Summary report: Rusty Blackbird habitat suitability on wintering grounds and during spring migration

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Overview of methods

Assessment of habitat suitability for winter and spring blitz periods required several processing steps, including: processing bird observation data, model development and calibration, processing of land cover and climatic data, model evaluation, and statistical interpretation of models. Because habitat suitability predictions and their interpretation are highly dependent on each of these steps, below I provide a brief overview of each of these steps.

- Processing bird observation data: Observations from the Spring and Winter Blitz as well as from the larger eBird database were used throughout this analysis. To ensure that collection of eBird and Blitz observations used similar protocols, eBird data were subset such that only travelling counts were considered for this analysis. Because the spatial extent of a study area can bias suitability models and large extents can lead to exaggerated measures model performance, observations were subset to those within the 99th percentile spatial distribution of Rusty Blackbird Observations. Observation data were grouped into sampling periods, with Winter Blitz observations grouped by year and Spring Blitz observations grouped into two-week intervals for each year. To maximize independence of samples (i.e., to avoid double-counting individuals) observations were aggregated to a 4 km resolution grid (see below), with grid cells representing the maximum count of Rusty Blackbirds during each sampling period. Finally, because the collection of eBird data is biased towards certain environments (e.g., warmer temperatures and close to human development), we evaluated habitat suitability of presence locations relative to locations in which eBird lists did not contain Rusty Blackbird observations.
- Processing land cover and climatic data: Land cover data were obtained from the USGS National Gap Analysis Program (http://gapanalysis.usgs.gov). These data are provided at a resolution of 30 m with classification of land cover in natural areas dependent on the plant community present at a given site. Land cover data were re-classified to habitat types expected to be predictive of Rusty Blackbird distribution. For each land cover type, we then aggregated the proportional cover to a resolution of 4 km, a spatial resolution thought to be representative of the spatial habitat use by wintering Rusty Blackbirds. Climatic data were obtained from the PRISM Climate Group (http://prism.oregonstate.edu/) and included average daily precipitation and minimum daily temperatures at a resolution of 4 km. Precipitation for both winter and spring migration analyses was evaluated as the mean daily precipitation across each sampling period (i.e., 1 Jan 14 Feb 2009-2011; X Mar X Apr 2014-2016). For the winter analysis, we calculated the average minimum temperature across the period for each year in the study, whereas for the spring analysis we determined the minimum temperature associated with each bird observation. After processing, land cover and climatic data were extracted to bird observation locations.
- Model development and calibration: Model development involves fitting the observed distibution of Rusty Blackbirds and observations (eBird lists) that do not include Rusty Blackbirds to the distribution of environmental covariates in a maximum entropy (MaxEnt) modeling framework. Importantly, because these models are developed in environmental rather than geographic space, these models do not predict the probability that a Rusty Blackbird will be present at a given location but rather that the environment at a given location is suitable for Rusty Blackbirds as a function of the distribution of Rusty Blackbird observations. Models were developed separately for Rusty Blackbird observations that fell into one of three flock size classes, including: small (1-19 individuals per observation), medium (20

- 99 individuals per observation), and large flocks (100 or more individuals per observation). For all variables with the exception of minimum temperature, only linear models were used to describe Rusty Blackbird habitat suitability. A quadratic term for minimum temperature was used to address the expected hump-shaped response of Rusties to minimum temperatures. Models were calibrated to avoid overfitting by excluding variables that are highly correlated and choosing models with the greatest explanatory power of the models relative to the number of variables used in their construction.
- Interpretation of models: Our goals in model interpretation were to determine: 1) How do Rusty Blackbird suitability models perform and did the inclusion of Blitz data improve model performance (formally tested for the Winter Blitz)? 2) Where is Rusty Blackbird habitat most suitable?; 3) Which environmental variables best predict Rusty Blackbird distributions?; and 4) Do large flocks of Rusty Blackbirds occupy a different environmental niche than small and medium size flocks (formally tested for the Winter Blitz)? Model performance is evaluated by comparing model sensitivity (i.e., the true positive rate – the proportion of correctly identified sampled at a given threshold of habitat suitability) and specificity (the false positive rate – in species distribution modeling this is described the proportional predicted area for the model at a given threshold of habitat suitability). To address the suitability of habitat, we used the relationship between Rusty Blackbird distributions in environmental space to predict suitability models for small, medium, and large flocks of Rusty Blackbirds in environmental space. We then evaluated the contribution of the environmental covariates to model performance to estimate which variable (habitat and climatic) best explains observed Rusty Blackbird distributions Finally, to address whether different flock size classes occupy a different environmental niche, we tested whether there are differences in relation to the environment in which each flock size class are observed and whether large flocks occupy a narrower niche space than small and medium flocks (i.e., are more constrained in their distribution about the environmental covariates). Further details for each step of this analysis are provided in the results below.

