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INCONSISTENT GEOGRAPHIC VARIATION IN THE CALLS AND DUETS OF BARRED OWLS (*STRIX VARIA*) ACROSS AN AREA OF GENETIC INTROGRESSION

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ABSTRACT.—Much of our understanding of vocal geographic variation in birds is based on the dialects of oscine songbirds that learn their songs. Recent studies have revealed that nonosine vocal behavior is more complex than previously thought, yet we still have a rudimentary understanding of how vocalizations of suboscine and nonpasserine birds are influenced by genetic and geographic variation. We examined geographic variation in male calls, female calls, and duets of Barred Owls (*Strix varia*) among 10 locations across the southeastern United States. Recent molecular work revealed two genetically distinct clades of Barred Owl at either end of our transect, with substantial introgression in between. We predicted that calls would vary with genetic distance in a clinal pattern, but that duets and duetting behavior might exhibit dialects similar to that of learned bird song. Discriminant analysis did not reveal any components of vocalizations or vocal behavior that could be used to assign vocalizations to the correct recording location. There were no relationships between any aspect of vocal structure or behavior and geographic distance. Some characteristics of male and female calls and duets varied among locations, but there was no discernible geographic pattern. We suggest that such inconsistent geographic variation in vocalizations is not unexpected for non-song-learning species. The lack of geographic pattern in vocalizations may be due, in part, to high levels of individual variation, recent signal evolution, and local adaptations. We discuss the application of these results to the ontogeny and evolution of complex, coordinated vocal behavior in nonpasserines. *Received 23 September 2011, accepted 18 April 2012.*

Key words: Barred Owl, duets, geographic variation, signal evolution, *Strix varia*.

Variación Geográfica no Consistente en los Llamados y Duetos de *Strix varia* a través de un Área de Introgresión Genética

RESUMEN.—Buena parte de nuestro entendimiento de la variación geográfica en las vocalizaciones de las aves se basa en los dialectos de aves canoras oscinas que aprenden sus cantos. Estudios recientes han revelado que el comportamiento vocal de las aves no oscinas es más complejo de lo que se pensaba previamente, aunque todavía tenemos un entendimiento rudimentario de cómo las vocalizaciones de aves suboscinas y no paserinas se ven influenciadas por la variación genética y geográfica. Examinamos la variación geográfica en los llamados de machos, llamados de hembras y duetos de *Strix varia* entre 10 localidades a través del sureste de Estados Unidos. Un trabajo molecular reciente reveló que existen dos clados genéticamente distintos de *S. varia* en los extremos de nuestro transecto, con introgresión sustancial en el medio. Predijimos que los llamados debían variar con la distancia genética en un patrón clinal, pero que los duetos y el comportamiento de duetos podría exhibir dialectos similares a los de los cantos de aves que son aprendidos. El análisis discriminante no reveló ningún componente de la vocalización o del comportamiento vocal que pudiera ser usado para asignar vocalizaciones a la localidad de grabación correcta. No hubo relación entre ningún aspecto de la estructura vocal o el comportamiento y la distancia geográfica. Algunas características de los llamados de machos y hembras y de los duetos variaron entre localidades, pero no hubo un patrón geográfico discernible. Sugerimos que tal inconsistencia en la variación geográfica de las vocalizaciones no es inesperada para aves que no aprenden sus cantos. La falta de un patrón geográfico en las vocalizaciones podría deberse, en parte, a altos niveles de variación individual, evolución reciente de la señal y adaptaciones locales. Discutimos la aplicación de estos resultados para comprender la ontogenia y la evolución del comportamiento vocal complejo y coordinado en aves no paserinas.

PATTERNS OF GEOGRAPHIC variation in bird vocalizations can provide insight into the ecology and evolution of animal sounds and vocal behavior (Mundinger 1982, Beecher and Brenowitz 2005, Podos and Warren 2007). Many oscine songbirds exhibit vocal dialects—multiple vocal characteristics are shared among

groups of individuals, with abrupt changes in those characteristics in relation to individuals at other nearby locations (Marler and Tamura 1962; reviewed in Mundinger 1982). These micro-geographic patterns arise mainly from vocal copying and song sharing associated with the process of song learning (i.e., oscine

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Passeriformes, Psittaciformes, and Trochilidae; Munding 1982, Podos and Warren 2007). Conversely, the innate vocalizations of most suboscines and nonpasserines are traditionally understood to exhibit macrogeographic patterns that should match large-scale patterns of genetic variation (Munding 1982, Zink and Remsen 1986). Some research on suboscine and nonpasserine species with presumably innate vocalizations has shown that their calls vary over large geographic scales, which is expected for a genetically controlled trait (Isler et al. 2005, Mager et al. 2007, Nyári 2007). Other studies of non-song-learning suboscine and nonpasserine species reveal more variable, small-scale patterns of variation (Peake and McGregor 1999, Leger and Mountjoy 2003, Saranathan et al. 2007, Fitzsimmons et al. 2008). Although typically not attributed to non-song-learning species, shorter-range or mosaic patterns of geographic variation could easily arise from a variety of genetically associated mechanisms, such as local adaptation, low dispersal, or drift (Podos and Warren 2007). Nevertheless, very few studies on nonoscine species have directly compared vocal and genetic geographic patterns to explore potential deviations between vocal variation and large-scale genetic patterns (exceptions include Isler et al. 2005, Nyári 2007, Saranathan et al. 2007).

Suboscine and nonpasserine birds exhibit a diversity of vocal geographic patterns (e.g., Goldstein 1978, James 1985, Galeotti et al. 1996, Peake and McGregor 1999, Ríos Chelén et al. 2005, Fernández-Juricic et al. 2009). Buff-breasted Flycatchers (*Empidonax fulvifrons*) and Willow Flycatchers (*E. traillii*) both have individually distinctive vocalizations that vary geographically, and similar vocal signatures are often found in the same location (Lein 2008, Fernández-Juricic et al. 2009). Like some song-learning species (Marler and Tamura 1962, Byers 1996), Bright-rumped Attilas (*Attila spadiceus*) exhibit different geographic patterns between their dawn versus daytime song, and Corn Crakes (*Crex crex*) share vocalizations between neighbors at levels greater than expected by chance (Peake and McGregor 1999, Leger and Mountjoy 2003). Blue Petrels (*Halobaena caerulea*), European Storm-Petrels (*Hydrobates pelagicus*), and Manx Shearwaters (*Puffinus puffinus*) have differences in their vocalizations among geographically separated archipelagos, but vocal variation does not necessarily correspond to geographic distance (James 1985, Bretagnolle and Genevois 1997). Tawny Owl (*Strix aluco*) vocalizations differ among genetically distinct subspecies, but they also vary among farmland and woodland habitats (Galeotti et al. 1996, Appleby and Redpath 1997, Brito 2005).

