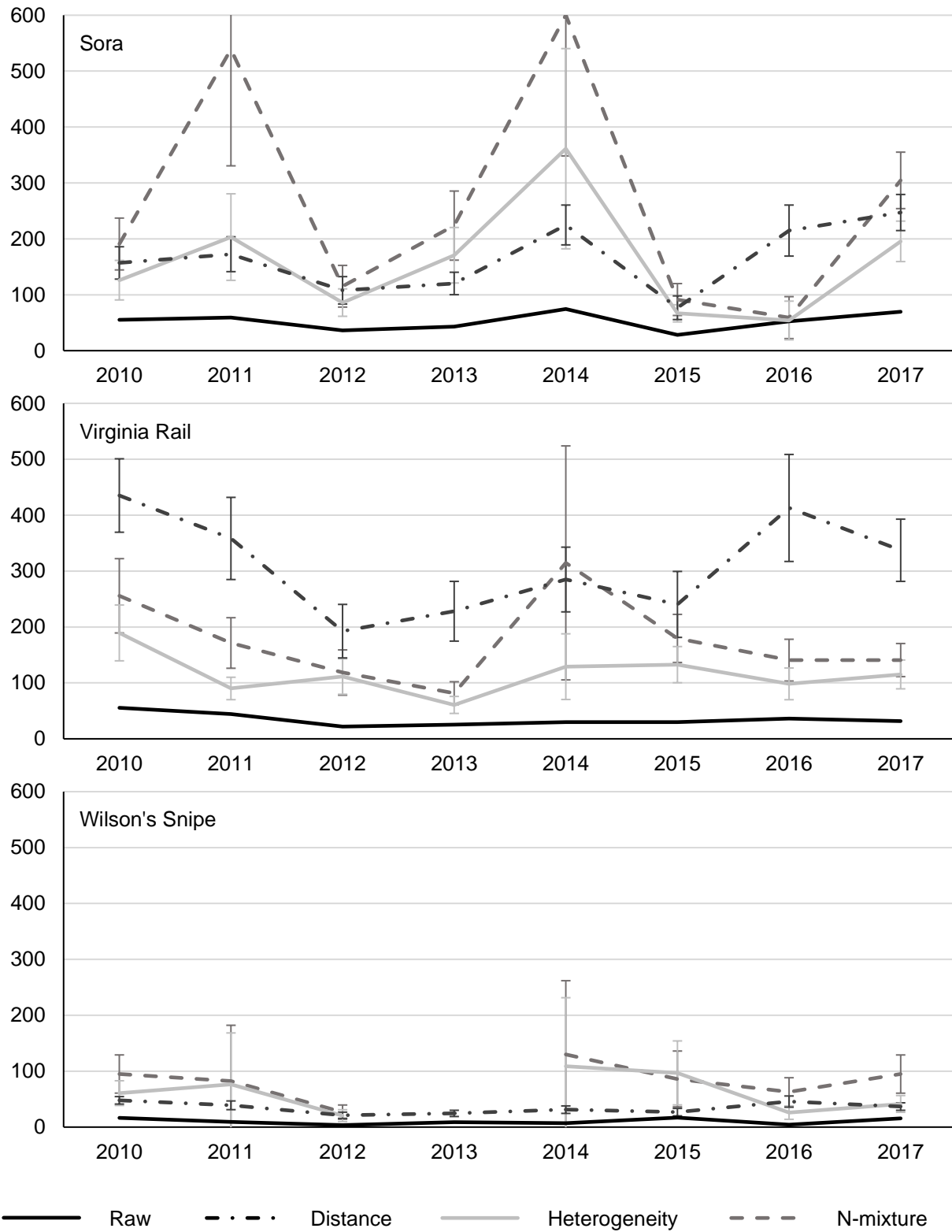


Figure D2, continued. Estimated population size (thousands) using the narrow habitat definition for BCR 23 by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

