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Research Article

Estimates of Tidal-Marsh Bird Densities Using Bayesian Networks

WHITNEY A. WIEST,[1,2] *Department of Entomology and Wildlife Ecology, University of Delaware, 250 Townsend Hall, Newark, DE 19716, USA*
MAUREEN D. CORRELL, *School of Biology and Ecology, Climate Change Institute, University of Maine, 204 Clapp Greenhouse, Orono, ME 04469, USA*
BRUCE G. MARCOT, *U.S.D.A. Forest Service, Pacific Northwest Research Station, 620 SW Main Street, Portland, OR 97205, USA*
BRIAN J. OLSEN, *School of Biology and Ecology, Climate Change Institute, University of Maine, 200 Clapp Greenhouse, Orono, ME 04469, USA*
CHRIS S. ELPHICK, *Department of Ecology and Evolutionary Biology and Center for Conservation and Biodiversity, University of Connecticut, 75 North Eagleville Road, U-43, Storrs, CT 06269, USA*
THOMAS P. HODGMAN, *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA*
GLENN R. GUNTENSPERGEN, *U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA*
W. GREGORY SHRIVER, *Department of Entomology and Wildlife Ecology, University of Delaware, 250 Townsend Hall, Newark, DE 19716, USA*

ABSTRACT Conserving tidal-marsh bird communities requires strategies to address continuing pressures from human development to the effects of increasing rates of sea-level rise. Knowing tidal-marsh bird distributions and population sizes are important for developing these strategies. In the Northeast United States, where estimates of sea-level rise are 3 times higher than the global average, 5 bird species are tidal-marsh specialists: clapper rail (*Rallus crepitans*), willet (*Tringa semipalmata*), Nelson's sparrow (*Ammospiza nelsoni*), saltmarsh sparrow (*A. caudacuta*), and seaside sparrow (*A. maritima*). We used a regional marsh bird survey to develop Bayesian network models to identify factors that influence patch-scale species density and to estimate regional population sizes. We modeled species density as a function of habitat covariates at the patch, local, landscape, and regional spatial scales. Densities were most sensitive to patch location and dimension, patch geomorphic setting, indices of human development, and changes in mean sea level. We estimated 110,000 clapper rails (95% CI = 61,000–159,000), 111,000 willets (95% CI = 70,000–152,000), 7,000 Nelson's sparrows (95% CI = 4,000–10,000), 60,000 saltmarsh sparrows (95% CI = 40,000–80,000), and 234,000 seaside sparrows (95% CI = 112,000–356,000) from the United States–Canada border to, and including, the mouth of the Chesapeake Bay, Virginia, USA. Our abundance estimates can be used to identify priority conservation areas at multiple geographic scales and our models help identify key habitat and landscape components for tidal-marsh restoration and management to benefit tidal-marsh birds and can be modified for other species. © 2018 The Wildlife Society.

KEY WORDS Bayesian network, density, model-based, monitoring, Northeast USA, predictive model, tidal-marsh birds.

Estimation of wildlife population status and trends is an important initial step in guiding conservation priorities and management actions (McCarthy and Possingham 2007, Jones et al. 2013, Moqanaki et al. 2018). Without knowledge of wildlife population sizes and basic demographic parameters, it is difficult to set meaningful population objectives, an activity mandated by many government agencies charged with managing wildlife. The absence of accurate population estimates leads to biased or spurious perceptions of conservation priorities, limits the ability to determine the effects of management actions, and can lead to inefficient uses of limited funding for conservation.

The North Atlantic coast of the United States (Maine to Virginia; i.e., Northeast) tidal salt marshes support several specialist bird taxa adapted to tidal marshes that are high conservation priorities (Greenberg 2006, Rosenberg et al. 2016). In the Northeast, the extent of tidal marshes has been reduced by ≥38% percent since the 1800s (Gedan and Silliman 2009) and sea-level rise contributes to the declining trend in salt marsh area (Dahl 2011). Five specialist birds are of concern in the Northeast region: clapper rail (*Rallus crepitans*), willet (*Tringa semipalmata*), Nelson's sparrow (*Ammospiza nelsoni*), saltmarsh sparrow (*A. caudacuta*), and seaside sparrow

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[1] *E-mail: whitney_wiest@fws.gov*
[2] *Present Address: U.S. Fish and Wildlife Service, South Carolina Ecological Services, 176 Croghan Spur Road, Suite 200, Charleston, SC 29407, USA.*

(*A. maritima*). These 5 species are recognized as conservation priorities by various designations, such as Species of Greatest Conservation Need in state Wildlife Action Plans (e.g., Maryland Department of Natural Resources 2015, New Hampshire Fish and Game Department 2015), high concern on the 2016 Watch List (North American Bird Conservation Initiative 2016), and globally endangered on the International Union for Conservation of Nature Red List (saltmarsh sparrow; BirdLife International 2017). Tidal-marsh birds are not adequately sampled by the North American Breeding Bird Survey because these roadside counts do not sufficiently sample wetlands (Gibbs and Melvin 1993, Lawler and O'Connor 2004). As a result, tidal-marsh bird population status and trends have only recently been estimated (Wiest et al. 2016, Correll et al. 2017) and conservation strategies setting specific population objectives are now being developed. Three species have documented negative population trends: the global population of saltmarsh sparrow is declining by 9.0% annually, and within the Northeast, clapper rails are declining by 4.6% annually and Nelson's sparrows (Acadian subspecies *A. n. subvirgatus*) are declining by 4.2% annually (Correll et al. 2017). Focusing conservation efforts on coastal marshes in the Atlantic Flyway and setting population objectives is a priority for the Atlantic Coast Joint Venture, making population estimates especially relevant for focusing regional and state-level actions that could reduce the declines and stabilize the population trajectories for these specialist birds (http://acjv.org/flagship-species-initiative, accessed 23 Jun 2018).