The vocal geographic variation seen in these suboscine and nonpasserine species suggest two patterns of geographic variation that might be expected for innate vocalizations. (1) Innate vocalizations may show clinal variation or other large-scale patterns whereby vocalizations decrease in similarity with increasing geographic distance or with genetic variation over large areas (e.g., Goldstein 1978, Isler et al. 2005, Nyári 2007). (2) Alternatively, innate vocalizations may show diffuse, unpatterned variation, with different vocal features varying among different locations in a way that is not correlated to geographic distance or large-scale genetic variation, but may be related to other short-range genetic differences (e.g., Lindell 1998, Peake and McGregor 1999, Lein 2008). Although the former is traditionally attributed to non-song-learning species, either form of variation could reflect genetic

variation and, therefore, can be expected for the innate vocalizations of suboscines and most nonpasserines. Although some species, such as Variable Antshrikes (*Thamnophilus caerulescens*), show a clinal pattern of vocal variation that corresponds with clinal genetic variation (Brumfield 2005, Isler et al. 2005), certain traits—perhaps especially signals that are important in communication—are susceptible to rapid evolution caused by environmental adaptation, sexual selection, or drift among populations with low gene flow, all of which would lead to haphazard patterns of vocal geographic variation among locations (Podos and Warren 2007). In addition, haphazard vocal variation could also arise because of selection on some other aspect of a bird's phenotype that affects vocal production, without direct selection on the vocalization specifically. For example, Common Loons (*Gavia immer*) in the northwestern United States are smaller than in other parts of their range and have higher-pitched calls (Mager et al. 2007). Whether directly or indirectly selected, recent vocal variation may not be reflected in large-scale genetic geographic patterns, but both forms of vocal variation described above could have a genetic component. Additionally, both types of variation described above should be contrasted with a third pattern: (3) vocalizations may vary according to dialects, as is observed in some song-learning species (Marler and Tamura 1962). Dialects differ from the second pattern we describe because in the case of dialects, multiple vocal features change across the same boundary such that songs from one dialect are recognizably different from the songs at another location (Munding 1982).

In addition to having diverse patterns of vocal geographic variation, many suboscine and nonpasserine birds have surprisingly complex vocalizations (e.g., Trainer et al. 2002; Lovell and Lein 2004a, b; Leger 2005). Many nonoscine species perform complex, coordinated vocal displays with their mates, known as duets (Farabaugh 1982, Malacarne et al. 1999, Hall 2004). Mated pairs of male and female Yellow-naped Parrots (*Amazona auropalliata*) combine their vocalizations into duets that have a specific syntax (Wright and Dahlin 2007), and Barred Owls (*S. varia*) have duet-specific call types that they perform at particular points in the duet (Odom and Mennill 2010a). Because of the precision and complexity of many avian duets, researchers have suggested that duets may require coordination or learning between duet partners (Harcus 1977, Levin 1996, Mann et al. 2009). However, remarkably little attention has been given to patterns of geographic variation in complex vocal behaviors such as duets (exceptions include Trainer and Parsons 2001, Mennill and Rogers 2006), and no studies to date have looked at geographic variation in syntax of duets. Comparing patterns of geographic variation of calls versus duets in species with otherwise innate vocalizations offers an interesting opportunity to explore additional levels of complexity in nonoscine vocalizations, as well as how duets might be coordinated in a species with innate vocalizations.

Barred Owls provide an interesting system for examining vocal variation because they have well-described stereotyped calls, and breeding partners combine their vocalizations into complex duets with distinct male and female components (Odom and Mennill 2010a). We analyzed recordings of Barred Owls in 10 locations along a transect from eastern Texas to southern North Carolina, covering most of the range of the Florida Barred Owl subspecies (*S. v. georgica*; Fig. 1), with our northeastern-most recording

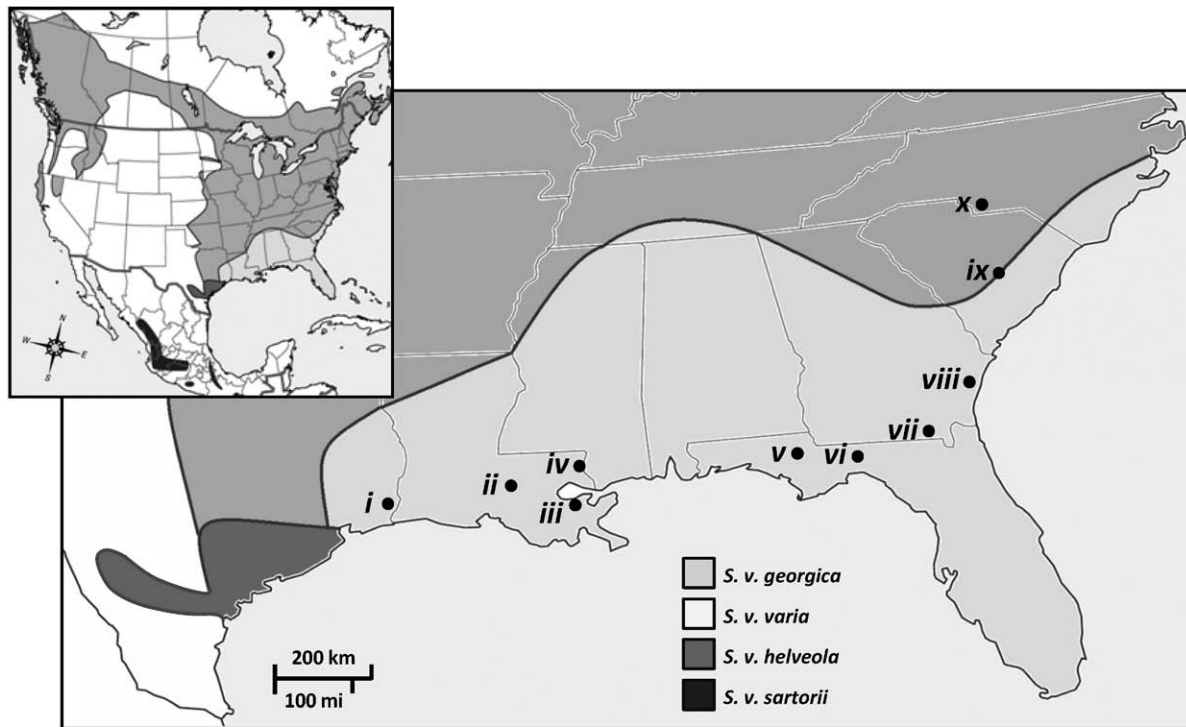


FIG. 1. Map of the range of the Barred Owl (*Strix varia*), showing traditional subspecies boundaries (inset). Ten recording locations through the geographic range of *S. v. georgica* are shown in the expanded section: (i) Big Thicket National Preserve, Texas; (ii) Sherburne Complex Wildlife Management Area, Louisiana; (iii) Barataria Preserve, Louisiana; (iv) Pearl River Wildlife Management Area, Louisiana; (v) Choctawhatchee River Basin, Florida; (vi) Apalachicola National Forest, Florida; (vii) Suwannee River Basin, Georgia; (viii) Harris Neck National Wildlife Refuge, Georgia; (ix) Congaree National Park, South Carolina; and (x) Charlotte, North Carolina. Entire species range boundary is modified from Mazur and James (2000), and subspecies boundaries are based on Bent (1938) and Eckert (1974). Two genetically divergent clades of Barred Owl also exist across the sampled range, with one clade prominent in Texas and the other clade prominent in North Carolina, and substantial introgression in between (Barrowclough et al. 2011).