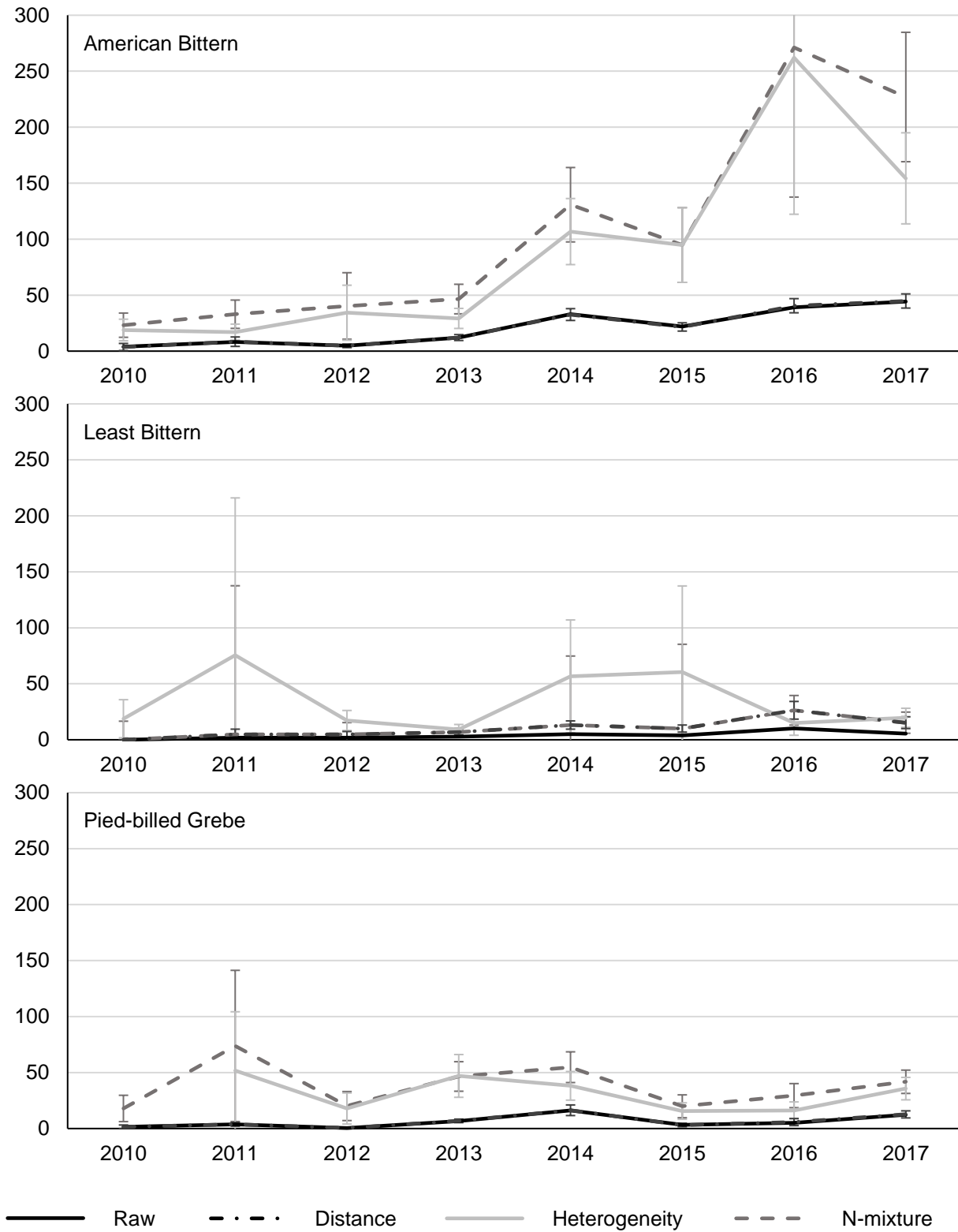


Figure D3. Estimated population size (thousands) using the narrow habitat definition for Michigan by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