Initial population estimates (Wiest et al. 2016) provided information at the regional scale (Northeast) but did not predict abundance in unsurveyed marshes and were not spatially explicit. Therefore, we used a Bayesian modeling framework to predict species density and estimate population sizes across all Northeast tidal marshes and to determine factors that influenced density. Bayesian networks (BNs) can be structured to depict causal, correlational, or logical relationships among variables, linked by conditional probabilities (Koski and Noble 2011). Variables are typically depicted with discrete nominal, cardinal, ordinal, or continuous states, each with associated probability values calculated according to Bayes' Theorem. BNs can be more robust to collinearity and variations in sample size than traditional frequentist, multivariate approaches (Sebastiani and Perls 2008, Pawson et al. 2017). Additionally, BN machine-learning algorithms derive network model structures and probability parameters to better deal with missing data and produce models representing working hypotheses that can be further calibrated, evaluated, and updated with new data (Marcot et al. 2006, Marcot 2012). Our primary goal was to use BNs to develop spatially explicit estimates of density and abundance that could be used to set population objectives at the state and regional levels and focus conservation and management actions. The specific objectives of our descriptive study were to develop BN models to estimate density in all marsh patches, evaluate the sensitivity of species density to different patch characteristics, and develop regional population estimates covering surveyed and unsurveyed patches.

STUDY AREA

We conducted this research during the spring and summer, 2011–2012, in predominantly polyhaline tidal marsh from Lubec, Maine, USA to the mouth of the Chesapeake Bay, Virginia, USA. Our study area consisted of 280,722 ha of coastal marsh classified as Acadian coastal salt marsh and Northern Atlantic Coastal Plain tidal salt marsh (Comer et al. 2003, Ferree and Anderson 2013). Acadian coastal salt marsh ranges from Newfoundland, Canada to northern Massachusetts, USA and is characterized by small patches interspersed in the rocky Gulf of Maine coastline. Northern Atlantic Coastal Plain tidal salt marsh ranges primarily from Cape Cod, Massachusetts to the Chesapeake Bay, and irregularly from Cape Cod to the southern coast of Maine. Coastal Plain marshes are more extensive in area than northern Acadian marshes and are associated with the saltwater bays of barrier beaches and the outer mouths of tidal rivers. Both marsh types were largely dominated by smooth cordgrass (*Spartina alterniflora*) and saltmeadow cordgrass (*S. patens*), and included patches of other graminoids and forbs (Comer et al. 2003, Ferree and Anderson 2013). Common fauna included fiddler crabs (*Uca* spp.), marsh crabs (*Sesarma* spp.), grass shrimp (*Palaemonetes* spp.), marsh periwinkle (*Littoraria irrorata*), eastern mudsnail (*Tritia obsoleta*), ribbed mussel (*Geukensia demissa*), eastern oyster (*Crassostraea virginica*), diamondback terrapin (*Malaclemys terrapin*); and various fish, bird, and mammal species (Bertness 1999).

The average day of the first bloom in our study area was 30 May in Lubec, Maine and 3 April in Fisherman Island National Wildlife Refuge, Virginia (spring index based on a 30-year dataset, 1981–2010; http://data.usanpn.org/npn-viz-tool/, accessed 20 Aug 2018). Precipitation at the northern boundary of our study area averaged 117 cm/year and temperatures averaged −10°C to −1°C in January and 12°C to 24°C in July. At the southern boundary, precipitation averaged 107 cm/year and temperatures averaged −1°C to 8°C in January and 21°C to 30°C in July. Our study area was situated in a highly developed coastal region of the United States that has a history of human impacts to large drainage systems (e.g., Connecticut, Hudson, Delaware, and Susquehanna rivers) and supports high-traffic ports (e.g., Boston, New York City, and Philadelphia). Historical land use of tidal marshes in the region included filling for development, grazing and haying, ditching for mosquito control, and the creation of impoundments (Greenberg 2006).

METHODS

Design-Based Abundance Estimates and Patch Attributes

We developed BN models and regional population estimates based on previous work summarized here. We surveyed the 5 tidal-marsh specialist birds as part of a Northeast tidal-marsh bird survey (Wiest et al. 2016) where we counted individuals based on visual and auditory detections (Conway 2011). We distributed 1,780 unique survey points across 8 subregions defined by geomorphology (Fig. 1) and surveyed these points 2–3 times (Wiest et al. 2016). We surveyed 1,642 points during the 2011 breeding season (167 points visited only twice) and 1,714 points during 2012 (91 points visited only twice; Wiest et al. 2016). We delineated the tidal marsh in our study area into habitat patches and used the unmarked package in Program R (Fiske and Chandler 2011; www.r-project.org, accessed 8 Aug 2014) to estimate density, and in turn abundance, in each sampled marsh patch (Wiest et al. 2016; design-based abundance models). We used unmarked's multinomPois function to estimate abundance using a general multinomial-Poisson mixture model (Royle 2004). We accounted for detection probability in our models using the time-of-detection method (Farnsworth et al. 2002), and we made the assumption that populations were closed during our sampling period (i.e., the breeding season; Wiest et al. 2016).

For each patch, we compiled 22 covariates describing location and dimension, land cover, geomorphic setting, sea-level trend, and human disturbance (Tables 1 and 2; Supplemental Material A, available online in Supporting Information). We chose patch features that influence bird