location falling in the subspecies range of the Northern Barred Owl (*S. v. varia*). Current taxonomic subspecies designations are based on morphology, including overall plumage color, size, and amount of feathering on the toes (Mazur and James 2000). Our transect also crosses a region of genetic introgression (Barrowclough et al. 2011). A recent molecular phylogeographic analysis (Barrowclough et al. 2011) established that two major clades of Barred Owl exist throughout the majority of their range in the United States and Canada. These two clades likely reflect two historically isolated populations in two separate geographic regions. Today, Barred Owls in the south-central United States, including Texas, Kansas, and Tennessee, belong predominantly to one clade, whereas Barred Owls on the east coast from North Carolina to Nova Scotia belong to a separate, divergent clade, with substantial introgression of the two clades throughout the southeastern United States. Our westernmost recording location falls within an area predominated by one clade, while our easternmost recording location falls within the range of the other clade (Fig. 1: populations i and x, respectively), with samples in between crossing the genetically introgressed region.

In the present study, our goal was to examine patterns of vocal geographic variation in the fine structure of the stereotyped male and female calls and complex duets of Barred Owls and

compare this variation with the known pattern of genetic introgression. We also sought to examine the potential for geographic variation in two components of duetting behavior: how frequently do Barred Owls use particular call types within their duets, and how often do Barred Owls transition between particular types of calls within their duets. We evaluated geographic variation in Barred Owl calls, duets, and duetting behavior on the basis of the three possible patterns described above: (1) a dialect-like pattern similar to that seen in many oscine songbirds; (2) a clinal pattern, whereby calls and duets vary with geographic distance; or (3) a haphazard pattern of variation, whereby vocal characteristics show no relationship to geographic distance. Given that the calls of Barred Owls are presumed to be innate, we predicted that geographic variation in calls would vary with the established pattern of genetic introgression (i.e., Barrowclough et al. 2011). Given that vocal duets may require partner-directed learning, we predicted that the coordinated duets and duetting behavior of Barred Owls might exhibit dialects similar to that of learned bird song. Alternatively, a third possibility is that Barred Owl calls and duets could be subject to environmental adaptation or other localized processes, in which case we predicted that Barred Owl calls and duets would vary haphazardly but might show a relationship with characteristics of the recording site.

METHODS

We recorded Barred Owl calls and duets from 10 locations across 5 southeastern states along a 1,350-km transect from eastern Texas to south-central North Carolina (Table 1 and Fig. 1). This transect covered the majority of a single morphological subspecies (*S. v. georgica*; Mazur and James 2000) and the genetically introgressed region described by Barrowclough et al. (2011). We recorded 6 to 11 pairs of Barred Owls at each of the 10 recording locations (Table 1). The majority of these locations were predominantly bottomland hardwood forest, characterized by low to substantial levels of standing water year round and large numbers of Bald Cypress (*Taxodium distichum*). Harris Neck National Wildlife Refuge, Georgia, possessed only small portions of bottomland forest and was otherwise dominated by wax myrtle (*Myrica* spp.), juniper (*Juniperus* spp.), and Virginia Live Oak (*Quercus virginiana*). Owls recorded in Charlotte, North Carolina, were recorded in upland suburbs directly surrounding the city, also dominated by Virginia Live Oak.

We spent 3 to 5 days at each location, recording 6 to 11 pairs per site (Table 1). The majority of recordings were collected between 21 February and 8 April 2008, except in the Choctawhatchee River, where we recorded Barred Owls from 23 January to 15 February 2008 while conducting playback experiments for another study (Odom and Mennill 2010b). February through April in the southeastern United States corresponds to the incubation and early nestling periods of Barred Owls (Mazur and James 2000, K. J. Odom pers. obs.). Barred Owls are nonmigratory, and pairs maintain year-round territories (Mazur and James 2000).

Equipment and Recording Protocol

All Barred Owls were recorded with a Marantz PMD-670 solid-state digital recorder and a Sennhieser ME67 shotgun microphone with K6 power module. Recordings were collected as WAV files at a sampling frequency of 44.1 kHz with 16-bit accuracy. Most recordings were made between 0200 and 0800 hours (in the dark or early twilight of dawn). Less than half of the pairs at Big Thicket, Choctawhatchee, Apalachicola, and Congaree were recorded between 1800 and 2400 hours (twilight of late evening or in the dark). Focal recordings used for analysis were made 10–40 m from the focal pair, but usually at a distance of ~20 m.

Separate pairs were recorded at a distance of ≥ 500 m from other pairs. We considered this distance sufficient to detect separate pairs of Barred Owls in the southeastern United States on the basis of detection of multiple pairs from single recording locations in northwest Florida and radiotelemetry studies that indicated contiguous territories averaging 200 m in diameter in North Carolina (R. Bierregaard, Jr., pers. comm.). Vocalizations of individual Barred Owls have been shown to be spectrographically distinct (Freeman 2000), so we visually inspected spectrographs of individuals that approached from adjacent recording locations. If we doubted that two recordings from adjacent locations were separate pairs, we eliminated one of the recordings from our analyses, resulting in the final sample sizes presented in Table 1.

We solicited calls and duets from all pairs using a standardized playback stimulus consisting of two tracks of common vocalizations: (1) 1 min and 40 s of eight two-phased hoots alternating between male and female, and (2) 3 min of ascending hoots by both males and females (for full description of calls, see Odom and Mennill 2010a). We played track 1 once and track 2 up to three times at a location, with 5 min of silence between playbacks. We stopped playback as soon as individuals responded vocally. If individuals did not respond within 5 min of the end of the third playback of track 2, we moved to a new location. Both playback stimuli were prepared from recordings of mated pairs of wild Barred Owls from the Choctawhatchee River Basin in northwest Florida.

Sound Analysis

Sounds were visualized as spectrograms, and measurements were made using SYRINX-PC (J. Burt, Seattle, Washington; settings: Blackman FFT, transform size 1,024 points, providing an effective time resolution of 1.2 ms and frequency resolution of 43 Hz). To assess vocal variation in call structure, duet structure, and duetting behavior, we measured multiple variables for each of five vocalization types or vocal behaviors (Table 2). These included three fine-structural measurements of calls and duets: structure of male calls, structure of female calls, and structure of duets. We also measured two components of duet behavior: how often specific calls occur within duets (hereafter “call occurrence”), and the frequency with which male and female duet partners transition between specific call types within their duets (hereafter “transition frequencies”).

