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Environmental Niche Modeling Reveals Climatic Differences among Breeding Ranges of Orchard Oriole Subspecies

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ABSTRACT.—Environmental niche parameters of breeding ranges for two subspecies in the Orchard Oriole complex (Icterus spurius spurius and I. s. fuertesi) were characterized via ecological niche modeling. Niche models formulated from museum specimen collections largely agree with published breeding ranges of both taxa. Furthermore, our findings identify likely suitable habitat of migratory double breeding in I. s. spurius. Models successfully identify suitable habitat as illustrated by threshold dependent and independent statistical tests and overlap very little in geographic space. Principal component analysis (PCA) identifies two axes explaining 99.0% of variation in the climate data and reveals that each breeding range exhibits unique ecological characteristics, as they occur in nonoverlapping PCA space. Multivariate analysis of variance (MANOVA) identifies significant differences along both axes (PC1, $P < 0.0001$; PC2, $P < 0.0001$). A newly formulated metric for niche similarity ($I$) agrees with PCA and ENM results and, further, indicates that environmental niche differences are more likely a result of differences in habitat availability than habitat preference. Our results may indicate rapid change in environmental niche within the Orchard Oriole group as these taxa have been diverging for approximately 200,000 y. The Orchard Oriole group provides an example of niche lability that contrasts with evidence of niche conservatism between many other Mexican species pairs.

INTRODUCTION

The ecological niche, as defined by Hutchinson (1957), describes the set of conditions, both biotic and abiotic, in which a population is able to persist. Niche variables can be classified into two general categories: resource variables (bionomic variables) and condition variables (or scenopoetic variables). Bionomic variables describe availability and consumption of resources, whereas scenopoetic variables describe the climate and physical features of the landscape (Hutchinson, 1978). Aspects of a species’ ecological niche, like other traits, are able to change through evolutionary time. Theory predicts that ecological niche evolution should occur slowly over time, because adaptation rates are typically slower than extinction rates under conditions outside the fundamental niche (Gomulkiewicz and Holt, 1995).

Recently, geographic information systems (GIS), global climate data and museum specimen collection databases have allowed rigorous testing of niche evolution rates via the application of ecological niche modeling (ENM). ENM is a general technique in which current climatic, or physical conditions at known organism occurrence points are used to ‘predict’ the geographic range of that organism. The climatic conditions throughout this predicted range represent an organisms’ environmental niche. Environmental niche is used as opposed to ecological niche because ENM only accounts for scenopoetic variables. ENM has identified cases of slow niche evolution (niche conservatism) (Peterson et al., 1999; Eaton et al., 2008) as well as fast niche evolution (niche lability) (Losos et al., 2003; Graham et al., 2004). These contradictory results are partly due to differing statistical analyses (Warren et al., 2008); thus, examination of environmental niche differences using multiple metrics could help identify cases of niche lability and niche conservatism more reliably.

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Using ENM, museum collection databases and global climatic data we characterize the environmental niches of two recently diverged oriole taxa: the Orchard Oriole (Icterus spurius spurius) and the Fuertes’s Oriole (I. s. fuertesi). The two taxa are divergent in male breeding color (Kiere et al., 2007), and qualitative differences have been suggested for song (Chapman, 1911; Graber and Graber, 1954). However, analysis of mtDNA shows a lack of reciprocal monophyly, most likely due to recent divergence, but hybridization is another possible explanation for this mitochondrial paraphyly (Baker et al., 2003). Icterus spurius spurius has a large breeding range in the eastern US and into central Mexico. Icterus spurius fuertesi occupies a much smaller breeding range along the Gulf Coast of Mexico in Tamaulipas and Veracruz states (Fig. 1). Icterus spurius spurius is a long-distance migrant while I. s. fuertesi migrates shorter distances suggesting a likely case of peripheral isolate speciation, in which I. s. fuertesi could result from a founder population from a more widespread I. s. spurius like ancestor. Indeed, the loss of migration may facilitate speciation in orioles via the creation of founder populations (Kondo et al., 2008), which could rapidly change in plumage as has been suggested for dabbling ducks (Omland, 1997). Under this model, one might also expect to find differences in ecology as the two ranges are geographically disjunct. Here, we test for these differences by assessing overlap in ENM and PCA space and by using a new metric of niche similarity in conjunction with null modeling (Warren et al., 2008).

