Mapping habitat suitability at range-wide scales: Spatially-explicit distribution models to inform conservation and research for marsh birds

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Abstract
Habitat loss is a primary cause of species decline, and predicting the distribution of quality habitats across broad scales is needed for conservation of rare species. Secretive marsh birds are a group of emergent-wetland specialists that include multiple threatened and endangered species whose populations have been impacted by wetland loss and modification. Habitat suitability for marsh birds is poorly mapped, and predictions of habitat quality over broad scales are primarily generated via expert judgment. We developed data-driven models to predict fine-resolution habitat quality for 13 marsh bird species across their ranges within the U.S. We demonstrate how these models are useful for conservation by quantifying range contraction, assessing the usefulness of existing protected areas, and assessing the vulnerability of habitats to global change for rare species. These tools provide a quantitative foundation for broad-scale conservation, research, and monitoring efforts, and a starting point for adaptive conservation of marsh bird breeding habitat over broad spatial extents.

KEYWORDS
black rail, hierarchical occupancy model, Rallidae, Ridgway’s rail, species distribution model, wetland birds

1 | INTRODUCTION

Species diversity is declining and the defaunation of ecological communities is occurring at unprecedented rates (Dirzo et al., 2014; Young, McCauley, Galetti, & Dirzon, 2016). Loss and degradation of habitat is a primary driver of species decline, rarity, and extinction (Potts et al., 2010; Sodhi, Brook, & Bradshaw, 2009). Habitat loss is commonly caused by anthropogenic modifications of landscapes (Martinuzzi et al., 2015; Norris, 2008), and such change has occurred both rapidly and over broad spatial extents (Dahl, 2006; Meyer & Turner, 1992; Ramankutty & Foley, 1999). The effects of habitat alteration are also exacerbated by other stressors, and the scope and scale of these changes across a species’ range pose challenges to implementing conservation efforts that potentially can halt or reverse population declines (Brook, Sodhi, & Bradshaw, 2008; Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Segan, Murray, & Watson, 2016). Given the pace and scale of habitat alterations and their ubiquitous impacts to species, spatially-explicit predictions of the location of high-quality habitat across broad spatial extents for sensitive species are...
needed. Such maps are vital for conservation planning and decision-making (Guisan et al., 2013; Scott et al., 2002).

While spatially-explicit models that project habitat quality throughout a species' range are vital for conservation planning, map-based decision-support tools are commonly derived from expert judgment due to a lack of rigorous field data (Clevenger, Wierzchowski, Chruszcz, & Gunson, 2002; Drew & Perera, 2011). Expert-judgment models of habitat suitability often have limited connection with actual field data and involve ad hoc weighting of variable importance for covariates that contribute to habitat quality (rather than biological effects estimated directly from data). This disconnect between data and prediction can limit the predictive accuracy of models derived from expert judgment, which is often unknown, making it more difficult to identify important areas for conservation and assess the vulnerability of populations to future disturbance (Johnson & Gillingham, 2004; Seoane, Bustamante, & Díaz-Delgado, 2005).

We demonstrate the utility of generating data-driven, spatially-explicit habitat models at range-wide extents for species of conservation concern. We illustrate this for secretive marsh birds, a group of emergent-wetland specialists whose populations have been negatively impacted by continental-scale destruction and modification of wetlands (Eddleman, Knopf, Meanley, Reid, & Zembal, 1988; Stevens & Conway, 2020). Emergent wetlands have dramatically declined over the past century in North America, largely due to conversion of wetlands for human uses (Brinson & Malvárez, 2002; Dahl, 2006). Marsh bird populations have declined, and the breeding ranges of several species are contracting (Conway, Eddleman, & Anderson, 1994; Conway & Sulzman, 2007; Eddleman et al., 1988; Stevens & Conway, 2020). Consequently, multiple species are federally protected by endangered species legislation in the United States, Canada, and Mexico (COSEWIC, 2002, Diario Oficial de la Federacion, 2002). Concerns over marsh birds are widespread (U.S. Fish and Wildlife Service, 2005, U.S. Fish and Wildlife Service, 2008), but the distribution of high-quality habitat for these birds is poorly understood and has not been mapped across their ranges. As such, broad-scale assessments of habitat suitability needed for conservation planning are often based on expert judgment (e.g., Bolenbaugh, Cooper, Brady, Willard, & Krementz, 2012), and data-driven models that map spatial heterogeneity in habitat quality over broad spatial extents are needed to inform conservation and research. Here, we provide fine-resolution spatial models developed to predict habitat suitability across the broad extents of each species' breeding range.