TABLE 1. Locations and samples sizes for Barred Owl (*Strix varia*) recordings collected throughout the southeastern United States.

Number	Location name	State	County	Pairs(<i>n</i>)
i	Beaumont Unit and John's Lake, Big Thicket National Preserve	Texas	Jefferson and Hardin	9
ii	Sherburne Complex Wildlife Management Area	Louisiana	Pointe Coupee Parish	7
iii	Barataria Preserve, Jean LaFitte National Park	Louisiana	Jefferson Parish	8
iv	Pearl River Wildlife Management Area	Louisiana	St. Tammany Parish	9
v	Choctawhatchee River, Northwest Florida Water Management District	Florida	Holmes, Walton, and Washington	10
vi	Florida and Stix Rivers, Apalachicola National Forest	Florida	Liberty	8
vii	Suwannee River	Georgia	Clinch	10
viii	Harris Neck National Wildlife Refuge	Georgia	MacIntosh	6
ix	Congaree National Park	South Carolina	Richland	11
x	Charlotte	North Carolina	Mecklenburg	6

TABLE 2. Summary of variables measured to assess vocal geographic variation in call structure, duet structure, and duetting behavior of Barred Owls.

Vocal category	Vocalization type or behavior	Number of variables	Variables
Call structure	Male call (gurgle)	5	Number of notes, call duration (s), maximum frequency (F_{\max} ; kHz), minimum frequency (F_{\min} ; kHz), duration of the final note (s)
Call structure	Female call (one-phrased hoot)	5	Number of notes, call duration (s), maximum frequency (F_{\max} ; kHz), minimum frequency (F_{\min} ; kHz), duration of the final note (s)
Duet structure	Duet section (female call + male gurgle + female one-phrased hoot)	6	Number of calls, duration of entire duet (s), start of the first female call to the start of the male gurgle (s), start of the male gurgle to start of the female one-phrased hoot (s), end of the male gurgle to end of the female one-phrased hoot (s), male F_{\max} – female F_{\max} (kHz)
Duet behavior	Call occurrence	11	Numbers of two-phrase hoots, one-phrase hoots, ascending hoots, short ascending hoots, fast ascents, gurgles, mumbles, two-notes, three-notes, other
Duet behavior	Transition frequencies ^a	11	Numbers of ascending hoots to ascending hoots, ascending hoots to gurgles, gurgles to ascending hoots, gurgles to gurgles, gurgles to one-phrased hoots, gurgles to short ascending hoots, one-phrased hoots to gurgles, one-phrased hoots to one-phrased hoots, one-phrased hoots to short ascending hoots, short ascending hoots to gurgles, short ascending hoots to one-phrased hoots

^a Eleven most common transition frequencies used in multivariate comparisons, but all call transition combinations were used to create dissimilarity matrix.

To evaluate male and female call structure, we measured structural features of two types of calls that occur frequently in Barred Owl duets: male gurgle calls and female one-phrased hoots (Fig. 2; Odom and Mennill 2010a). Both calls were isolated from consecutive gurgle to one-phrased hoot transitions within duets. We selected these vocalizations because gurgles and one-phrased hoots are the most common calls and the most common transition within Barred Owl duets (Odom and Mennill 2010a, K. J. Odom and D. J. Mennill unpubl. data), thus providing us with elements that could be measured across all recordings and duets. We counted number of notes and measured call duration, maximum frequency (F_{\max}), minimum frequency (F_{\min}), and duration of the final note for each male gurgle and female one-phrased hoot (Table 2 and Fig. 2).

For duet structure analysis, we counted number of calls within the duet and measured duration of the entire duet. We also measured time delays and frequency differences between the gurgle call, the one-phrased hoot, and the preceding female call. These measures included delay from the start of the first female call to the start of the male gurgle; delay from the start of the male gurgle to the start of the female one-phrased hoot; delay from the end of the male gurgle to the end of the female one-phrased hoot; and the frequency difference between male gurgle F_{\max} and female one-phrased hoot F_{\max} (male F_{\max} – female F_{\max} ; Table 2 and Fig. 2). We selected gurgle to one-phrased hoot duet sections from the first duet in a recording in which the entire duet was of sufficiently high recording quality to allow each call within the duet to be readily identified. We isolated only one gurgle to one-phrased hoot duet section from one duet for each recorded pair. We modified this procedure from Klenova et al. (2008) in order to obtain a comparable section of a duet from each pair. In several locations, gurgle to one-phrase hoot transitions were less common. If we could not find a gurgle to one-phrased hoot transition for a pair, we measured the same variables in the next-most-similar call combination, gurgle to short ascending hoot or gurgle to ascending hoot transitions (call type definitions in Odom and Mennill 2010a).

We examined geographic variation in duetting behavior by counting call occurrence and transition frequencies within duets.

The same duet from each pair used for fine-scale measurements was used in these two analyses. For call occurrence, we counted how often each of 10 common call types occurred within each duet (call descriptions based on Odom and Mennill 2010a). We added any additional rare calls to a category of “other,” for 11 call-occurrence categories in total, covering the range of vocalizations produced by Barred Owls (Odom and Mennill 2010a). For transition frequencies, we sequenced the order of each type of call within duets. We then counted the number of each type of transition within a duet. We analyzed only the 11 most common transitions in our multivariate analyses. We used all possible transitions to create proximity matrices for comparisons to geographic distance. Duets varied in length among pairs, so both call occurrence and transition frequencies were calculated and evaluated as the proportion of calls or transitions in a duet.

Statistical Analysis

We conducted three analyses to assess the patterns of geographic variation in Barred Owl calls and duets laid out by our three predictions. (1) We used canonical discriminant analysis to determine whether calls, duets, and duetting behavior could be assigned to geographic location on the basis of the measurements outlined above. (2) We used Mantel tests to compare geographic distance between recording locations to similarity in calls, duets, and duetting behavior. (3) We used multivariate comparisons (multivariate analysis of variance and log-linear regression) to assess differences in variation within and between all locations for all measured variables for calls, duets, and duetting behavior. For each set of analyses, we tested all five vocalization measurements (male call structure, female call structure, duet structure, call occurrence, and transition frequencies). We compensated for testing all five features of Barred Owl vocalizations by accepting a significance threshold of $P = 0.01$, as determined by Bonferroni correction.