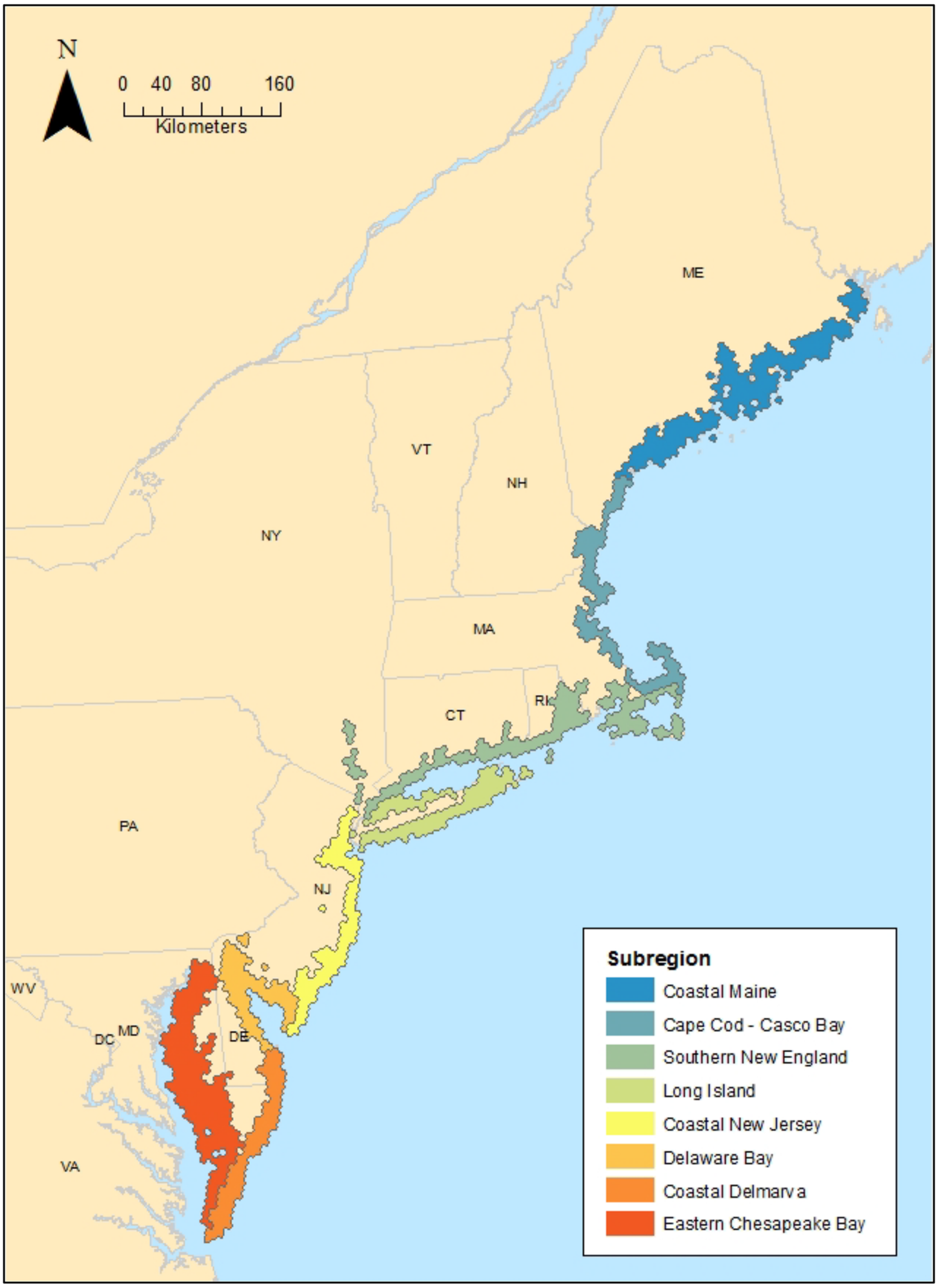

Figure 1. The sampling universe for surveys of tidal-marsh birds in the Northeast United States, delineated into subregions, 2011–2012. Subregions are composed of 40-km^2 hexagons containing estuarine intertidal emergent wetlands. We developed subregion boundaries based on suggestions by Conway and Droege (2006).

Table 1. Tidal-marsh patch covariates, grouped by category, developed to predict the density of tidal-marsh specialist birds in the Northeast United States in 2011–2012 using Bayesian network models.

Category and covariate	Definition	Unit of measure	Source citation	Geographic level[a]
Location and dimension				
State	U.S. state the patch is located in based on the patch's centroid.	Category	Wiest et al. 2016	Regional
Subregion	Marshbird monitoring area the patch is located in; geographic areas for marshbird monitoring were defined into discrete units based on major geomorphological features.	Category	Conway and Droege 2006, Wiest et al. 2016	Regional
Longitude	Angular distance of the patch's centroid from the meridian at Greenwich, England.	Decimal degrees	Wiest et al. 2016	Regional
Latitude	Angular distance of the patch's centroid from the earth's equator.	Decimal degrees	Wiest et al. 2016	Regional
Area	Size of the patch.	ha	Wiest et al. 2016	Patch
Perimeter	Length of the patch's perimeter.	m	None	Patch
Land use and land cover				
High marsh	Extent of the patch that is dominated by saltmeadow cordgrass (*Spartina patens*), smooth cordgrass (short form, *Spartina alterniflora*), saltmeadow rush (*Juncus gerardii*), or saltgrass (*Distichlis spicata*).	Proportion	M. D. Correll, University of Maine, unpublished data	Patch
Natural 150	Extent of natural lands within a 150-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Local
Agriculture 150	Extent of agricultural lands within a 150-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Local
Developed 150	Extent of developed lands within a 150-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Local
Open water 150	Extent of open water within a 150-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Local
Marsh 150	Extent of marsh within a 150-m buffer around the patch (index of habitat connectivity).	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Local
Natural 1,000	Extent of natural lands within a 1,000-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Landscape
Agriculture 1,000	Extent of agricultural lands within a 1,000-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Landscape
Developed 1,000	Extent of developed lands within a 1,000-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Landscape
Open water 1,000	Extent of open water within a 1,000-m buffer around the patch.	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Landscape
Marsh 1,000	Extent of marsh within a 1,000-m buffer around the patch (index of habitat connectivity).	Proportion	Comer et al. 2003, Ferree and Anderson 2013	Landscape
Geomorphic setting				
Primary geomorphic setting	Dominant physical setting of the patch; settings are characterized by differences in hydrodynamics, sediment sources, and plant community characteristics.	Category	Cahoon et al. 2009, classification scheme modified from Reed et al. 2008 (based on Woodroffe 2002 and Cahoon 2006)	Regional
Secondary geomorphic setting	Second most dominant physical setting of the patch, if applicable; settings are characterized by differences in hydrodynamics, sediment sources, and plant community characteristics.	Category	Cahoon et al. 2009, classification scheme modified from Reed et al. 2008 (based on Woodroffe 2002 and Cahoon 2006)	Regional
Tertiary geomorphic setting	Third most dominant physical setting of the patch, if applicable; settings are characterized by differences in hydrodynamics, sediment sources, and plant community characteristics.	Category	Cahoon et al. 2009, classification scheme modified from Reed et al. 2008 (based on Woodroffe 2002 and Cahoon 2006)	Regional
Sea-level trend				
Sea-level trend	Change in mean sea level (rise or fall) documented by the tide gauge located in the area associated with the patch.	mm/year	National Ocean Service, Center for Operational Oceanographic Products and Services 2013, 2014	Landscape
Human disturbance				
Road density	Density of roads within the patch and a 500-m buffer around the patch (index of human disturbance).	m/ha	U.S. Census Bureau 2013	Local

