

Environmental variability and acoustic signals: a multi-level approach in songbirds

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Among songbirds, growing evidence suggests that acoustic adaptation of song traits occurs in response to habitat features. Despite extensive study, most research supporting acoustic adaptation has only considered acoustic traits averaged for species or populations, overlooking intraindividual variation of song traits, which may facilitate effective communication in heterogeneous and variable environments. Fewer studies have explicitly incorporated sexual selection, which, if strong, may favour variation across environments. Here, we evaluate the prevalence of acoustic adaptation among 44 species of songbirds by determining how environmental variability and sexual selection intensity are associated with song variability (intraindividual and intraspecific) and short-term song complexity. We show that variability in precipitation can explain short-term song complexity among taxonomically diverse songbirds, and that precipitation seasonality and the intensity of sexual selection are related to intraindividual song variation. Our results link song complexity to environmental variability, something previously found for mockingbirds (Family Mimidae). Perhaps more importantly, our results illustrate that individual variation in song traits may be shaped by both environmental variability and strength of sexual selection.

Keywords: acoustic adaptation; birdsong; environmental variability; selection; sensory drive; song variation

1. INTRODUCTION

The sensory drive hypothesis predicts that signals associated with mate choice should evolve to maximize conspicuousness relative to other stimuli, especially for species where sexual selection is intense [1]. For acoustic mating signals, adaptive signal evolution in response to local habitat features has often been referred to as the acoustic adaptation hypothesis and is well documented in birds [2,3]. Evidence for acoustic adaptation has typically been restricted to comparisons between strongly dissimilar habitats [2], often without considering a key aspect of the sensory drive hypotheses: the strength of sexual selection [2,3], which, when strong, should favour song traits that are more readily perceived by

females for mate-choice criteria [1]. Additionally, most studies have used acoustic traits (e.g. frequency, song length) averaged per population or species, but recent studies show that signal variation at the level of the individual can also be important for acoustic communication in a variety of environments [4–7].

Whether selection via sensory drive may also explain intraindividual signal variation is unknown, but such variability may facilitate communication for individuals exposed to heterogeneous environments and may facilitate signal variation among individuals or populations inhabiting distinctly different environments (figure 1a). Although not all species appear capable of adjusting signals to changing environmental conditions [4], intraindividual song variability may be used to maximize signal transmission in variable environmental conditions, such as in response to seasonal changes or urban noise [5]. In contrast, intraspecific variation via adaptation to local conditions may be most common when species have large geographical ranges or if sexual selection is especially strong [8]. Still, it remains to be seen whether such variation is consistently associated with variation in particular environmental variables.

Here, we examine the ubiquity of the sensory drive hypothesis by determining how spatial and temporal variation in environmental factors (representative of habitat structure) and sexual selection are associated with the evolution of individual and species-level song variation in songbirds (figure 1b). Additionally, given previously reported relationships between environmental factors and song complexity [9], we also examine the roles of environment and sexual selection in explaining short-term song complexity and test for relationships between short-term song complexity and song repertoire size, a measure of long-term complexity.

2. MATERIAL AND METHODS

We analysed recordings of songs from 429 individuals from 44 North American passerine species (mean number of individuals per species: $n = 9.720$, s.e. = 0.042, range: 6–10). We chose taxonomically diverse pairs of species in the same genus with different range sizes and environmental requirements (see electronic supplementary material). We used high-quality recordings from audio archives (xeno-canto.org; macaulaylibrary.org) that contained five or more songs and strove to use recordings from throughout each species' range.

We measured song characteristics of five randomly selected songs per recording. We measured peak, minimum and maximum frequency (kHz), song length (s), duration of syllables (s) and the intervals between them (s). Peak frequency was measured automatically in RAVENPRO v. 1.4 and minimum and maximum frequency were measured using a threshold of –30 dB relative to the peak frequency (see electronic supplementary material, figure S1). For short-term song complexity, we used number of unique notes divided by total number of notes, number of repeated syllables divided by total number of syllables per song and the number of different song types sampled and the presence or absence of harmonics per recording.

We reduced the song data dimensionality using principal components analysis (PCA) for measures of song complexity, and intraspecific and intraindividual variation. We reduced the four complexity measures to a single component representative of song complexity ($PC_{\text{complexity}}$, 48.54% of variance, electronic supplementary material, table S1), which was positively related to the proportion of unique notes (loading: 0.68) and negatively related to the proportion of repeated syllables (–0.67).

For intraspecific song variation, we calculated mean values per individual for eight spectral and temporal variables, and then calculated the coefficient of variation (CV) among individuals. Dimension reduction resulted in a single $PC_{\text{intraspecific}}$ (35.15%) with strong positive loadings for spectral and temporal variables (see electronic supplementary material, table S2).