**METHODS**

**DATA SOURCES AND GEOREFERENCING**

We used 20 bioclimatic variables (Table 1), here referred to as ‘climate layers,’ to describe the environmental niches of the focal taxa, Icterus spurius spurius and I. s. fuertesi. These climate layers were interpolated from the WorldClim dataset (available at http://www.worldclim.org/) as described by Hijmans et al. (2005), using ANUSPLIN, a thin plate smoothing spline algorithm. Climate data resolution was five arc minutes (approximately 10 km²). We collected point occurrence data for I. s. spurius and I. s. fuertesi using two searchable online databases, the Ornithological Information System (ORNIS; http://olla.berkeley.edu/ornisnet/) and the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/). Additionally, we added I. s. fuertesi specimens recently collected by our lab to the data set.

We considered records based only on tangible specimens for the data set and excluded any specimens collected outside of the core breeding season (20 May–10 Jul.). After compiling entries from all data sources, we removed duplicate records from the same collection locality so that each specimen record represented a unique locality. When more than 10 records of Icterus spurius spurius occurred in a single state or province, we chose 10 records at random to include in the dataset, reducing geographic bias. The same procedure was not applied to I. s. fuertesi because of its limited range. We excluded one record of I. s. spurius collected during the breeding season from Chiapas, Mexico because the locality was well outside the established breeding range for I. s. spurius (Howell and Webb, 1995; Jaramillo and Burke, 1999).

Records without latitude and longitude coordinates were georeferenced using BioGeomancer (BG) (available at http://bg.berkeley.edu/latest/) and visually assessed for accuracy. BG automatically assigns latitude and longitude coordinates using the written locality data included with specimen records from databases such as GBIF and ORNIS. It also computes uncertainty for each georeferenced point using the point-radius method as described by Wieczorek et al. (2004). Average uncertainty for our locality data was <10 km
Fig. 1.—Georeferenced points and final descriptive niche models for (a) *I. s. spurius* and (b) *I. s. fuertesi*. Shading corresponds to the number of preliminary models that included a given area as suitable habitat (9–10 models – dark grey, 7–8 models – medium grey; 5–6 models – light grey). Overlap of the two models is shown in (c). Note the localities and predicted range of *I. s. spurius* in northwestern Mexico, corresponding to areas of migratory double breeding.
which is appropriate for the resolution of the climate data (∼10 km²).

**CLIMATE DATA EXTRACTION AND ANALYSIS**

Georeferenced specimen records and climate layers were imported into ArcGIS (version 9, ESRI). We extracted climate layer values at each point occurrence and, in SPSS (version 19, IBM, Corp.), performed a principal components analysis (PCA) as well as multivariate analysis of variance (MANOVA) in which species was a fixed factor; and the principal component scores were the dependant variables. We analyzed only the first two principal components. Factor scores for each specimen record were imported into ArcGIS and we created minimum convex polygons for each taxon using Hawth’s Tools (version 3, available at http://www.spatialecology.com/htools/download.php). Any overlap in the minimum convex polygons implies overlap in ecological variables.

**ECOLOGICAL NICHE MODELING**

We used Maxent (Phillips et al., 2006, version 3.3.3e, available at http://www.cs.princeton.edu/~schapire/maxent/), a maximum entropy modeling algorithm, to produce ecological niche models. Maxent predicts the geographic distribution of a target species by estimating a probability distribution that has the maximum entropy (i.e., that is most spread out, or uniform) given certain constraints. In the case of maximum entropy modeling, the constraint is that the expected values of each feature (i.e., climate variables) must equal the empirical average (i.e., average value at known occurrence points). We assigned 50% of input data points for training and the remaining points for testing (Icterus spurius spurius: n_{training} = 72, n_{testing} = 71; I. s. fuertesi: n_{training} = 9, n_{testing} = 9). Training data is used to formulate the model parameters whereas testing data points are used to assess the accuracy.