[a] Covariates were grouped at 4 geographic scales: patch, local, landscape, and regional, to develop our Bayesian network models. Patch-level covariates described the individual marsh patches, local-level covariates described conditions up to 500 m away, landscape-level covariates described conditions up to 1,000 m away, and regional-level covariates described location and geomorphic conditions relative to the entire Northeast United States.

Table 2. Tidal-marsh patch covariates, grouped by geographic context, and covariate bin categories developed to predict the density of tidal-marsh specialist birds in the Northeast United States in 2011–2012 using Bayesian network models. The X marks indicate covariates included in a particular model. Land use and land cover covariates (i.e., natural, agriculture, developed, open water, and marsh) are proportions.

Geographic level[a] and covariate	Model[b]							Bin categories[c]
	Patch	500-m subset	500 m	1,000-m subset	1,000 m	Regional subset	Global	
Patch								
Area	X	X	X	X	X	X	X	0–5, 5–50, 50–100, ≥100 ha
Perimeter	X	X	X	X	X	X	X	137–700, 700–2,500, 2,500–15,000, ≥15,000 m
High marsh	X	X	X	X	X	X	X	0.0–0.01, 0.01–0.15, 0.15–0.50, 0.50–1.0
Local								
Natural 150		X	X	X	X	X	X	0.0–0.25, 0.25–0.50, 0.50–1.0
Agriculture 150		X	X	X	X	X	X	0.0–0.01, 0.01–0.15, 0.15–0.53
Developed 150			X		X		X	0.0–0.10, 0.10–0.25, 0.25–0.99
Open water 150			X		X		X	0.0–0.10, 0.10–0.25, 0.25–0.92
Marsh 150		X	X	X	X	X	X	0.0–0.05, 0.05–0.10, 0.10–0.47
Road density		X	X	X	X	X	X	0.0–20.0, 20.0–50.0, 50.0–230.0 m/ha
Landscape								
Natural 1,000					X		X	0.0–0.25, 0.25–0.50, 0.50–1.0
Agriculture 1,000				X	X	X	X	0.0–0.01, 0.01–0.15, 0.15–0.61
Developed 1,000				X	X	X	X	0.0–0.10, 0.10–0.25, 0.25–0.91
Open water 1,000					X		X	0.0–0.10, 0.10–0.25, 0.25–0.93
Marsh 1,000				X	X	X	X	0.0–0.05, 0.05–0.10, 0.10–0.59
Sea-level trend				X	X	X	X	1.70–2.0, 2.0–2.63, 2.63–5.48 mm/year
Regional								
State							X	DE, CT, MA, MD, ME, NH, NJ, NY, RI, VA
Subregion							X	Coastal Maine, Cape Cod to Casco Bay, Southern New England, Long Island, Coastal New Jersey, Delaware Bay, Coastal Delmarva, Eastern Chesapeake Bay
Longitude						X	X	−77.380 to −73.965, −73.965 to −71.855, −71.855 to −66.800
Latitude						X	X	36.400 to 40.490, 40.490 to 41.400, 41.400 to 45.100
Primary geomorphic setting						X	X	Back-barrier lagoon marsh, Estuarine brackish marsh, Estuarine embayment, Open coast, Tidal fresh marsh
Secondary geomorphic setting						X	X	Back-barrier lagoon marsh, Estuarine brackish marsh, Estuarine embayment, None
Tertiary geomorphic setting						X	X	Tidal fresh marsh, None

[a] Covariates were grouped into 4 geographic scales: patch, local, landscape, and regional, to develop our Bayesian network models. Patch-level covariates described the individual marsh patches, local-level covariates described conditions up to 500 m away, landscape-level covariates described conditions up to 1,000 m away, and regional-level covariates described location and geomorphic conditions relative to the entire Northeast United States.

[b] Model names were derived from the approximate scale of covariates contained within each model.

[c] Bin categories do not overlap. Continuous covariates are discretized into bins that approximately capture an even distribution of the covariate's values.

species distribution and abundance and that can be obtained from remote sensing data for the entire Northeast (Comer et al. 2003; Conway and Droege 2006; Cahoon et al. 2009; Ferree and Anderson 2013; National Oceanic and Atmospheric Administration, National Ocean Service, Center for Operational Oceanographic Products and Services 2013, 2014; U.S. Census Bureau 2013; Wiest et al. 2016; M. D. Correll, University of Maine, unpublished data). We used ArcGIS 9.3 for all geospatial calculations unless stated otherwise (Environmental Systems Research Institute, Redlands, CA, USA; see Supplemental Material A for the methods used to define patch features and for a summary of associated results).

Bayesian Network Models to Estimate Species Density

We developed BN models that related design-based density estimates with patch characteristics to project these estimates to unsurveyed patches and ultimately generate regional population estimates. For each species, we developed a series of 7 models with different sets of covariates, from which we selected the best-performing model. We used the BN modeling shell Netica 5.16 (Norsys Software Corp., Vancouver, British Columbia, Canada) and followed Marcot et al. (2006) for model development and analysis.