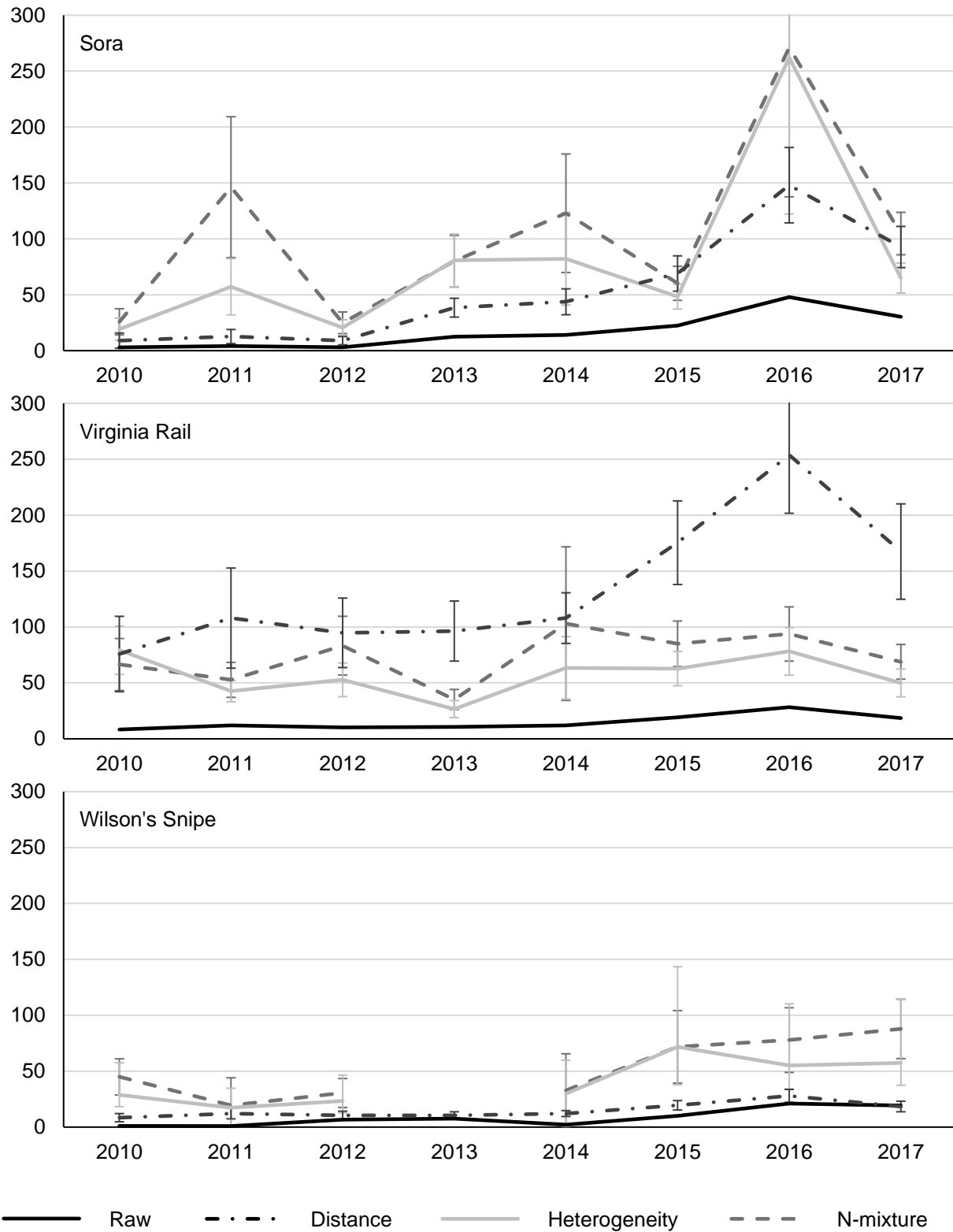


Figure D3, continued. Estimated population size (thousands) using the narrow habitat definition for Michigan by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

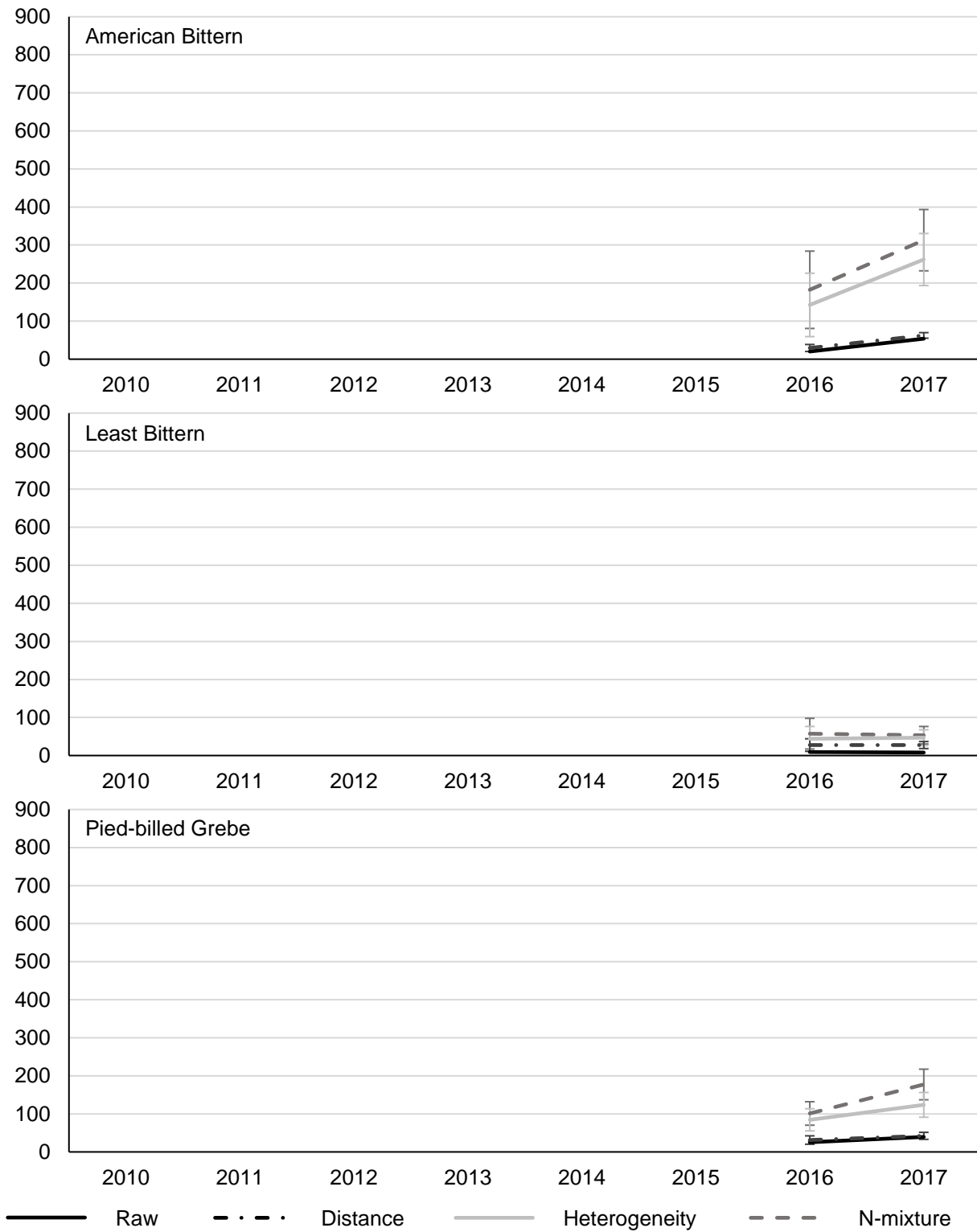


Figure D4. Estimated population size (thousands) using the narrow habitat definition for Minnesota by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