Discriminant analysis.—We conducted discriminant analysis using a cross-validation technique. We constructed discriminant analysis using a randomly selected 80% of the data and then

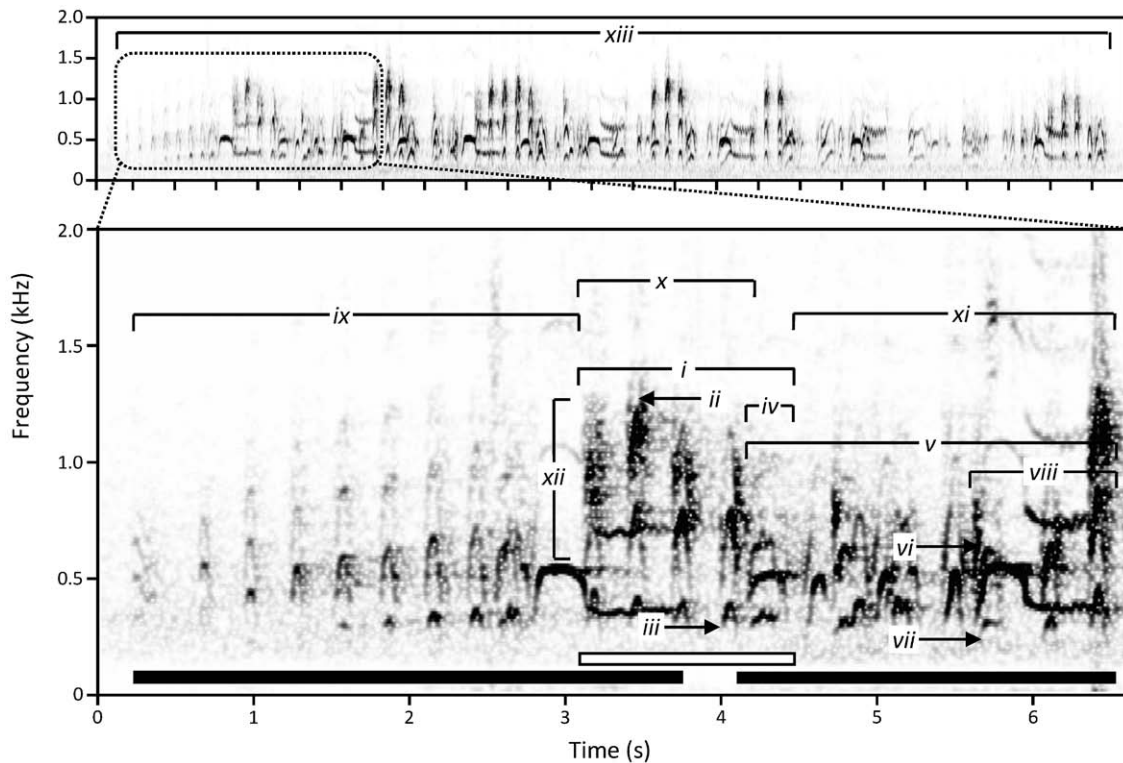


FIG. 2. Top: spectrogram of a Barred Owl duet. Bottom: spectrogram of a portion of a duet, showing structural components measured for a female–male–female gurgle call to one-phrased hoot duet section. Female contributions are underlined in black, and male contributions are underlined in white. Thirteen variables were measured: (i) male call duration, (ii) male call maximum frequency (F_{\max}), (iii) male call minimum frequency (F_{\min}), (iv) male call duration of the final note, (v) female call duration, (vi) female call F_{\max} , (vii) female call F_{\min} , (viii) female call duration of the final note, (ix) start of the first female call to the start of the male gurgle, (x) start of the male gurgle to start of the female one-phrased hoot, (xi) end of the male gurgle to end of the female one-phrased hoot, (xii) male gurgle F_{\max} minus female one-phrased hoot F_{\max} (male F_{\max} – female F_{\max}), and (xiii) duration of the entire duet.

evaluated the predictive ability of the discriminant analysis using the remaining 20% of the data. Correct discrimination was evaluated by a chi-square analysis of known location by the predicted location from the discriminant analysis. We report correct classification as the proportion of the subset of 20% of the data used for validation that was correctly classified to location. Discriminant analysis and chi-square tests were carried out in JMP, version 5.0.1 (SAS Institute, Cary, North Carolina).

Geographic distance, dissimilarity matrices, and Mantel tests.—We used Mantel tests to compare a matrix of geographic distances between each of the recording sites with dissimilarity matrices for each of the five vocal features. We calculated geographic distance using central latitude and longitude coordinates converted from Universal Transverse Mercator coordinates measured at each location with a handheld global positioning system. We calculated distance between each pair of locations in kilometers to create a matrix of geographic distances. Dissimilarity matrices were constructed by between-group linkage using Euclidean distances for male call, female call, and duet fine-scale measurement data sets, such that large values reflected greater differences in vocal characteristics between populations. For call occurrence and transition frequencies, we specified chi-square measures as the data type in place of Euclidean distance to compensate for count data. Fine-scale measurement data were standardized as

Z-scores. All matrices were rescaled to range from zero to 1. Each test included the 10 locations.

If vocalizations and duets varied with geographic distance, we predicted that vocal features would become less similar with geographic distance. Because we compared a distance matrix to dissimilarity matrices, given the above prediction, an increase in geographic distance should correspond to increasing dissimilarity of vocal features. Therefore, we expected positive correlations for each of the Mantel tests. Mantel tests were performed in ISOLATION BY DISTANCE, version 3.16 (Jensen et al. 2005), and dissimilarity matrices were constructed in SPSS, version 17.0 (SPSS, Chicago, Illinois).

Multivariate comparisons.—We used general linear models to compare locations in a multivariate analysis of variance (MANOVA) for both continuous fine-scale measurements and count data. For male call structure, female call structure, and duet structure measurements, we ran three separate multivariate general linear models with all variables specified as dependent and location as a fixed factor. We used repeated-measures general linear models to compare count data of call occurrence and transition frequencies as log-linear regressions on expanded data sets. The data sets for each were structured as contingency tables of presence or absence of each vocalization type or transition for each call or pair of calls within a duet. We specified 11 factors, treating

each of the 11 variables of call type or transitions as a within-subjects factor. Location was specified as an among-subjects factor. All models were run with a full factorial design and type III sum of squares. For tests with significant results, we ran planned post hoc comparisons to evaluate which variables and locations were significantly different. MANOVA and log-linear regression were conducted in SPSS.

RESULTS

Discriminant function analysis.—No aspects of Barred Owl calls or duets could be used to assign recorded vocalizations to the correct recording location using a multivariate discriminant analysis with cross-validation. This analysis could not correctly classify male or female calls to location better than expected by chance; only 6.3% of male calls ($\chi^2 = 44.0, P = 0.88, n = 16$) and 20.0% of female calls ($\chi^2 = 47.6, P = 0.93, n = 15$) were correctly classified on the basis of fine-scale measurements. Fine-scale measurements of duets also could not be used to assign the correct recording location, with only 25.0% of duets classified to the correct location ($\chi^2 = 45.6, P = 0.84, n = 16$). Call occurrence and transition frequencies could not be used to assign the correct recording location either, with only 23.5% ($\chi^2 = 52.3, P = 0.96, n = 17$) and 25.0% ($\chi^2 = 41.2, P = 0.93, n = 16$) of duets assigned to the correct location, respectively. There was substantial overlap among the 95% confidence intervals for nearly all locations for all comparisons, shown by the initial discriminant analysis using 80% of each data set. Therefore, none of the variables we measured appeared to show a signature of where they were recorded.