Model development.—We constructed and selected from BN models representing various combinations of covariates. We grouped the covariates at 4 geographic scales: patch, local, landscape, and regional (Table 2). Three patch-level covariates described the individual marsh patches, 6 local-level covariates described conditions within 500 m, 6 landscape-level covariates described conditions within 1,000 m, and 7 regional-level covariates described location and geomorphic conditions relative to the entire Northeast (Table 2). We constructed models of increasing complexity by incorporating covariates from each geographic scale in succession starting with the patch scale (the smallest scale). We developed 1 patch-scale model (patch), 2 local-scale models (500 m subset and 500 m), 2 landscape-scale models (1,000 m subset and 1,000 m), and 2 regional-scale models (regional subset and global); the subset models differed from their counterparts in that not all covariates were included in the subset models (Table 2). Because avian response to marsh isolation and development can vary by species, within species, and by geographic region, we chose to develop a series of models that incorporated covariates that increasingly described different levels and aspects of the surrounding landscape (Shriver et al. 2004). To facilitate model development for the subset models at the local, landscape, and regional scales, we assessed the covariate relationships within each of these geographic groups using Pearson correlation coefficients. When the relationship was $|r| \geq 0.4$ for 2 covariates in the same geographic group, we used our previous knowledge of tidal-marsh birds (Shriver et al. 2004) to decide which covariate to prioritize and keep in the subset models.

Covariates were represented as nodes in the BN structure. We discretized each continuous predictor variable (i.e., the patch features) into 3 or 4 state ranges (bins; Table 2), and the target variable, bird species density, into 3 states (0–$<10^{-5}$ birds/ha, 10^{-5}–<1 birds/ha, and ≥ 1 bird/ha). We used a tree-augmented naïve (TAN) algorithm to build the BNs from the existing case file data set (Friedman et al. 1997) describing the sample of surveyed marsh patches with density estimates from design-based models (Wiest et al. 2016). Following TAN, we built the simplest network linking covariates to outcomes for the most parsimonious explanatory structure and linked correlated variables so as not to assume their independence. We fitted conditional probability values for each covariate using the expectation maximization (EM) algorithm (McLachlan and Krishnan 1996, Dempster et al. 1977; see Supplemental Material B for examples of developed models).

Model evaluation.—To ensure independence between data used for model building and model testing, we used 5-fold cross-validation to evaluate the predictive accuracy of our models (Boyce et al. 2002). We evaluated each model series by comparing model complexity and classification performance metrics. We defined and quantified model complexity based on the number of covariates and probabilities (unconditional priors and conditional probabilities) in each model. We used these 2 metrics because complexity metrics are not necessarily correlated and multiple metrics can provide a more holistic assessment of model structure and parsimony than a single metric alone (Marcot 2012). We assessed model classification performance by comparing the most likely species densities produced by our models to our data using spherical payoff and confusion error rates (Marcot 2012). Spherical payoff is calculated from state probabilities and is a continuous measure of the predictive accuracy of the model ranging from 0–1, with 1 indicating perfect model performance and lower values denoting greater uncertainty (error rates) of model predictions (Hand 1997, Marcot 2012). We considered models with spherical payoff >0.70 as having good model performance. Confusion error rates are the percentage of cases for which a model classifies the state incorrectly, where classification is defined as the dominant probability outcome; in this way, confusion error is a measure of discrete outcomes, whereas spherical payoff accounts for continuous probability values. We calculated confusion error rates from confusion matrices for false positives (Type I error), false negatives (Type II error), and their sum, to assess model calibration performance and model validity (Kohavi and Provost 1998, Marcot 2012).

Because of the novel application of our BN approach, rules for model selection are not clearly defined, so we developed selection rules that emphasized high prediction performance as measured by spherical payoff and mean confusion error for the greatest density state (≥ 1 bird/ha; ≥ 1 error rate). Because we tested the models against the same data used to build them, the confusion error rates for calibration performance provided a test of fit, and the mean confusion error rates for cross-validation evaluated true prediction accuracy (Marcot 2012). We prioritized low error for the greatest density state to minimize the number of false positives. We made this decision on the premise that conservation actions will be more costly and species recovery may take longer when a species is predicted to occur in greater density than it actually does. Species recovery may also take more time when false negatives are not minimized; however, conservation would not occur at the expense of risking extinction as could be the case if false positives are not addressed.

Our steps for model selection were as follows: first, we selected the models that had the highest spherical payoff and lowest ≥ 1 error rate. If the model with the highest spherical payoff did not have the lowest ≥ 1 error rate, but the rate was within 5% of the lowest ≥ 1 error rate in the species' model series, we selected that model. If the model's ≥ 1 error rate was $>5\%$ higher than the lowest ≥ 1 error rate in the species' model series, we disregarded the model with the highest spherical payoff and evaluated the model with the second highest spherical payoff. If the next model had the lowest ≥ 1 error rate, or the rate was within 5% of the lowest ≥ 1 error rate in the species' model series, we selected that model. We used the final selected models to project species density in unsurveyed marsh patches.

Species abundance projections.—We used the expected species density values estimated by the BNs to calculate species abundance in each unsurveyed patch that occurred within a species' regular breeding range (Wiest et al. 2016). We calculated the expected density values by multiplying the probability of each density state by the mid-point value of that density state, and summing over all states. When the final state is open-ended, its mid-point is calculated based on the spread of values of the previous state, which is the calculation built into the BN modeling program (Netica). For example, in the 3-state bird density models, the density ranges in each state are 0 to $<10^{-5}$, 10^{-5} to <1, and ≥ 1. Because the third state is open-ended, we used the mid-point based on the previous state whose mid-point was $0.5 \times (1 - 10^{-5})$, or approximately 0.5, so the mid-point of the third state is $1 + 0.5$, or 1.5. We acknowledge that this could bias low the expected value calculations, but this bias was held constant across all bird species and patches. We then multiplied the expected density of each species by patch area to project species abundance within each unsurveyed marsh patch during the breeding season; see Supplemental Material C for patch geospatial data, including patch covariate values and final species density and abundance estimates (geospatial data can also be downloaded from www.tidalmarshbirds.org).