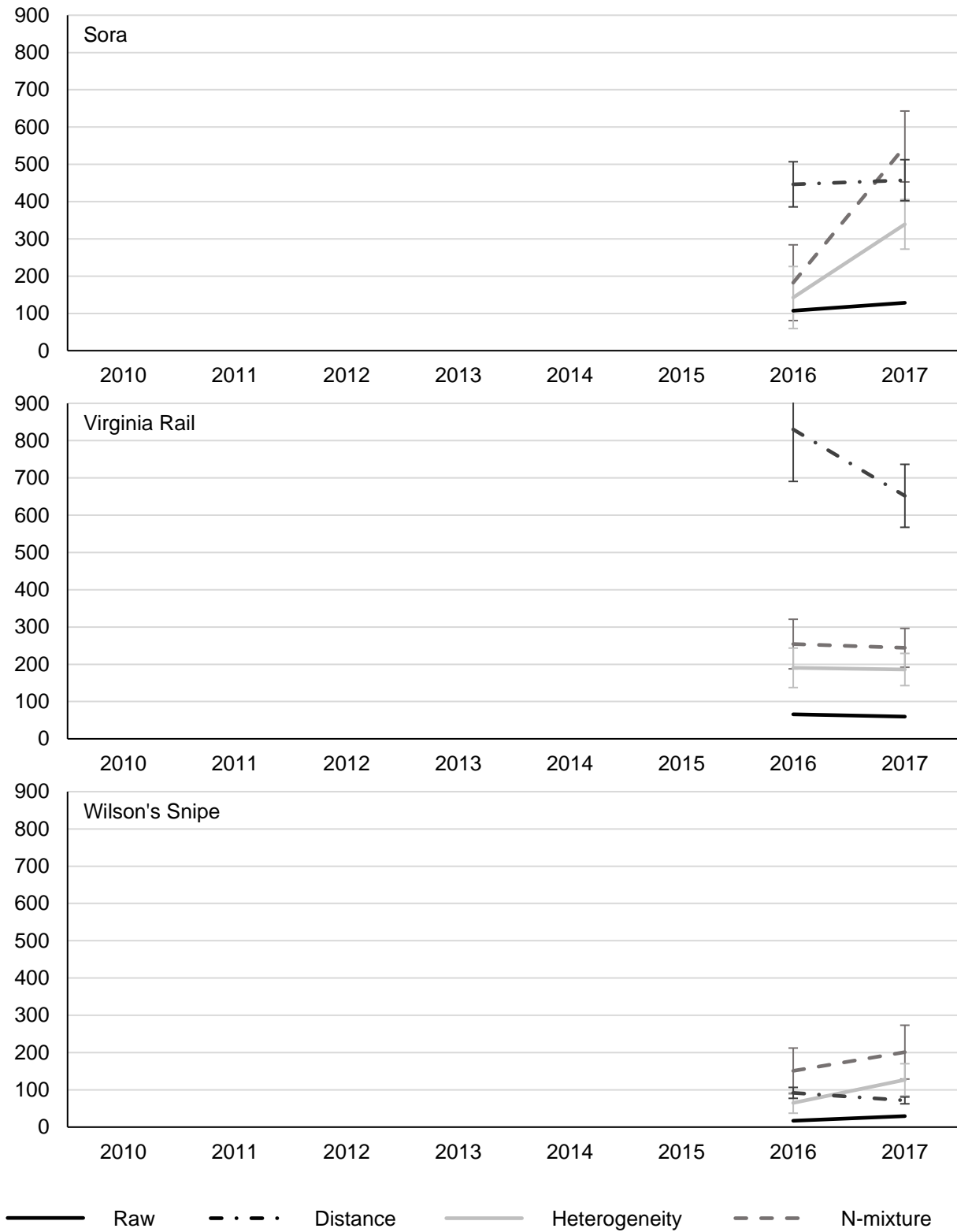


Figure D4, continued. Estimated population size (thousands) using the narrow habitat definition for Minnesota by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