Summary of results

1. Model evaluation

To evaluate the performance of models we assessed the area under the receiver operator curve (ROC, AUC, see Fig. 1A). While the details of AUC are outside of the goals of this document, AUC describes the sensitivity and specificity of models, with values of 0.5 representing equivalent model performance relative to random, 0.7 - 0.8 representing "fair" performance, 0.8 - 0.9 "good" performance, and 0.9 - 1.0 "excellent" model performance. AUC was calculated by separating samples into 5 "folds" of training and test samples and examining how well training samples predict test samples (cross-validation with k-fold partitioning). We found strong evidence that model performance increased with increased flock size, with fair performance for small flocks and good perforance for medium and large flocks (across observation methods, Fig. 1B). Because the number of samples used to develop models decreased with flock size, this suggests that larger flocks are observed across a narrower range of the environmental covariates (formally tested in Number 4, below). We tested whether the predictive capacity of models varied by flock size by comparing training AUC across folds for a given flock size class against a null distribution developed by randomizing two flock size classes (e.g., large vs. small flocks). Similarly, to determine whether Blitz data improved estimates evaluate the performance of models relative to observation methods (eBird or Blitz, Winter Blitz only), we compared observed AUC against a null distribution developed by randomizing eBird and Blitz samples. Our findings show that models developed using eBird and Blitz data, combined, performed better than either eBird and Blitz alone (Fig. 1B). With the exception of small flocks, for which Blitz observations had a greater predictive capicity than eBird observations, there was not evidence for a difference in predictive capacity between Blitz and eBird samples. There was, however, strong evidence that the inclusion of Blitz data (i.e., in combined Blitz and eBird observation methods) greatly improved model performance for large and medium flock size classes.

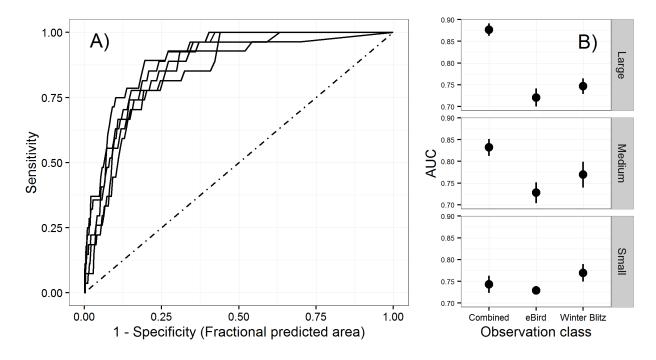


Figure 1: A: Example receiver operator curves (ROC) for cross-validation runs of large flocks during the Winter Blitz period, 2009-2011. The dotted line represents the null model of random model perfomance. B:Area under the receiver operator curve (AUC) across flock size and observation classes for the Winter Blitz period, 2009-2011. Error bars represent the 95% confidence interval about mean AUC values across cross-validation runs.

2. Habitat suitability for small, medium, and large flocks of Rusty Blackbirds

Winter suitability maps generated for each flock size class (Fig. 2) show potential hotspots in the southern Mississippi River Basin, the Blackbelt region of Alabama and Mississippi, and the coastal plains of the southeastern states. Note that the predicted suitability appears to decrease with increasing flock size (formally tested in Number 4, below). Surprisingly, the Piedmont region of the southeastern states appears to be of moderate suitability for large flocks, however, low sample sizes for this flock size class mean that some samples (e.g., an observation in Piedmont forest) may have a strong effect on habitat suitability estimates.

3. The contribution of environmental variables to habitat suitability

To determine which environmental variables best predict Rusty Blackbird distributions for each flock size class, we compared the contribution of each variable to model performance after calibrating models (see above for model calibration). Across flock size classes minimum temperature had the greatest influence on the suitability models (Fig. 3, left). With the exception of temperature (Fig. 3, right), floodplain forest had the greatest influence on model performance, with the contribution of this variable to large flock distributions nearly double that of small and medium-sized flocks. The predicted suitabilility for each flock size class was positively associated with floodplain forest (i.e., λ coefficient > 0). Among the remaining variables, row crops and pasture also strongly contributed to model performance across flock size classes ($\lambda > 0$ for both variables), while the proportion of highly developed land contributed to large flock distributions ($\lambda < 0$) but not small or medium-sized flocks.

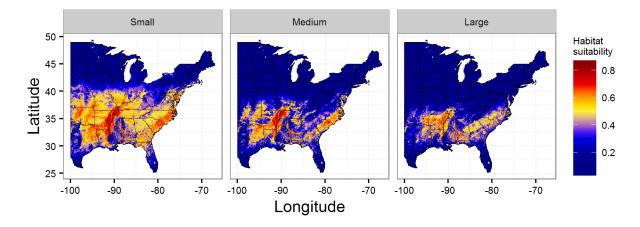


Figure 2: Winter habitat suitability predictions for small medium, and large flock size classes across observation methods, generated using winter 2009 precipitation and minimum temperatures.