Geographic distance.—Variation in Barred Owl calls, duets, and duetting behavior was not related to geographic distance. Similarity in the fine structure of male calls and female calls showed no relationship with geographic distance (Mantel test: males, $r = -0.11, P = 0.74, n = 10$ locations; females, $r = 0.13, P = 0.19, n = 10$ locations). Duet structure was not related to geographic distance ($r = -0.27, P = 0.96, n = 10$ locations). Lastly, neither aspect of duet behavior was significantly related to geographic distance (transition frequencies: $r = -0.05, P = 0.54, n = 10$ locations; call occurrence: $r = -0.26, P = 0.96, n = 10$ locations).

Multivariate comparisons.—Barred Owl calls and duetting behavior varied among locations, but there was no discernible geographic pattern to this variation (Figs. 3 and 4). Male calls varied significantly among locations (MANOVA: $F = 1.8, df = 45$ and $307, P = 0.002$), a pattern driven by significantly fewer notes in calls given at site iii than at site vii and significantly higher minimum frequencies at site iv than at sites vi, vii, viii, or ix (Fig. 3A, B). Females gave significantly shorter calls at sites vi and vii than at site viii ($F = 1.8, df = 45$ and $303, P = 0.002$; Fig. 3C). Duet structure varied among locations, but not significantly after corrections for multiple comparisons ($F = 1.4, df = 54$ and $336, P = 0.05$).

Duetting behavior varied among locations across several variables, but, as with our analysis of solo vocalizations, there was no discernible geographic pattern (Fig. 4). Call use within duets differed significantly among locations (log-linear regression: $F = 2.6, df = 9, P = 0.005$). At site iv, Barred Owls gave more two-phrased hoots (Fig. 4A), and at site vi, they gave more three-note calls (Fig. 4B) than at most other locations. Barred Owls also gave fewer short ascending hoots at site iv than at site x, more one-phrased hoots at site vii than at sites viii and x, and more fast

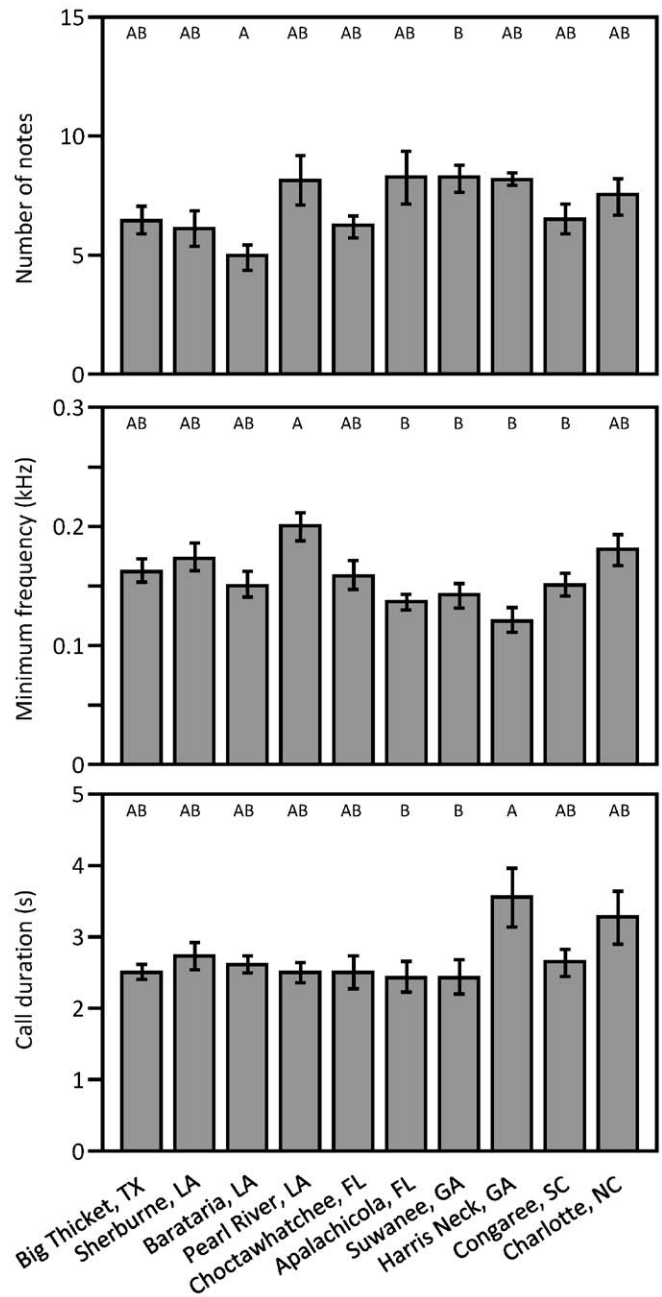


FIG. 3. Comparisons of Barred Owl calls among 10 locations throughout the southeastern United States based on fine-structural features of the number of notes of male calls, minimum frequency of male calls, and female call duration. Error bars represent standard error. Letters above the bars indicate statistical significance; sites that are not connected by the same letter are statistically different.

ascents at site ii than at most other locations. Transition frequencies of Barred Owl duets also varied significantly among locations ($F = 2.8, df = 9, P = 0.003$), with individuals at site vi performing more ascending hoot to ascending hoot combinations than at site ix and individuals at site x gave fewer one-phrased hoot to gurgle transitions than at sites iv and vii.