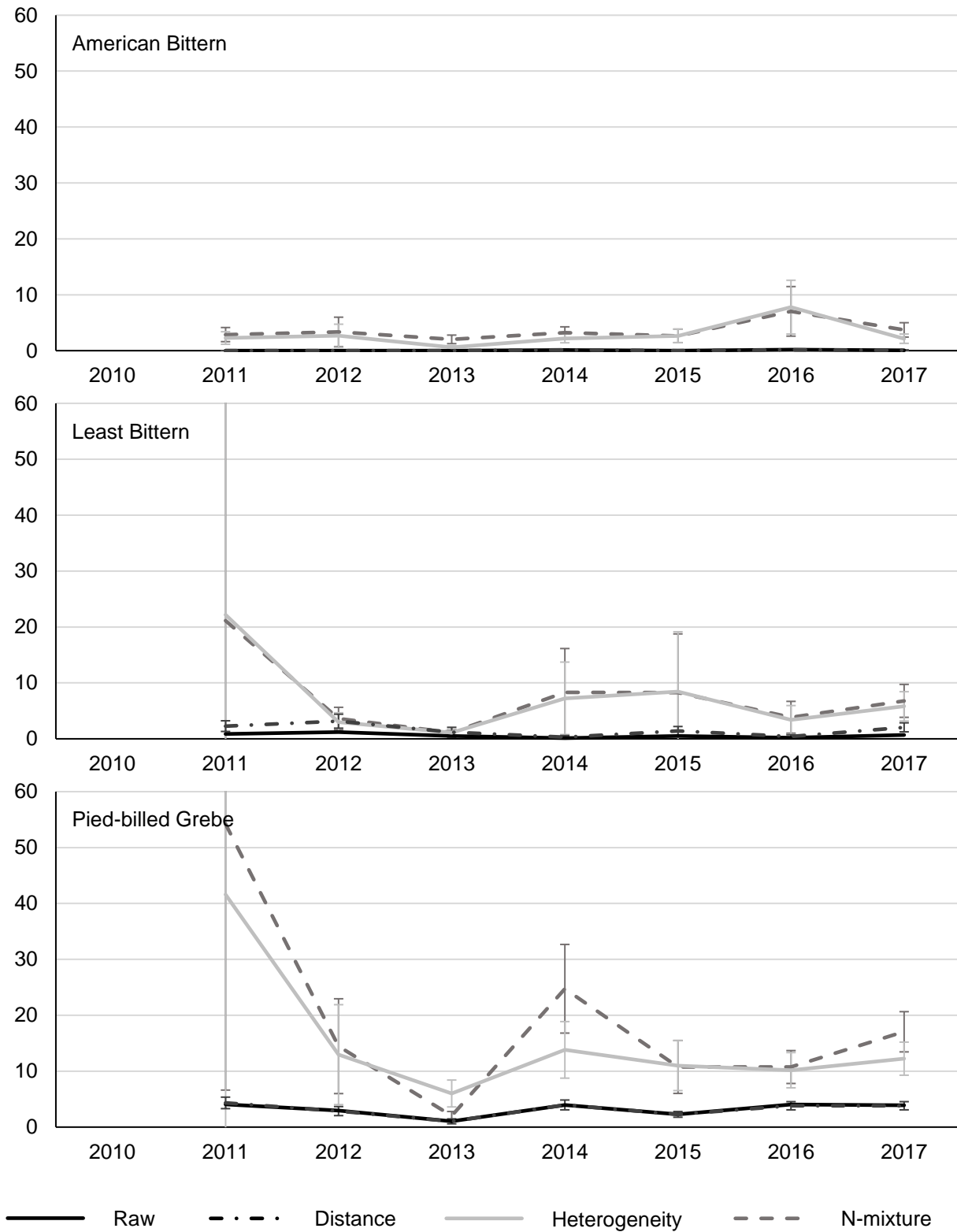


Figure D5. Estimated population size (thousands) using the narrow habitat definition for Ohio by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

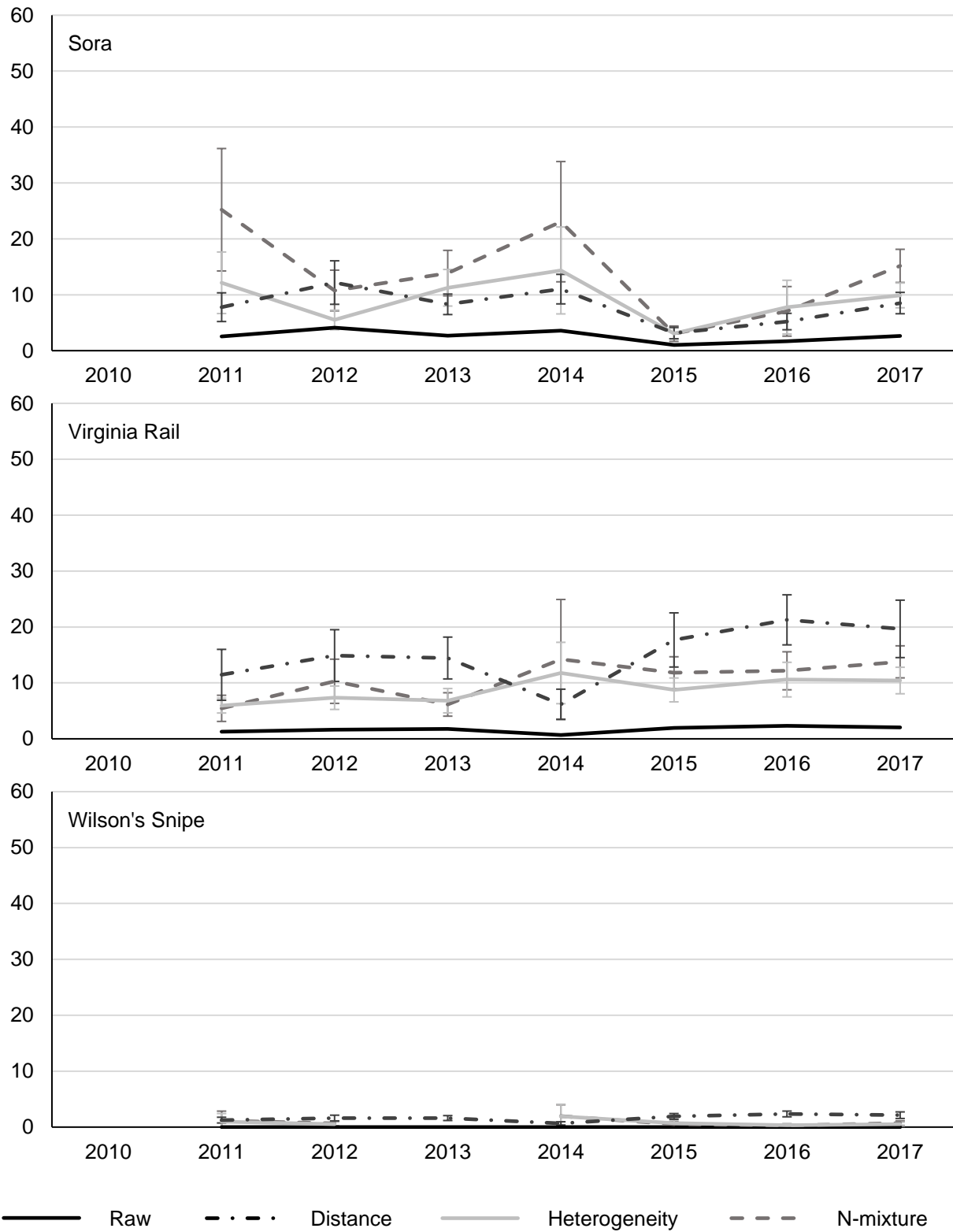


Figure D5, continued. Estimated population size (thousands) using the narrow habitat definition for Ohio by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