Sensitivity analyses.—We conducted sensitivity analyses of the best-performing models to determine the relative influence of each patch covariate on species density (Marcot et al. 2006, Marcot 2012). We set input covariates to their default prior probability distributions based on frequencies of values derived from the case files, and set realistic upper bounds on the real value of species density using the maximum densities estimated in our baseline assessment (rounded up to the nearest whole number; Wiest et al. 2016). We calculated sensitivity by calculating variance reduction for continuous variables and entropy reduction (mutual information) for categorical variables (Marcot 2012). We evaluated the rank-order of the covariates to compare covariate influence: the greater the reduction value, the more likely it was that a particular covariate node changed the posterior probability values of a given species density node.

Regional population estimates.—We estimated region-wide population sizes for each species by combining the abundance values calculated from the best-performing BNs for unsurveyed patches with those calculated from the R package unmarked during our baseline survey for surveyed patches (Wiest et al. 2016). We used the function total.est in the spsurvey package in Program R (Kincaid and Olsen 2012) to estimate population totals with 95% confidence intervals. We used the Horvitz–Thompson estimator for a single-stage sample to calculate population totals and used a normal distribution multiplier to calculate the confidence intervals (Horvitz and Thompson 1952, Diaz-Ramos et al. 1996, Kincaid et al. 2015). We used the species abundance value for each patch as the response value (i.e., the abundance projections for the unsurveyed patches and the design-based abundance estimates for the surveyed patches; Wiest et al. 2016), and weighted patches equally (weight = 1). We report population sizes and confidence bounds to the nearest 1,000 or 100 depending on the magnitude of the estimates.

RESULTS

The BN models varied in their complexity; the number of covariates ranged from 3 to 22 and the number of probabilities ranged from 111 to 1,815 (Table 3). Model classification performance also varied, but all models had spherical payoff values >0.70 (Table 3). Total confusion error rates ranged from 11% to 40% for calibration performance and from 23% to 43% for model validation (Table 3). In general, model prediction accuracy improved with increasing model complexity.

On average, models most accurately predicted when a patch supported no birds (clapper rail, willet, and Nelson's and seaside sparrow models) and least accurately predicted when a patch supported ≥ 1 bird/ha (clapper rail, willet, and Nelson's and saltmarsh sparrow models; Table 3). The exception to this being that saltmarsh sparrow models performed best when predicting 10^{-5}–<1 birds/ha, whereas seaside sparrow models were least effective at predicting this density category (Table 3). Overall there was more variation (greater spread) in the error rates for the ≥ 1 and 10^{-5}–<1 density states than for the 0–$<10^{-5}$ density state.

The global model for clapper rail and willet met our first rule for model selection; these models had the highest spherical payoff values (0.90 and 0.87, respectively) and lowest model validation confusion error rates for ≥ 1 bird/ha (45% and 77%, respectively) in their model series (Table 3). We choose the global model for saltmarsh sparrow using our second rule, which had the highest spherical payoff, 0.90, and a ≥ 1 error rate (94%) within 5% of the lowest reported rate (92%; Table 3). No model for Nelson's sparrow or seaside sparrow met our first 2 selection steps, so we evaluated each model series using our third step. The models with the second highest spherical payoff values both had ≥ 1 error rates within 5% of the lowest rate and so were selected for the 2 species. Nelson's sparrow's global model had 79% error (76% was the lowest ≥ 1 error rate in the series) and seaside sparrow's regional subset model had 47% error (this was the lowest ≥ 1 error rate in the series) for the ≥ 1 density category (Table 3). Although high confusion error for the ≥ 1 density category was a large source of the total error, total error rates from the 5-fold cross-validation were all $<30\%$ for the final selected models (Table 3). The 5 selected models were overall more accurate but also more complex than the other models considered (see Supplemental Material B for figures of the final selected models).

Our species density predictions varied in sensitivity to the different input variables (Table 4). Clapper rail density was most sensitive to the state and subregion categories, followed by the proportion of human development within 1,000 m, total patch area, and latitude. Uncertainty associated with willet density was most sensitive to the subregion and then state categories, followed by the dominant geomorphic setting of a patch, density of roads, and the proportion of marsh within 1,000 m. Nelson's sparrow density was most

Table 3. Model complexity, calibration performance, and validation values of Bayesian network models used to predict tidal-marsh bird density (birds/ha) in the Northeast United States, 2011–2012, as a function of patch covariates. The best-scoring value(s) for each species are indicated by an asterisk.