We developed habitat models over the extent of the entire U.S. breeding range for 13 marsh bird species. We projected statistical species distribution models (SDMs) that were optimized for spatial prediction, and generated predictions using species-specific models and covariates mapped at a 30-m resolution over the contiguous U.S. We demonstrate how these models provide a quantitative baseline for guiding scientifically-driven conservation, monitoring, and research of marsh birds. We emphasize tangible examples of how these models can be used for a variety of applied purposes that will inform conservation. These models provide an unprecedented fine-resolution depiction of breeding habitat quality over broad spatial extents for marsh birds in the U.S.; however, the general approach is not taxa-specific and could be applied to any species for conservation planning at the extent of a species' range.

2 | METHODS

2.1 | Range-wide spatial models

We built models to project habitat suitability over the breeding range within the contiguous U.S. for each of 13 marsh birds: pied-billed grebe (Podilymbus podiceps), American bittern (Botaurus lentiginosus), least bittern (Ixobrychus exilis), American coot (Fulica americana), common gallinule (Gallinula galeata), purple gallinule (Porphyrio martinicus), limpkin (Aramus guarauna), king rail (Rallus elegans), clapper rail (Rallus crepitans), Ridgway’s rail (Rallus longirostris), Virginia rail (Rallus limicola), black rail (Laterallus jamaicensis), and yellow rail (Coturnicops noveboracensis). We identified the range extent for each species from the U.S. Geological Survey’s Gap Analysis Project (USGS-GAP; Gergely & McKerrow, 2013), and projected models of habitat suitability that were species-specific within those ranges.

We used raster regression to build spatially-explicit models that predict breeding habitat quality. Predictions were generated from multiscale hierarchical occupancy models built using field data collected over a 14-year period across the U.S. (Stevens & Conway, 2019, 2020). We used the optimally predictive model for each species to predict occupancy probability as a function of rasters that measured habitat and disturbance covariates over a variety of spatial extents via moving-window analyses (see Appendix A for details). Moving-window analyses quantified the values of covariates measured over a range of spatial extents (100, 224, and 500 m) around each 30-m raster pixel and assigned each pixel the value for
each covariate based on its measurement over those broader extents around that pixel. We also considered anthropogenic disturbances (agriculture, development, and modification of hydrology) at broader extents within a watershed, which were important for some species (Tables A1 and A2). Both the specific covariates and the spatial extents at which each covariate was measured were species-specific and optimized for out-of-sample spatial prediction (i.e., to predict at new locations in space; Stevens & Conway, 2019, 2020). These analyses allowed for fine-resolution (30 m) prediction of habitat quality for each species based on ecological effects of habitat and disturbance variables that could operate over a range of spatial extents that are relevant to these birds (Glisson, Conway, Nadeau, & Borgmann, 2017; Stevens & Conway, 2020). Thus, we used occupancy probability (ψ) as an indicator of habitat quality, where ψ was predicted for each 30-m pixel as a function of wetland attributes, anthropogenic disturbances near wetlands, and anthropogenic modifications of hydrology within watersheds (Tables A1-A2). We used the raster calculator tool within ArcMap 10.5.1 (ESRI, Redlands, CA) to build spatial models, and have made each species’ habitat model publicly available (Appendix B).

2.2 | Example 1: Temporal change in status

These models provide an unprecedented baseline for assessing changes in the distributions of marsh birds and their habitats within the U.S. To illustrate this potential, we used our models to estimate area of the occupied breeding range at several points in time for black rails, a species of conservation concern whose eastern sub-species (Laterallus jamaicensis jamaicensis) has been recommended for listing under the U.S. Endangered Species Act. We estimated the area of occupied black rail habitat as the sum of all ψ values at each unique pixel multiplied by its area (900 m² for each pixel; Royle & Dorazio, 2008; Appendix A). The statistical model used for predicting black rail occupancy included a decreasing time trend over the 14-year period used to collect field data for model building (1999–2012; Stevens & Conway, 2020; Table A2). Because the model for black rails included a time trend covariate, we could easily illustrate changes in the breeding area occupied over time. Thus, we replicated range-wide spatial modeling and calculation of the area occupied at four discrete years: 2000, 2006, 2012, and 2018. This quantified range contraction from 2000 to 2012 and provided a more recent estimate of breeding range size based on extrapolation of the trend in occupancy estimated during that period.