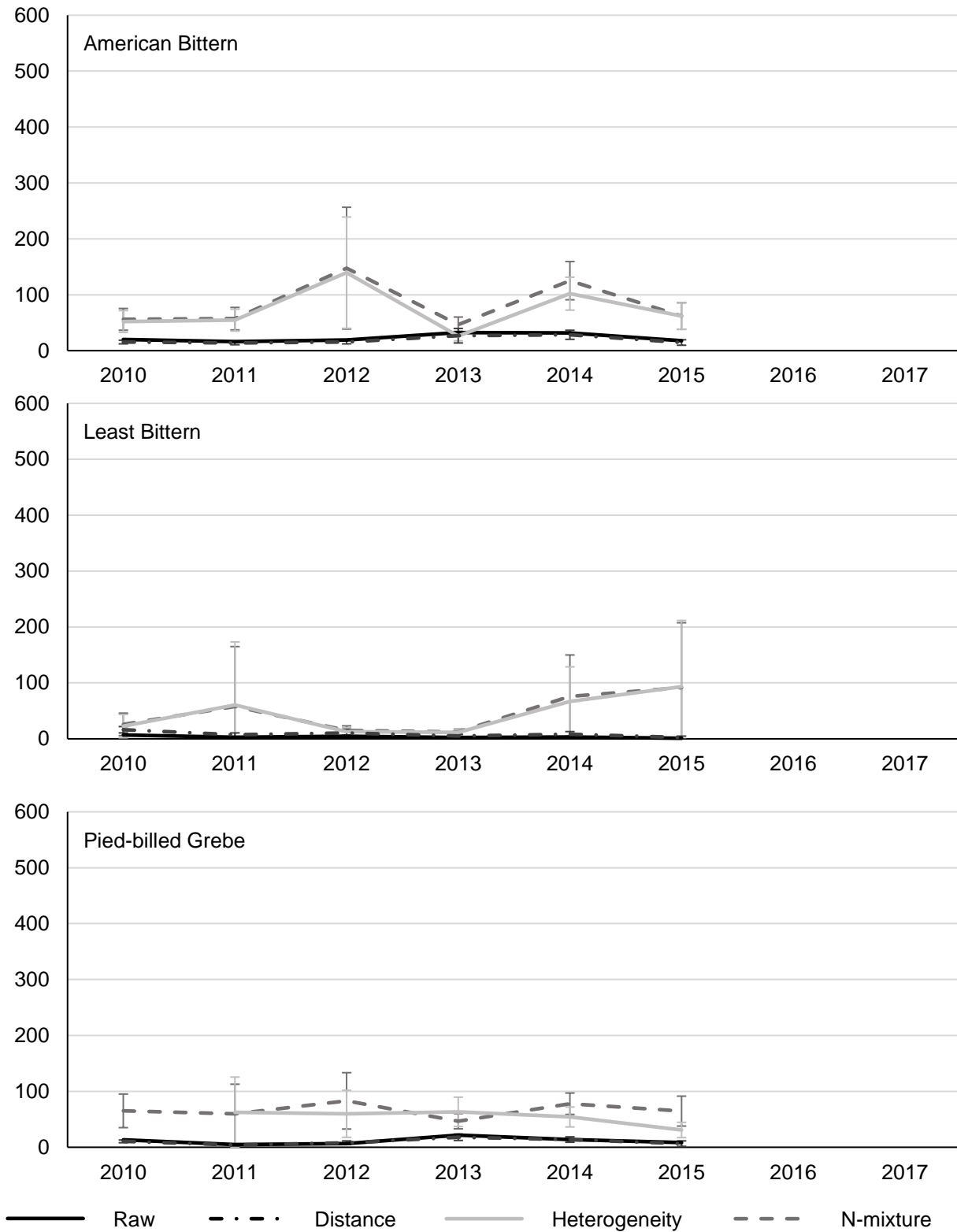


Figure D6. Estimated population size (thousands) using the narrow habitat definition for Wisconsin by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix D. Annual marsh bird population estimates for 2010-2017 at BCR and state scales.