		Model complexity		Model calibration performance, confusion error rates, %				Model validation (5-fold), mean confusion error rates, mean %			
Species and model[a,b]	**Spherical payoff**	**Number of covariates**	**Number of probabilities**	**0–<10^{-5} birds/ha**	**10^{-5}–<1 birds/ha**	**≥1 bird/ha**	**Total**	**0–<10^{-5} birds/ha**	**10^{-5}–<1 birds/ha**	**≥1 bird/ha**	**Total**
Clapper rail											
Patch	0.82	3	111	9*	41	85	24	15	38	100	29
500-m sub	0.86	7	237	10	21	55	17	15	32*	72	26
500 m	0.87	9	291	10	25	50	17	16	38	92	28
1,000-m sub	0.88	11	336	9*	24	25	15	15	39	65	26
1,000 m	0.90*	15	444	9*	23	15*	16	11*	41	63	25*
Regional sub	0.89	16	498	9*	25	15*	14	14	37	65	25*
Global[b]	0.90*	22	1,248	9*	20*	15*	13*	17	45	45*	28
Willet											
Patch	0.81	3	111	5*	55	98	23	8*	56*	100	25*
500-m sub	0.83	7	237	6	48	73	20	8*	57	90	25*
500 m	0.83	9	291	9	53	62	22	9	58	91	25*
1,000-m sub	0.84	11	345	9	49	64	22	12	63	86	28
1,000 m	0.84	15	453	12	41	44*	20	12	61	83	28
Regional sub	0.83	16	507	12	43	51	21	15	57	80	29
Global[b]	0.87*	22	1,734	7	33*	58	16*	12	56*	77*	27
Nelson's sparrow											
Patch	0.82	3	111	6	56	83	24	10	65*	93	30
500-m sub	0.87	7	255	7	41	48	18	14	70	85	33
500 m	0.87	9	300	7	29	44	16	13	67	76*	31
1,000-m sub	0.89	11	354	5*	27	35	12	12	75	84	32
1,000 m	0.91*	15	471	5*	18*	35	11*	9	66	88	29
Regional sub	0.90	16	414	5*	21	35	11*	10	74	84	30
Global[b]	0.90	22	531	5*	24	30*	11*	8*	70	79	28*
Saltmarsh sparrow											
Patch	0.71	3	111	57	18	100	40	60	21	100	43
500-m sub	0.75	7	246	37	23	82	33	49	30	95	42
500 m	0.76	9	300	37	24	78	33	45	34	100	42
1,000-m sub	0.82	11	345	20	21	59	23	29	28	92*	32
1,000 m	0.83	15	453	19	22	55	22	29	27	92*	31
Regional sub	0.83	16	492	20	21	48	22	25	28	97	30
Global[b]	0.90*	22	1,815	13*	12*	22*	13*	20*	19*	94	23*
Seaside sparrow											
Patch	0.77	3	111	8	85	58	30	10*	86	80	34
500-m sub	0.81	7	246	14	60	29	26	15	70	51	31
500 m	0.81	9	291	12	62	29	25	14	69	53	31
1,000-m sub	0.83	11	345	11	55	19	22	15	69	53	31
1,000 m	0.84	15	444	11	50	13*	21	16	61	59	32
Regional sub[b]	0.86	16	528	10	35	19	17	16	56	47*	28
Global	0.90*	22	1,365	6*	26*	13*	12*	10*	46*	63	23*

[a] Number of cases in each species data set used to parameterize the models: clapper rail = 255, willet = 582, Nelson's sparrow = 193, saltmarsh sparrow = 509, and seaside sparrow = 390. The subset models (sub) differed from their counterparts in that not all covariates were included in the subset models.

[b] The final selected model for each species.

influenced by the 2 covariates measuring patch dimension, area and perimeter, followed by the dominant geomorphic setting of a patch, changes in mean sea level, and the proportion of open water within 1,000 m. Saltmarsh sparrow density was most sensitive to the subregion and state categories, followed by changes in mean sea level, the dominant geomorphic setting of a patch, and the proportion of marsh within 150 m. Seaside sparrow density was most influenced by latitude and longitude, followed by total patch area, the proportion of human development within 1,000 m, and the density of roads.

We determined that, of the specialist species, Nelson's sparrow had the smallest estimated population size in the region, whereas seaside sparrow had the largest (Table 5). Population size estimates and 95% confidence intervals were similar for clapper rail and willet (Table 5). Our regional population estimate for saltmarsh sparrow also represents the global population estimate for this species (Table 5).

DISCUSSION

Our model-based approach provides spatially explicit density estimates for tidal-marsh birds of high conservation concern across marsh patches in the Northeast. The flexibility of the BN model estimates is such that estimates can be scaled to any geographic level of conservation interest, where patch-specific extrapolation was not possible with the design-based estimates (Wiest et al. 2016). Our patch-level estimates allow for the identification and targeting of areas for conservation, and because our BNs integrated geospatial

Table 4. Sensitivity of findings for the best-performing Bayesian network models predicting tidal-marsh bird density in the Northeast United States, 2011–2012, as a function of patch covariates. The 5 highest-scoring covariates for each species are indicated with an asterisk; NA implies not applicable because a given variable was not included in the final model.

	Variance reduction				
Geographic level[a] and covariate	**Clapper rail**	**Willet**	**Nelson's sparrow**	**Saltmarsh sparrow**	**Seaside sparrow**
Patch					
Area	0.0715*	0.0327	0.1158*	0.0103	0.0934*
Perimeter	0.0433	0.0251	0.0976*	0.0125	0.0579
High marsh	0.0432	0.0154	0.0037	0.0091	0.0265
Local					
Natural 150	0.0025	0.0036	0.0021	0.0033	0.0015
Agriculture 150	0.0020	0.0059	0.0014	0.0011	0.0318
Developed 150	0.0570	0.0198	0.0102	0.0053	NA
Open water 150	0.0395	0.0247	0.0062	0.0036	NA
Marsh 150	0.0199	0.0318	0.0132	0.0223*	0.0245
Road density	0.0405	0.0417*	0.0151	0.0087	0.0664*
Landscape					
Natural 1,000	0.0010	0.0154	0.0191	0.0028	NA
Agriculture 1,000	0.0018	0.0181	0.0001	0.0031	0.0267
Developed 1,000	0.0764*	0.0162	0.0138	0.0057	0.0800*
Open water 1,000	0.0193	0.0329	0.0341*	0.0169	NA
Marsh 1,000	0.0244	0.0373*	0.0144	0.0031	0.0042
Sea-level trend	0.0529	0.0240	0.0410*	0.0400*	0.0327
Regional					
State	0.1487*	0.0576*	0.0131	0.0751*	NA
Subregion	0.1051*	0.0745*	0.0173	0.0769*	NA
Longitude	0.0528	0.0279	0.0000	0.0193	0.0988*
Latitude	0.0603*	0.0319	0.0000	0.0194	0.1086*
Primary geomorphic setting	0.0072	0.0451*	0.0606*	0.0353*	0.0061
Secondary geomorphic setting	0.0029	0.0028	0.0000	0.0019	0.0662
Tertiary geomorphic setting	0.0004	0.0002	0.0000	0.0132	0.0180

[a] Covariates were grouped into 4 geographic scales: patch, local, landscape, and regional, to develop our Bayesian network models. Patch-level covariates described the individual marsh patches, local-level covariates described conditions up to 500 m away, landscape-level covariates described conditions up to 1,000 m away, and regional-level covariates described location and geomorphic conditions relative to the entire Northeast United States.

habitat data and other covariates that influence variation in bird density, the estimates provide insight to the factors that influence density for these species and better account for underlying uncertainty than our design-based estimates from our initial baseline assessment (Wiest et al. 2016). We developed our BN models using publicly accessible geospatial databases as economical and presumably reliable sources of data, and so patch covariates and density estimates can be readily updated and recalculated in the models when geospatial data are improved and updated by external sources.