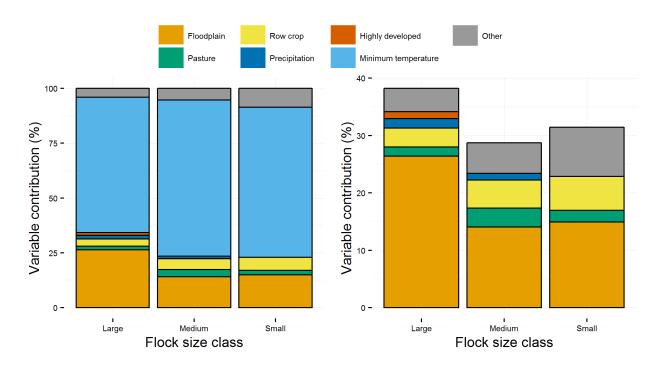


Figure 3: Variable contribution by flock size class of the environmental variables most predictive of observed Rusty Blackbird distributions. The plot on the left includes minimum temperature while the plot on the right shows variable contributions in the absence of minimum temperature.

4 Differences in environmental niche across flock size classes

To assess differences in Rusty Blackbird's environmental distribution across flock size classes, we assessed prevalence (i.e., the average predicted suitability for each map pixel), predicted area of suitable habitat, and compared distributions across and among environmental variables. Prevalence and predicted area of suitable habitat are measures of environmental niche width, as smaller values of each represent a narrower distribution in environmental space. For the Winter Blitz, differences in prevalence and predicted area between flock size classes were statistically evaluated by comparing the observed values for a given flock with a null distribution developed by permuting flock size classes. In both the Winter and Spring Blitz periods, prevalence decreased with increasing flock size. There was strong evidence that large flocks had lower prevalence than small flocks (Fig. A, top panel), but observed prevalence values for large flocks were statistically indistinguishable from a null distribution of medium and large flock size classes. The observed prevalence of medium-sized flocks was significantly lower than that of small flocks and higher than large flocks (Fig A, bottom panel). Fractional predicted area was calculated at the logistic threshold of equal model sensitivity and specificity and decreased with increasing flock size. During the Winter Blitz period, predicted area for large flocks was significantly lower than small and medium-sized flocks (Fig. B, top panel) while the predicted area for medium flocks was statistically indistinguishable from that of small and large flocks (Fig. B, bottom panel). Combined, our observation that prevalence and fractional predicted area decrease with flock size provide strong evidence that the distribution of larger flocks exhibit a narrower environmental niche than that of smaller flocks.

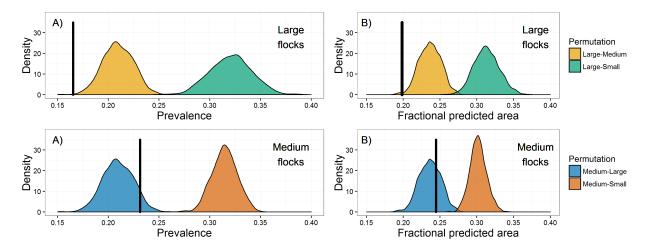


Figure 4: Comparison of observed prevalence (A) and fractional predicted areas (B), solid lines, with the distribution of prevalence and fractional predicted area developed by permuting observations among flock size classes. V.

The distributions of flock size classes across environmental variables were compared for winter flocks by evaluating the niche equivalency among flock size classes (see Fig. 2). We calculated differences in environmental niche as the degree of similarity between habitat suitability maps (modified-Hellinger distance, an index from 0-1 with 1 representing identical environmental niches) and tested whether observed differences were significant by generating and comparing suitability maps developed by randomly permuting flock class labels. We found that flock size classes occupy similar portions of environmental space (e.g., the modified-Hellinger similarity between large and small flocks was 0.89) but the each of significantly different portions of environmental space. analyzing the degree of niche equivalency. We compared the observed distributions of flock size classes of wintering Rusty Blackbirds across individual environmental variables using two-tail Kolmogorov-Smirnov tests of the null hypothesis that samples were drawn from the same distribution.

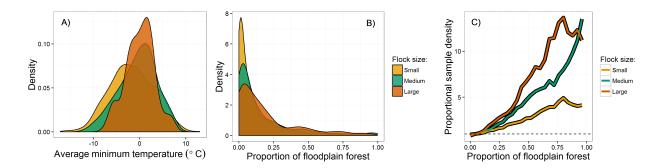


Figure 5: Comparison of observed prevalence (A) and fractional predicted areas (B), solid lines, with the distribution of prevalence and fractional predicted area developed by permuting observations among flock size classes. V.