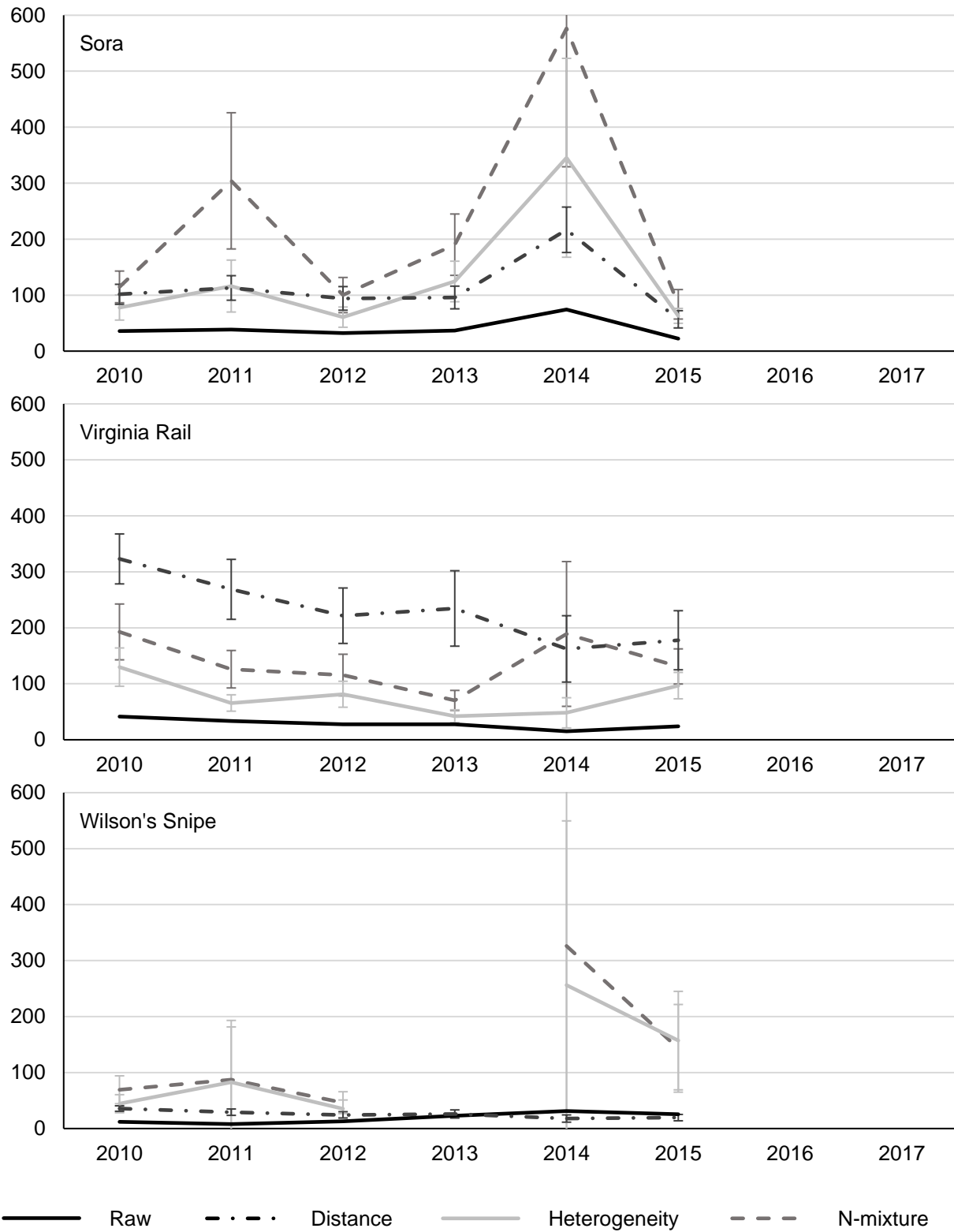


Figure D6, continued. Estimated population size (thousands) using the narrow habitat definition for Wisconsin by species, model type, and year (2010-2017). Error bars represent the mean plus and minus the standard error.

Appendix E. Parameter estimates from multi-season occupancy models developed for seven marsh bird species.

Table E1. Parameter estimates from multi-season occupancy models developed for seven marsh bird species in the upper Midwest during 2010-2017 ($n = 621$).

Parameter	American Bittern		American Coot		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Occupancy (2010)	0.098	0.049	0.106	0.050	0.088	0.060	0.144	0.038	0.184	0.079	0.341	0.078	0.167	0.080
Occupancy (2011)	0.142	0.025	0.090	0.034	0.099	0.032	0.162	0.027	0.240	0.035	0.351	0.054	0.143	0.048
Occupancy (2012)	0.181	0.024	0.096	0.029	0.105	0.027	0.174	0.023	0.270	0.027	0.346	0.046	0.174	0.042
Occupancy (2013)	0.211	0.027	0.102	0.029	0.108	0.029	0.182	0.023	0.286	0.028	0.337	0.045	0.196	0.041
Occupancy (2014)	0.235	0.030	0.108	0.031	0.109	0.030	0.187	0.025	0.296	0.030	0.328	0.047	0.219	0.044
Occupancy (2015)	0.253	0.034	0.114	0.034	0.110	0.032	0.190	0.027	0.301	0.031	0.319	0.049	0.239	0.047
Occupancy (2016)	0.267	0.037	0.120	0.037	0.110	0.033	0.192	0.029	0.361	0.048	0.310	0.052	0.258	0.050
Occupancy (2017)	0.278	0.040	0.125	0.041	0.111	0.033	0.194	0.031	0.307	0.033	0.303	0.055	0.275	0.054
Rate of change (2010-2011)	1.953	0.892	2.892	3.706	1.141	0.458	1.288	0.285	1.702	0.758	1.191	0.259	1.200	0.360
Rate of change (2011-2012)	1.274	0.133	1.904	0.191	1.066	0.187	1.118	0.093	1.170	0.100	1.021	0.078	1.273	0.234
Rate of change (2012-2013)	1.152	0.058	1.473	0.052	1.034	0.092	1.062	0.052	1.073	0.036	0.987	0.047	1.150	0.088
Rate of change (2013-2014)	1.098	0.035	1.320	0.024	1.019	0.051	1.036	0.035	1.037	0.017	0.975	0.036	1.125	0.051
Rate of change (2014-2015)	1.068	0.025	1.242	0.013	1.010	0.031	1.022	0.024	1.021	0.010	0.971	0.030	1.101	0.033
Rate of change (2015-2016)	1.049	0.020	1.194	0.008	1.006	0.019	1.013	0.017	1.012	0.006	0.970	0.027	1.085	0.023
Rate of change (2016-2017)	1.037	0.016	1.162	0.006	1.004	0.013	1.009	0.012	1.007	0.004	0.970	0.025	1.073	0.017
Colonization (2010-2011)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Colonization (2011-2012)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022

Appendix E. Parameter estimates from multi-season occupancy models developed for seven marsh bird species.