2.3 | Example 2: High-quality habitats

These models enable identification of high-quality breeding habitat across broad-scales that is useful for conservation planning and monitoring. To illustrate this, we mapped breeding habitat quality for the Ridgway’s rail, a federally endangered species, within the lower Colorado River basin in Arizona, California, and Nevada, USA. In addition, to identify multispecies hotspots of high-quality habitat for the conservation of breeding rails (i.e., birds in the Rallidae family), we used a stacked distribution modeling approach (Calabrese, Certain, Krann, & Dormann, 2014; Appendix A) calculated over the same geographic area. The stacked distribution approach summed ψ values for >1 species at each pixel, providing a composite measure of habitat quality for the group of species. We also compared the distribution of high-quality habitat for rails to the location of existing National Wildlife Refuge (NWR) lands in the region to assess the extent to which these areas are protecting high-quality habitat for marsh birds.

2.4 | Example 3: Vulnerability to global change

These models provide a baseline for assessing vulnerability of breeding habitat to global change. To illustrate this, we projected effects of sea level rise on predicted black rail habitat. The black rail is the smallest rail in North America and is sensitive to changes in water depths that exceed their wading ability (Eddleman et al., 1988), suggesting coastal populations are vulnerable to increases in sea level. We used the habitat model for black rails projected to 2018 (described in Example 1), and then overlaid GIS layers projecting a 0.61 m sea level rise (i.e., a 2 ft. rise from the National Oceanic and Atmospheric Administration Sea Level Rise Viewer; https://coast.noaa.gov/digitalcoast/tools/slr.html) for the western Gulf Coast. From this analysis, we calculated the area of habitat that would be affected, as well as summary metrics of habitat quality from the original area and the remaining habitat after a 0.61-m sea level rise. Thus, we demonstrate how the models can provide baselines of broad-scale habitat suitability that can be used to assess vulnerability of breeding habitat to future change.

3 | RESULTS

Our analyses provide data-driven and range-wide predictions of breeding-season habitat quality for each of 13 species of marsh birds (Table A2, Appendix B). These models also provide baselines for assessing future change in habitat quality and species’ distributions over broad extents, as
demonstrated by our examples. Example 1 suggested the area occupied by black rails decreased by 71% from 2000 to 2018, a substantial breeding range contraction (2000:79,623 km²; 2006:56,092 km²; 2012:35,753 km²; 2018:23,037 km²). Example 2 mapped breeding habitat quality for three rails (black rails, Ridgway’s rails, and Virginia rails) within the lower Colorado River basin (Figure 1) and showed that NWR lands in this region are protecting slightly better-than-average breeding habitat for both the endangered Ridgway’s rail (Cibola NWR: $\psi = 0.65$, $SD_\psi = 0.02$; Havasu NWR: $\psi = 0.68$, $SD_\psi = 0.14$; Imperial NWR: $\psi = 0.63$, $SD_\psi = 0.02$; entire region: $\psi = 0.60$, $SD_\psi = 0.01$) and rails as a group (Cibola NWR: $\sum \psi = 1.46$, $SD_{\sum \psi} = 0.12$; Havasu NWR: $\sum \psi = 1.28$, $SD_{\sum \psi} = 0.22$; Imperial NWR: $\sum \psi = 1.33$, $SD_{\sum \psi} = 0.11$; entire region: $\sum \psi = 1.19$, $SD_{\sum \psi} = 0.18$). Lastly, Example 3 showed that black rails occupying the western Gulf Coast region of Texas and western Louisiana are vulnerable to sea level rise; a 0.61 m increase to sea level would inundate 27% of the breeding habitat (6,974.2 km²) (Figure 2). Moreover, the quality of areas projected to be inundated by sea level rise was slightly better than that of remaining sites (inundated: $\psi = 0.25$, $SD_\psi = 0.04$; remaining: $\psi = 0.23$, $SD_\psi = 0.06$).