**Table 1.** The 20 bioclimatic variables used to describe the ecological niches of I. s. spurius and I. s. fuertesi

<table>
<thead>
<tr>
<th>Bioclimatic variable</th>
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<tbody>
<tr>
<td>Annual Mean Temperature</td>
</tr>
<tr>
<td>Mean Diurnal Range of Temperature</td>
</tr>
<tr>
<td>Isothermality</td>
</tr>
<tr>
<td>Temperature Seasonality</td>
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<tr>
<td>Maximum Temperature of Warmest Month</td>
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<tr>
<td>Minimum Temperature of Coldest Month</td>
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<tr>
<td>Annual Range of Temperature</td>
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<tr>
<td>Mean Temperature of Wettest Quarter</td>
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<tr>
<td>Mean Temperature of Driest Quarter</td>
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<tr>
<td>Mean Temperature of Warmest Quarter</td>
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<tr>
<td>Mean Temperature of Coldest Quarter</td>
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<tr>
<td>Annual Precipitation</td>
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<td>Precipitation of Wettest Month</td>
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<tr>
<td>Precipitation Seasonality</td>
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<td>Precipitation of Coldest Quarter</td>
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<td>Precipitation of Warmest Quarter</td>
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<tr>
<td>Altitude</td>
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of the model. Preliminary models were assigned conservative thresholds equal to the lowest probability of occurrence recorded at a training point location, so that areas below this probability could be eliminated from the model. We compiled our final descriptive niche models using areas that appeared in a minimum of five of the 10 initial models. For visualization, map colors were assigned according to the number of initial models that included the area as suitable habitat: (i) 9–10 initial models (dark grey), (ii) 7–8 initial models (medium grey) and (iii) 5–6 initial models (light grey). We compared final models across taxa to assess predicted geographic overlap.

We assessed initial model performance using threshold dependant measures (one-tailed binomial test; e.g., Phillips et al., 2006) and threshold independent measures (area under the receiver operating characteristic curve; AUC; e.g., Elith et al., 2006; Hernandez et al., 2006; Phillips et al., 2006). Binomial test P-values indicate how many more test data points were located within the predicted range at a set threshold than would be predicted by random chance. Lower P-values indicate a higher number of points than would be predicted by chance. AUC values indicate the ability of a model to distinguish between presence locations and pseudo-absence background locations. An AUC of 0.5 would indicate a model performance equal to random prediction. These metrics are traditionally used to demonstrate model accuracy; however, problems have been identified with their use (Lobo et al., 2008). To ensure model accuracy, we use conservative thresholds and compiled multiple models to formulate our final descriptive models.

**NULL MODEL ANALYSIS**

In addition to our descriptive models, we also created comparative niche models which used all presence points to formulate the ENMs. These models are used for null model testing by, first, computing niche model similarity using $I$, calculated as:

$$I = 1 - 0.5(H(p_X, p_Y)^2)$$

in which $H(p_X, p_Y)$ is the Hellinger distance:

$$H = \sqrt{\sum_i (\sqrt{p_{X,i}} - \sqrt{p_{Y,i}})^2}$$

where $p_X$ and $p_Y$ correspond to the probability distribution of species occurrence for species X and Y, as calculated by an ENM algorithm. $I$ ranges from 0 (no overlap) to 1 (total overlap). This, and all further calculations of $I$ were carried out using ENMTools (version 1.1; available at http://enmtools.blogspot.com/; Warren et al., 2008). This value of $I$ ($I'$) was then compared to two null distributions of $I$-values. First, we tested for niche equivalency using the ‘identity test’ by comparing $I'$ to a null distribution of $I$-values calculated using 100 pseudoreplicate calculations. Each pseudoreplicate consisted of two niche models created using a random partition in the locality data for both species. $I$ is calculated for each pseudoreplicate by comparing the two niche models. Second, we tested if niche differences were more likely due to differences in habitat preferences between species or differences in habitat availability between ranges by conducting a ‘background test’. We compared $I'$ to two additional null distributions of $I$, representing the niche overlap between a model created using actual locality points of one focal species and a model created using randomly chosen background points from the nonfocal species’ known range. The background was assigned for each species as the minimum convex polygon drawn using the locality points for that species. Additional details on all tests can be found in Warren et al. (2008).
RESULTS

In total, we included 18 records of *Icterus spurius fuertesi* and 143 records of *I. s. spurius* in the final data set. Visual inspection of the georeferenced dataset indicates general agreement with known breeding ranges of *I. s. spurius* and *I. s. fuertesi*; however, a cluster of *I. s. spurius* occurrences in Sinaloa and Sonora are well outside published range estimates (Fig. 1).