Table E1, continued.

Parameter	American Bittern		American Coot		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Colonization (2012-2013)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Colonization (2013-2014)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Colonization (2014-2015)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Colonization (2015-2016)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Colonization (2016-2017)	0.099	0.016	0.032	0.013	0.058	0.018	0.056	0.014	0.168	0.023	0.083	0.025	0.073	0.022
Extinction (2010-2011)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2011-2012)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2012-2013)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2013-2014)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2014-2015)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2015-2016)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Extinction (2016-2017)	0.271	0.085	0.104	0.055	0.421	0.209	0.280	0.093	0.376	0.061	0.208	0.065	0.196	0.044
Detection (2010-1)	0.435	0.036	0.019	0.023	0.736	0.013	0.288	0.034	0.531	0.032	0.084	0.014	0.228	0.026
Detection (2010-2)	0.359	0.032	0.018	0.022	0.735	0.012	0.214	0.028	0.267	0.022	0.083	0.014	0.144	0.020
Detection (2010-3)	0.161	0.021	0.015	0.018	0.780	0.010	0.188	0.026	0.156	0.017	0.069	0.011	0.125	0.019
Detection (2011-1)	0.410	0.036	0.064	0.025	0.659	0.016	0.299	0.034	0.531	0.032	0.094	0.015	0.228	0.026
Detection (2011-2)	0.347	0.033	0.066	0.026	0.637	0.017	0.214	0.028	0.267	0.022	0.100	0.016	0.144	0.020

Appendix E. Parameter estimates from multi-season occupancy models developed for seven marsh bird species.

Table E1, continued.														
Parameter	American Bittern		American Coot		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Detection (2011-3)	0.160	0.022	0.060	0.023	0.673	0.015	0.188	0.026	0.156	0.017	0.090	0.015	0.125	0.019
Detection (2012-1)	0.423	0.035	0.033	0.014	0.617	0.018	0.293	0.034	0.531	0.032	0.097	0.016	0.228	0.026
Detection (2012-2)	0.364	0.032	0.034	0.015	0.604	0.019	0.216	0.028	0.267	0.022	0.100	0.016	0.144	0.020
Detection (2012-3)	0.162	0.021	0.031	0.013	0.621	0.017	0.199	0.026	0.156	0.017	0.094	0.015	0.125	0.019
Detection (2013-1)	0.433	0.035	0.137	0.030	0.591	0.019	0.309	0.034	0.531	0.032	0.116	0.018	0.228	0.026
Detection (2013-2)	0.358	0.033	0.142	0.030	0.560	0.020	0.224	0.027	0.267	0.022	0.125	0.019	0.144	0.020
Detection (2013-3)	0.162	0.021	0.138	0.029	0.574	0.019	0.202	0.026	0.156	0.017	0.121	0.019	0.125	0.019
Detection (2014-1)	0.410	0.036	0.076	0.018	0.659	0.016	0.303	0.034	0.531	0.032	0.057	0.012	0.228	0.026
Detection (2014-2)	0.355	0.033	0.086	0.021	0.615	0.018	0.215	0.028	0.267	0.022	0.065	0.013	0.144	0.020
Detection (2014-3)	0.159	0.021	0.071	0.017	0.683	0.015	0.189	0.026	0.156	0.017	0.053	0.011	0.125	0.019
Detection (2015-1)	0.420	0.035	0.050	0.016	0.612	0.018	0.309	0.034	0.531	0.032	0.121	0.017	0.228	0.026
Detection (2015-2)	0.359	0.032	0.046	0.015	0.630	0.017	0.225	0.027	0.267	0.022	0.115	0.016	0.144	0.020
Detection (2015-3)	0.162	0.021	0.046	0.015	0.633	0.017	0.197	0.026	0.156	0.017	0.114	0.016	0.125	0.019
Detection (2016-1)	0.426	0.034	0.087	0.029	0.643	0.017	0.293	0.034	0.531	0.032	0.118	0.014	0.228	0.026
Detection (2016-2)	0.349	0.032	0.087	0.029	0.638	0.017	0.219	0.028	0.267	0.022	0.118	0.014	0.144	0.020
Detection (2016-3)	0.155	0.021	0.089	0.030	0.629	0.018	0.182	0.026	0.156	0.017	0.124	0.015	0.125	0.019
Detection (2017-1)	0.438	0.035	0.057	0.018	0.578	0.020	0.295	0.034	0.531	0.032	0.117	0.016	0.228	0.026

Appendix E. Parameter estimates from multi-season occupancy models developed for seven marsh bird species.

Table E1, continued.														
Parameter	American Bittern		American Coot		Least Bittern		Pied-billed Grebe		Sora		Virginia Rail		Wilson's Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Detection (2017-2)	0.360	0.032	0.061	0.019	0.559	0.021	0.214	0.028	0.267	0.022	0.122	0.017	0.144	0.020
Detection (2017-3)	0.592	0.010	0.056	0.018	0.586	0.020	0.188	0.026	0.156	0.017	0.115	0.016	0.125	0.019