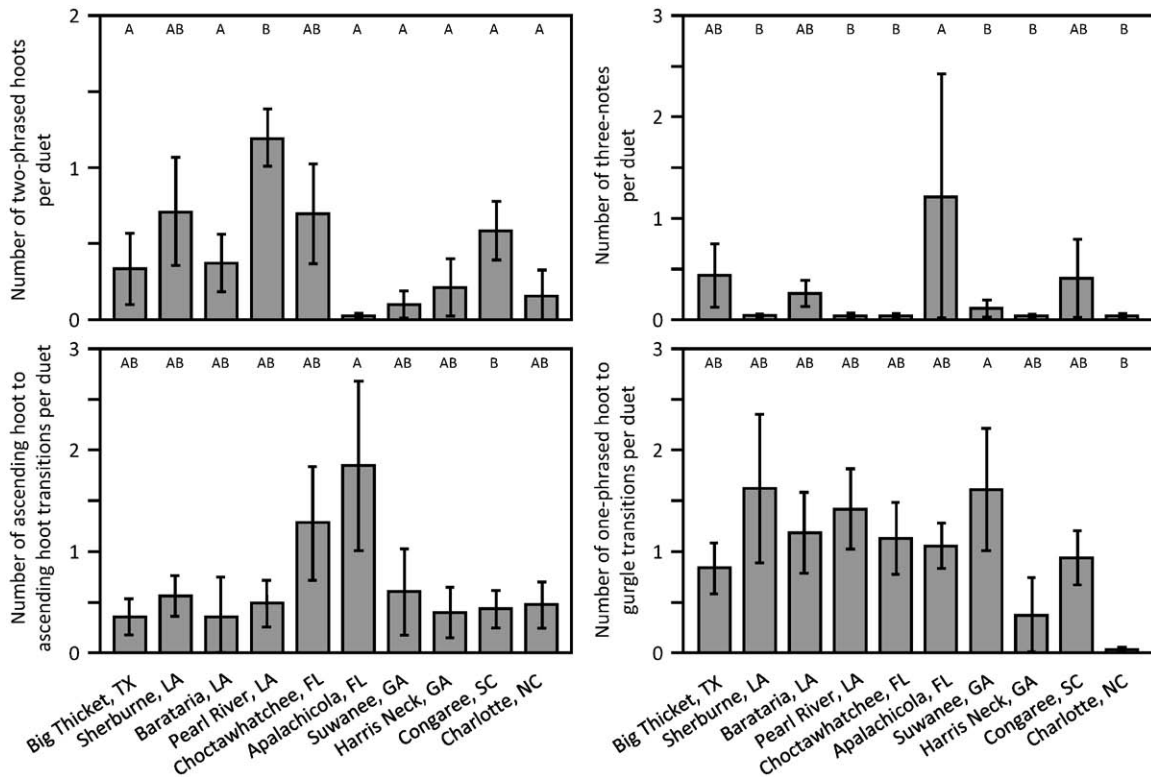


FIG. 4. Comparisons of Barred Owl calls among 10 locations throughout the southeastern United States based on call occurrence of two-phrased hoots and three-note calls, and transition frequencies between ascending hoots to ascending hoots and one-phrased hoots to gurgles. Error bars represent standard error. Letters above the bars indicate statistical significance; sites that are not connected by the same letter are statistically different.

DISCUSSION

Barred Owl calls, duets, and duetting behavior did not show a clinal or dialect-based pattern of geographic variation throughout a 1,350-km transect across the southeastern United States. No measured details of vocalizations or vocal behavior could be used to assign recordings to the correct location following discriminant analysis. No aspects of call structure, duet structure, or duetting behavior showed any relationship with geographic distance. There was some statistical variation among locations for call structure and duetting behavior; however, the locations that showed variation were not consistent across different variables. Our analysis of Barred Owl vocalizations and vocal behavior suggests that geographic variation in this species is haphazard. The pattern that we found does not match the clinal or macrogeographic pattern typically expected for an innate trait (Mundinger 1982), the genetic variation observed by Barrowclough et al. (2011), or dialect-like patterns common in learned traits (Marler and Tamura 1962). We suggest that the haphazard, inconsistent vocal variation that we observed in Barred Owl calls and duets is not unexpected for innate vocalizations of non-song-learning suboscine and nonpasserine species.

Vocal variation can result from selective pressures acting directly on vocalizations, such as habitat differences leading to acoustic adaptation, morphological adaptations that influence sound production, or drift (Galeotti et al. 1996, Mager et al. 2007;

reviewed in Podos and Warren 2007). The effects of these mechanisms have most notably been studied in the culturally transmitted songs of songbirds (Handford and Loughheed 1991, Podos 2001, Podos and Warren 2007). In songbirds and other song-learning species, vocalizations often show pronounced microgeographic dialect boundaries (Marler and Tamura 1962, Mundinger 1982). Yet adaptation of vocalizations or morphological features to local environments could lead to microgeographic variation in non-song-learning species as well. We suggest that this variation may be more haphazard in species with innate vocalizations, however, because these species lack song-copying and assortative mating that might reinforce dialect boundaries (Mundinger 1982). Below, we offer several explanations for the haphazard geographic variation that we detected in Barred Owls, including habitat differences, high levels of individual variation, and recent signal evolution coupled with local adaptation.

Some of the differences among locations could be attributed to habitat differences. Our recording locations included two upland sites: Harris Neck National Wildlife Refuge, Georgia (site viii), and Charlotte, North Carolina (site x). The eight remaining locations were similar in habitat, dominated by bottomland hardwood forest. Some geographic differences were associated with these sites (e.g., call duration in males was greater at Harris Neck, a higher-elevation site, than at two of the lowland sites, and the number of one-phrased-hoot to gurgle transitions was significantly lower in Charlotte, a higher-elevation site, than at the