Principal components analysis (PCA) of climate layers at each locality explains 99.0% of variation along two principal components (Fig. 2). Positive values on principal component 1 (PC1, x-axis, 94.4% of variation explained) correspond to areas with higher annual precipitation, while negative values correspond to areas of fluctuating seasonal temperature. Along principal component 2 (PC2, y-axis, 4.6% of variation explained), positive values correspond to areas with higher annual precipitation, while negative values correspond to areas with high elevation. MANOVA indicates significant separation along both PCI (P <
There is no observable overlap in the minimum convex polygons drawn for each taxon. Maxent models accurately predicted both taxon distributions as shown by AUC values and threshold dependant P-values (Table 2). Additionally, final descriptive models for each taxon (Fig. 1) generally agree with published breeding ranges of Icterus spurius spurius and I. s. fuertesi; however, overprediction is apparent in both models. Predicted ranges cover approximately 8,779,100 km$^2$ and 145,400 km$^2$ for I. s. spurius and I. s. fuertesi, respectively. Final models overlap a total of 24,700 km$^2$.

The observed $I$ value for the comparative models is 0.34. Overlap of environmental variables measured using the $I$ statistic reveals moderate amounts of similarity between the two breeding ranges. However, identity tests for environmental equivalency between the two breeding ranges reveal that they are not identical, as $I$ fell outside the null distribution (Fig. 3a; P < 0.0001). The background test indicates that environmental niche differences are most likely due to differences in habitat between the two ranges, rather than differences in habitat preference between species as $I$ fell within the null distributions (Fig. 3b; P > 0.05 in both cases).

**Discussion**

Multiple tests of niche similarity reveal differences in the environmental variables describing the breeding ranges of Icterus spurius spurius and I. s. fuertesi. First, environmental data at known occurrence locations for each species do not overlap in principal components space (Fig. 2). In addition, MANOVA reveals significant differences along both principal components. Second, ENM’s formulated using known occurrence points and digital climate data overlap very little (Fig. 1c; 0.3% of total predicted range for both species). Lastly, the identity test corroborates PCA and ENM results revealing that environmental parameters of the two breeding ranges are not identical. All three tests imply that the two breeding ranges differ in environmental parameters. A background test in ENMTools provides further insight and suggests that environmental differences are more likely a result of differences between habitat availability than differences between habitat preferences.

Compared to the reanalyzed Peterson et al. (1999) data (from Warren et al., 2008; see Table 1), the observed niche overlap for Icterus spurius spurius and I. s. fuertesi is lower than most species pair comparisons. Moreover, taxa included in Peterson et al.’s (1999) analysis have been diverging for 2.4 to $10^6$ y (Graham, 1993), whereas I. s. spurius and I. s.
fuertesi have been diverging for roughly 200,000 y (Baker et al., 2003). Changes in environmental parameters in such a short period of time in the Orchard Oriole group provides some support for the pattern of rapid evolutionary change perhaps facilitated by founder effects. As predicted by peripheral isolate divergence, changes have evolved rapidly between I. s. spurius and I. s. fuertesi in geographic isolation. Male color has diverged and the environmental parameters of each range are also different. Our results differ from the findings of the large study of Peterson et al. (1999) from southern Mexico; I. s. spurius and I. s. fuertesi have diverged in bioclimatic niche space. Peterson et al. (1999) argue that ‘speciation takes place in geographic, not ecological dimensions’; however, our results indicate the collaborative effects of both geography and environment in facilitating rapid changes between taxa.