4 | DISCUSSION

We developed data-driven, fine-resolution models to predict breeding habitat quality over range-wide extents within the U.S. for marsh birds of conservation concern. Models with this combination of fine spatial resolution and broad spatial extent were not possible until recently, because the assessment of habitat relationships for marsh birds has been primarily regional in nature (e.g., Bolenbaugh et al., 2012). Our models put range-wide prediction of breeding habitat quality on a data-driven foundation to guide future conservation and research efforts. These predictions provide quantitative baselines for measuring future change, including changes in species distributions over time (e.g., Example 1), distributions of high-quality habitat for one or multiple species (e.g., Example 2), and the vulnerability of marsh birds to global change (e.g., Example 3). Our example analyses also illustrate how the models provide a starting point to inform broad-scale and species-specific conservation relative to the distribution of high-quality habitat, and provide important stand-alone results for species of high conservation concern.

Our models provide quantitative, range-wide baselines for assessing changes to breeding distributions and habitat quality over time. Example analyses illustrated the assessment of changes to the occupied breeding area for black rails, and suggested their breeding range has contracted by more than 70% in the 21st century. Additional analyses with black rails also demonstrated how to pair predictive habitat models with predictions of sea level rise, and indicated that breeding habitat for this species in low-lying coastal areas is vulnerable to future...
changes (see also Roach & Barrett, 2015). Both of these results are particularly alarming for black rail conservation given the existing concerns over their status (Conway & Sulzman, 2007; Roach & Barrett, 2015) and the recent recommendation to list the eastern subspecies under the Endangered Species Act. Yet, data-driven assessments of marsh bird distributions and range contractions over their entire breeding ranges were not previously possible, and thus our models provide the ability to quantitatively assess changes in status over time. Similarly, the effects of sea level rise on coastal marsh bird populations is a prominent concern among biologists, yet quantitative models to facilitate vulnerability assessment over broad scales are lacking (Woodrey et al., 2012). Our example provides one assessment of habitat vulnerability to a 2 ft. sea level rise, but spatial accuracy of such projections is unknown and other projections exist. Moreover, the sea-level-rise predictions do not account for changes in coastline geomorphology, vegetation composition, and water depth that will likely occur as a result of rising seas (see https://coast.noaa.gov/data/digitalcoast/pdf/slr-inundation-methods.pdf), and thus their accuracy in predicting future sea levels may be spatially heterogeneous. Nonetheless, analyses similar to our example could be replicated over a range of sea-level-rise predictions (e.g., including but not limited to a 2 ft. rise) as part of scenario planning efforts to identify vulnerable habitat for coastal marsh bird populations. Our habitat suitability models could be used for each sea-level projection, and thus facilitate the best-possible conservation and scenario planning in the face of global change.

We also demonstrate how to use the models to provide a more thorough understanding of the effectiveness of conservation and recovery efforts for marsh birds. Example analyses used stacked species-specific SDMs to evaluate the effectiveness of the NWR System in the lower Colorado River basin for conserving high-quality breeding habitat for both the endangered Ridgway’s rail and other rail species, and indicated these protected areas are indeed conserving high-quality habitat for rails that is present within the region. The stacked SDM approach for assessing habitat quality for multiple species is highly informative, but can be challenging to implement over broad spatial extents because of spatial heterogeneity in species diversity and differences in range boundaries among species. At a minimum, our habitat models enable assessment of the effectiveness of existing reserve networks for conserving high-quality habitat for individual marsh birds over spatial extents not previously possible, and also enable identification of holes in protected-area networks where important areas could be conserved in the future. In addition, these models provide a spatial tool to help target species-specific monitoring efforts. Uncertainty about the broad-scale status of marsh bird populations could be reduced by more effective monitoring and the integration of monitoring and modeling efforts (Conroy et al., 2010; Conway, 2011; Johnson et al., 2009). Our models represent a step toward such integration that could help reduce uncertainty about the status and conservation of marsh birds, and thus directly benefit evidence-based assessment of the effectiveness of conservation efforts.