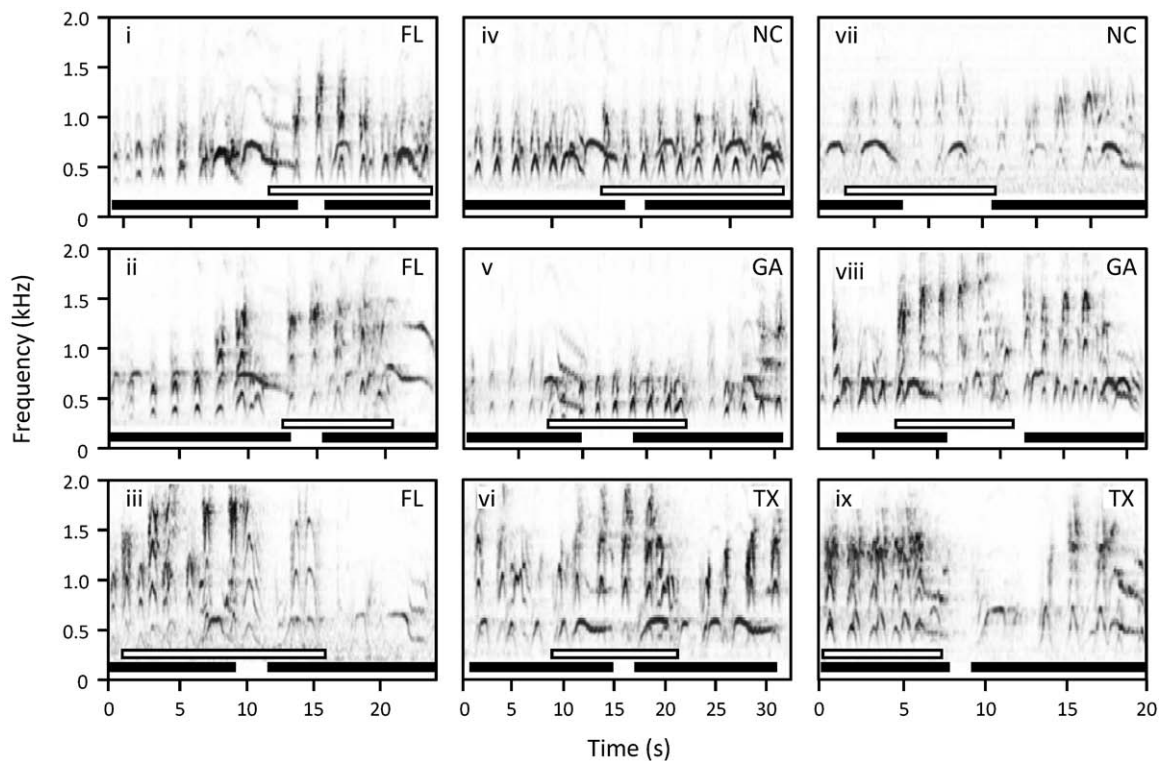


FIG. 5. Spectrographs of Barred Owl female-male-female gurgle to one-phrased hoot duet sections from the Choctawhatchee River, Florida (i-iii); Charlotte, North Carolina (iv and vii); Suwannee River, Georgia (v and viii); and Big Thicket Preserve, Texas (vi and ix). Time delays within duets (indicated by underlines: female = black; male = gray) at a single location can be very similar (i versus ii) or different (i versus iii). Comparatively, time delays between locations can be equally similar (i versus iv, or v versus vi) or different (iv, v, and vi versus vii, viii, and ix).

two lowland sites). However, less than one-third of the sites where significant differences were detected by MANOVA occurred between solely upland and lowland sites. In addition, no differences were observed between the two upland sites together versus the lowland sites, which suggests that these differences were not driven solely by upland-versus-lowland differences.

Barred Owls have individually distinct vocalizations that can be readily visually identified by spectrographs (Freeman 2000). We noticed obvious spectrographic differences among individuals within each location in our study as well. Duet structure and syntax were highly variable even among pairs from the same location (Fig. 5). We sampled only one call or duet per individual. Thus, high inter- and intra-individual variation may have prevented us from detecting a genetically linked macrogeographic pattern, if one exists. Nevertheless, high individual variability was revealed statistically by the large dispersion of points, by large, overlapping 95% confidence intervals in discriminant analysis, and by large error bars among MANOVA values for many measurements, particularly for duets and duetting behavior. Moreover, we observed duets of individuals from different populations that had equal or similar timing between calls but were very different in timing compared with individuals from their own population (Fig. 5). Our previous work with Barred Owls indicated that their duets vary drastically from bout to bout even within a pair (Odom and Mennill 2010b, K. J. Odom and D. J. Mennill unpubl. data).

Therefore, we suggest that high vocal variability across Barred Owl populations may have prevented us from detecting a pattern. High vocal variability may actually reduce vocal differentiation among geographically separated locations because all locations have large amounts of variation encompassing the same range of variants (Fig. 5).

Genetic change associated with recent signal divergence among populations is difficult to detect (Zink 2004, Ekblom and Galindo 2011). Traditional phylogeographic methods may not reveal recent evolution because of the time required for accumulation of mutations used for phylogenetic reconstruction based on neutral nuclear and mitochondrial markers (Crandall et al. 2000, Zink 2004). Researchers have found little support for morphologically based subspecies designations, perhaps partly because of this discrepancy (Zink 1996, 2004; Soltis et al. 2006). In fact, few avian phylogeographic studies have revealed any phylogenetic structure across large portions of North America (Zink 1996, Zink et al. 2004). In the southeastern United States, Yellow-throated Warblers (*Setophaga dominica*), for example, show little evidence of genetic differentiation but exhibit a clinal relationship in plumage coloration and bill size (McKay 2008, 2009). By contrast, a distinct genetic split occurs in the Carolina Chickadee (*Poecile carolinensis*) across the Tombigbee River in Alabama, but there is no noticeable corresponding change in plumage or vocal characteristics (Ward 1966, Gill et al. 1999).

Recent research reveals two genetically distinct clades of Barred Owl that arose as a result of isolation during Pleistocene glaciations, with subsequent introgression (Barrowclough et al. 2011). This isolation event is one possible source of variation in Barred Owl vocalizations, but many other selective pressures could have acted on the vocalizations of Barred Owls since their isolation and recolonization (Mayr 1956, Podos and Warren 2007). We suggest that the lack of any clear geographic pattern in the calls and duets of Barred Owls may be influenced by recent vocal changes, including local adaptation, either direct (e.g., habitat differences) or indirect (e.g., morphological or genetic differences that affect vocal production), as well as individual variation. Some recent genetic variation could potentially be detected using multiple molecular markers, including microsatellite markers. However, geographic variation in morphological features likely corresponds to selection or variation at specific loci, and we have only just begun to develop techniques to measure such variation (Eklom and Galindo 2011).

Our study is one of the first to examine vocal variation in a nonpasserine across an area of known genetic introgression. Although the haphazard vocal variation that we observed differs from the clinal or macrogeographic pattern usually expected for innate vocalizations (Mundinger 1982, Isler et al. 2005), many studies show alternative, localized geographic patterns in subsocial and nonpasserine species (Lindell 1998, Peake and McGregor 1999, Fernández-Juricic et al. 2009). More research on vocal variation in a diversity of subsocial and nonpasserine species across subspecies boundaries and areas of genetic introgression will help verify the potential for both patterns. Although difficult, future research that directly compares the amount of vocal and genetic variation in the same individuals will have the greatest ability to tease apart the relationships between genes and vocalizations.

Lastly, vocal geographic variation has been used as a tool for examining vocal learning in songs of a subsocial (Saranathan et al. 2007). We suggest that it may also be useful to explore learning of complex vocalizations and vocal behaviors, such as duets. Mennill and Rogers (2006) found that the female contributions to the duets of Eastern Whipbirds (*Psophodes olivaceus*) varied across the species' range, whereas male contributions were highly stereotyped across the range, suggesting different selection pressures on males versus females in a song-learning species. On the other hand, Trainer and Parsons (2001) found no geographic variation among three locations in the male–male duets of the subsocial Long-tailed Manakin (*Chiroxiphia linearis*). We suggest that the haphazard, inconsistent geographic variation in Barred Owl call structure, duet structure, and duetting behavior indicates that all aspects of vocalizations and vocal behavior are innate in Barred Owls. Nevertheless, evidence is accumulating that vocal learning is more widespread and plastic than originally thought (Brenowitz and Beecher 2005, Saranathan et al. 2007). More attention should be paid to vocal ontogeny in a diversity of vocalization types and behaviors. We encourage continued research on vocal geographic variation of subsocials and nonpasserines, particularly of complex, coordinated vocalizations, such as duets.

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