Our ENM’s largely agree with published breeding ranges for Icterus spurius spurius and I. s. fuertesi (Howell and Webb, 1995; Jaramillo and Burke, 1999). Overprediction in both models is limited and primarily occurs in areas not abutting the known breeding range. The latter indicates suitable habitat for both taxa outside their respective ranges, but historical and geographic factors likely prohibit colonization and use of such areas. Although relatively few specimen records were used for I. s. fuertesi, accurate Maxent models have been calculated using as few as 4–10 records (Hernandez et al., 2006; Pearson et al., 2007; but see Wisz et al., 2008). In addition, restricted ranges, as is the case for I. s. fuertesi, likely improve the accuracy of ecological niche models created using few specimen records (Hernandez et al., 2006). The I. s. spurius range is not generally depicted as extending into Sinaloa and Sonora, Mexico but specimen records from these states suggest that a population exists there. Recent work has shown that I. s. spurius is a migratory double breeder, migrating north from the southern winter range to breeding areas in northern latitudes; and then breeding a second time during southbound migration in these areas of Sinaloa and Sonora before returning to the winter range (Rohwer et al., 2009). The predicted range of I. s. spurius in northwestern Mexico may represent additional suitable habitat for migratory double breeding but further field work would be necessary to substantiate this claim.

Null modeling tests agree with PCA and ENM results while also providing further insight into environmental differences between each subspecies’ range. Background tests suggest
that differences between the ranges are likely a result of available habitat instead of habitat preferences by each subspecies. However, this conclusion is dependent upon what is considered the ‘background’ environment. The background environment is meant to represent the environment in which the taxon’s environmental niche has evolved. In assigning the background environment, we included the area bounded by known localities, a very restrictive assignment. As birds are extremely mobile and migrate thousands of kilometers, our test may have not included the entire background in which the habitat tolerances evolved. More likely, a larger area could be included; but our method provides the most conservative estimate of the background.

It is important to note that differences described here between environmental parameters of subspecies’ breeding ranges, may not indicate real physiological changes—changes in the fundamental niche of each taxon. Because *Icterus spurius spurius* does not co-occur with *I. s. fuertesi* does not mean that it is unable to co-occur with *I. s. fuertesi*. In fact, ENMs of breeding ranges fail to predict the wintering ranges of these taxa, implying quantitative differences between the two seasonal environments that are inhabited and utilized successfully by each taxon. That is, the breeding range of each species does not fully represent the environmental parameters tolerable by each species. While our results can not conclusively argue for changes in actual physiological constraints, similar work concerning the wintering range of Orchard Oriole subspecies may provide additional support for environmental differences between taxa. Common garden experiments would also be useful in determining physiological differences but would be impractical in this system.

The documentation of environmental differences between *Icterus spurius spurius* and *I. s. fuertesi* warrants continued examination of taxonomic ranks in the Orchard Oriole group. Throughout its history of study, the taxonomic rank of *I. s. fuertesi* has been debated (Baker et al., 2003; Kiere et al., 2007). *Icterus spurius fuertesi* was first described as a species by Chapman (1911) based on morphological and breeding range differences but was then lumped with *I. s. spurius* by Blake (1953) and subsequently Graber and Graber (1954) based on alleged, unquantified male color variation (but see Kiere et al., 2007). The presence of environmental differences in the Orchard Oriole group is another piece of evidence relevant to determining taxonomic rank using multiple criteria as described by de Queiroz (1998; 2005). Differences have now been documented in haplotype frequencies, male color, pigment usage and now habitat in the Orchard Oriole group (Baker et al., 2003; Kiere et al., 2007; Hofmann et al., 2007). Ongoing work in our lab examining multiple nuclear loci using coalescent methods could uncover additional evidence of differentiation in the Orchard Oriole group.

Multiple tests for niche differences agree that *Icterus spurius spurius* and *I. s. fuertesi* occupy environmentally different breeding ranges. While our study may not indicate actual physiological changes between taxa, it provides a preliminary analysis of environmental differences between Orchard Oriole subspecies. Our results present a striking contrast to Peterson et al. (1999) and document a likely case of niche lability between very closely related taxa.

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