Range-wide predictive habitat maps provide a foundation for additional model refinement to foster improved predictions of habitat quality for marsh birds, and ultimately the adaptive management of broad-scale conservation efforts (Conroy et al., 2010). Our rasters predict habitat suitability for each species, are publicly available (see Appendix B), and can be used to directly inform current marsh bird conservation efforts. Indeed, our predictions of habitat suitability for four species (black rail, king rail, yellow rail, limpkin) will be considered by the U.S. Fish and Wildlife Service in future purchasing decisions that may add land parcels to the NWR System. However, many covariate data sets used in our analyses

**FIGURE 2** Projected habitat quality in 2018 for black rails along the western Gulf Coast region of Texas and Louisiana, USA without (a) and with (b) a 0.61 m increase in sea level. The black line indicates the Gulf of Mexico coast and darker red-spectrum colors indicate better breeding habitat (i.e., higher occupancy probability), whereas solid black regions (b) are projected to be inundated by seawater.
are updated periodically (e.g., National Wetland Inventory data) and field sampling for marsh birds is ongoing in many regions. Thus, our models provide spatially-explicit predictions that can be refined as data are updated, and the Bayesian implementation of the SDMs (Stevens & Conway, 2020) projected with our spatial models provides a quantitative framework for adaptation using Bayesian learning (Hobbs & Hooten, 2015).

Quantitative updating of model predictions could be used for regional adaptation of habitat suitability maps (i.e., model adaptation in space), updating parameter estimates (and possibly adding additional covariates) with region-specific occupancy data to account for the possibility of spatial heterogeneity in habitat relationships (suggested by Woodrey et al., 2012). As an example, work is currently underway to adapt spatial predictions from our range-wide models for the eastern subspecies of black rails along the Atlantic Coast. Black rail survey data from the Atlantic Coast are being used to update model parameter estimates, test the predictive ability of additional, region-specific covariates, and ultimately adapt the maps for optimal spatial prediction of habitat for this area and subspecies. The parameter estimates and predictions from our range-wide models could also be updated over time as new data are collected, and such updating is a central tenant of adaptive management that can be used to improve species conservation in the face of anthropogenic disturbance and global change (Conroy et al., 2010; Johnson, Boomer, Williams, Nichols, & Case, 2015; Nichols et al., 2011). As such, the spatial models described here provide a predictive foundation for implementing adaptive management of marsh birds at regional scales, and thus provide practical utility for conservation of these birds across the U.S.

Lastly, while our models provide predictions of habitat quality for marsh birds across broad extents, these predictions are focused on the breeding season and on the U.S. portion of each species’ range. It remains unclear how the quality of breeding-season habitat may be different from quality of habitat used in other seasons, as most marsh bird research has focused on the breeding season. Our analyses also focused on the U.S. portion of each species range, as this is where the data used to build predictive SDMs were collected (Stevens & Conway, 2020) and where the habitat variables used to generate predictions were available. Some species have ranges that extend beyond the U.S. borders, however, and our maps do not predict habitat quality in these areas. Consequently, the models for species whose breeding range spans a U.S. border cannot fully capture range dynamics and changes in the breeding area occupied outside of the U.S. For example, multiple marsh birds have breeding ranges that extend into Canada (e.g., American bittern, least bittern, pied-billed grebe). If the breeding ranges of these birds began to shift northward as a result of climate change, then assessments of breeding range contraction in the U.S. portion of the range may not provide an entirely accurate assessment of the species status as a whole. Nonetheless, we provide the most spatially extensive set of habitat quality predictions available for these birds within the U.S., and thus provide a starting point for future work that could extend analyses and predictions in other seasons and beyond the U.S. borders.

ACKNOWLEDGMENTS

Department of Defense Legacy Program, U.S. Fish and Wildlife Service, Nebraska Game and Parks Commission, and the U.S. Geological Survey Gap Analysis Project provided funding. C. Nadeau, K. Borgmann, and W. Glisson helped compile rail survey data and spatial data. We thank J. Aycrigg and two anonymous reviewers whose comments improved the focus of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

AUTHOR CONTRIBUTIONS

B.S. and C.C. conceived the study and planned the analyses. B.S. conducted the spatial analyses and wrote the initial manuscript draft, where C.C. provided additional contributions and feedback that resulted in the finished manuscript.

ETHICS STATEMENT

No ethics approval was required for this research. Our analyses involved modeling output and predictions only and did not involve handling of live animals.

DATA AVAILABILITY STATEMENT

Marsh bird habitat models have been made publicly available on Figshare (links provided in Appendix B).

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SUPPORTING INFORMATION

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

How to cite this article: Stevens BS, Conway CJ. Mapping habitat suitability at range-wide scales: Spatially-explicit distribution models to inform conservation and research for marsh birds. Conservation Science and Practice. 2020;2:e178. https://doi.org/10.1111/csp2.178