The density of each bird in each patch was calculated from the expected value across all density range states, weighted by the associated probability of each state, and then summed across all states. This inherently accounts for the probability distributions across the density states and is not simply a mid-point. However, this approach also provides an estimate of the standard deviation of density values across all states, assuming a Gaussian distribution, which is essentially a measure of uncertainty of the expected value. We did not carry these patch-specific measures of standard deviation into the measures of bird density across patches at the regional scale, and we recognize that they add uncertainty to the overall signal. That is, the region-wide bird density estimates should be interpreted not as precise point values but as embedded in a range of potential values.

Table 5. Population estimates of tidal-marsh birds during the breeding season, 2011–2012, in the Northeast United States (Maine to Virginia).

Species	**Abundance (95% CI)**
Clapper rail	110,000 (61,000–159,000)
Willet	111,000 (70,000–152,000)
Nelson's sparrow	7,000 (4,000–10,000)
Saltmarsh sparrow	60,000 (40,000–80,000)
Seaside sparrow	234,000 (112,000–356,000)

We developed the BNs at the regional scale instead of smaller subregion or state scales, and thus had a large training data set with which to build the model probability structures, which contributed to more robust cross-validation analyses. Although there is no specific guideline for number of cases from which to induce BN model structures and parameters, BN models become more robust when the cases cover as many combinations of covariate conditions as possible, as was the condition of our data sets, so that any missing combinations pertain mainly to *non sequitur* or irrelevant conditions. Our training data set contained fewer records for the ≥ 1 bird/ha state compared to the other categories, and including additional cases where individuals are present at greater densities should improve model accuracy. Model performance patterns suggested that the magnitude of effect from selecting the wrong model would be greater if precedence was not given to minimizing ≥ 1 error.

Results of the sensitivity analyses indicated that, for these specialist tidal-marsh species, the bird species density response variables were most sensitive to local-scale variables of patch area and perimeter, the proportion of human development within 1,000 m, road density, and changes in mean sea level, and regional-scale variables including state, subregion, latitude and longitude, and primary geomorphic setting because they denoted large-scale geographic variation in abundance. Landscape context influences the factors that affect tidal-marsh birds in the Northeast (Shriver et al. 2004) and our results support the notion that regional management prescriptions will likely be most effective for this suite of species. For example, patch area was an important predictor of the densities of several of our specialist species in terms of density being affected by changes in patch size. The range of patch sizes, however, varies across our subregions such that what constitutes a large patch in one subregion may differ from another subregion; this explains why bird species density was sensitive to patch size and subregion. Generally, larger patches with less human development and smaller variation in mean sea level tend to be best for these specialist species. Patch-level density estimates can be used to set conservation targets within states, subregions, and across the Northeast by providing the ability to determine which combination of patches support the greatest number of birds for each species. Indeed, sensitivity results can be used to prioritize future monitoring and research efforts (Pollino and Hart 2008, Ayre and Landis 2012).

Incorporating better data into existing BNs is a major strength of this analytical tool (Ayre and Landis 2012) and if we update our BNs with more precise geospatial data in the future, we may reduce the overall uncertainty in our model results. Integrating more detailed and locally derived sea-level rise estimates for each patch would be especially beneficial given the effects that sea-level rise has on the timing of semidiurnal high tide events during the breeding season. Specifically, future changes in saltmarsh sparrow reproduction resulting from shifts in the magnitude of semidiurnal high tide events could cause extinction for this species as soon as 2035 (Field et al. 2017).

Our baseline mapping can provide conservation organizations with a way to identify initial marshes for conservation across a broad geographic area, and can be revisited and updated as more detailed geospatial data become available (e.g., remote sensing of saltmarsh vegetation zones). The Atlantic Coast Joint Venture has begun using our patch-level estimates to develop the Saltmarsh Sparrow Habitat Prioritization Tool, which scores and prioritizes the marsh patches needed to sustain this species in its breeding range (the Northeast). The tool can be used to help make land protection decisions and guide habitat management actions (tool available at http://acjv.org/saltmarsh-sparrow-2/).

The ability of land managers and conservation practitioners to continue species monitoring is critical to evaluating the efficacy of tidal-marsh habitat management decisions. Management tools are most useful when they are adaptive, incorporating species' responses to habitat changes and applying this information to counteract species' population declines. There are substantial challenges in developing these tools (and adapting them) because they need to be founded in science-based decision-making and incorporate climate change uncertainties at the same time (Conroy et al. 2010), but long-term monitoring will provide some guarantee that conservation efforts are targeting the most valuable habitat patches for bird populations. Incorporating data on land costs and availability, and on long-term viability of marshes also could be beneficial to future conservation planning (Wiest et al. 2014). Our ability to accurately identify marshes that are essential to sustaining tidal-marsh bird populations and maintain these areas as viable habitats will likely determine the future persistence of these species.

MANAGEMENT IMPLICATIONS

Our BN models provide a flexible framework built on baseline monitoring and spatial data that can be modified into an adaptive management tool and used to guide management decisions in response to avian species' interactions with tidal-marsh habitat. Managers interested in maintaining tidal marshes for marsh birds and other wildlife could concentrate on conserving patches with lower rates of sea-level rise and minimizing impacts from development. Habitat management actions that help maintain marsh habitat and increase reproduction of specialist birds that nest on and near the marsh surface can be incorporated into our models as decision variable information. The information can be used to evaluate the success of implemented actions and help make future management decisions that are based on empirical data. Updating our models with new data from bird monitoring, remote sensing, and sea-level rise and climate models also will improve the utility of such a tool to aid in managing this changing landscape.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.