For intraindividual song variation, we calculated the CV for each spectral and temporal variable from five songs per individual, and then calculated a mean intraindividual CV per species. This value

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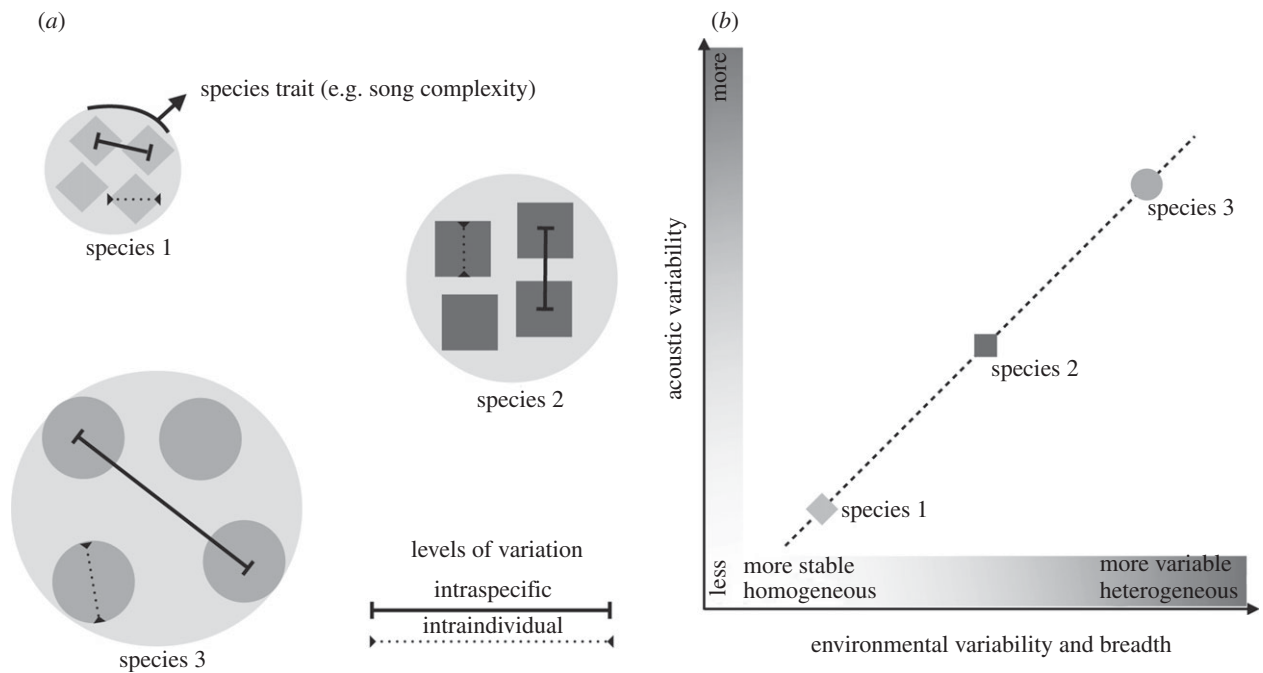


Figure 1. Predicted relationship between song variation and environmental factors. (a) Symbols represent individuals from species 1–3, each of which occupies a different ecological and hence acoustic environment. Arrows depict the levels of variation assessed in the study (but not song complexity). (b) Predicted relationship between environmental variability and intraindividual and intraspecific signal variation.

was divided by total number of song types per recording, providing a measure of intraindividual trait variation independent of song type number. Following the PCA, we obtained a single $PC_{\text{intraindividual}}$ (33%) with strong positive loadings from spectral and temporal variables (see electronic supplementary material, table S3).

From GIS shapefiles [10] of each species' range, we measured breeding range area and latitudinal mean, an oft-used index of sexual selection. We also measured temperature and precipitation seasonality and mean temperature and precipitation of the warmest quarter (corresponding with the breeding season) [11]. Temperature and precipitation can determine physiological limitations for birds but are also highly related to habitat structure (see electronic supplementary material, figure S2) and vegetation density [12]; therefore, they are associated with the acoustic environment and can serve as a proxy to understand song evolution. Corresponding with the breeding season, we calculated the CV for mean temperature and precipitation of the warmest quarter across each species range to reflect spatial variation in temperature (CV_T) and precipitation (CV_P), respectively, and the mean of temperature and precipitation seasonality.

Given the importance of sexual selection in promoting signal divergence [1,3], we used an index of colour dimorphism to represent sexual selection intensity for each species following Owen & Bennett's [13] protocol using drawings from Dunn *et al.* [14]. From *Birds of North America* [15], we collected repertoire size and habitat requirements (closed, mixed or open vegetation), plus migratory status because sexual selection may be more intense in migratory species [16].

We used phylogenetic generalized least-squares regression models to evaluate the influence of area, mean latitude, CV_P , CV_T , precipitation seasonality, temperature seasonality, habitat, colour dimorphism and migratory behaviour on song variation and song complexity. For each model, we estimated λ to account for phylogenetic relationships among species [17]. Higher λ -values indicate greater similarity in the relationship between predictor and response variables for closely related taxa; and when λ equals zero, the relationship between predictor and response variables is unrelated to phylogeny. For model selection, we dropped each non-significant term individually based on the highest p -value until only significant terms remained. The phylogenetic hypothesis used in all analyses was based on Barker *et al.* [18], upon which we added species that were not included using additional phylogenies (see electronic supplementary material, figure S3). Because the phylogeny was based on several sources, branch lengths were set such that node depth was proportional to number of taxa in a clade minus one [19]. All analyses were completed in R (r-project.org; electronic

supplementary material) and the data used for these analyses have been deposited at Dryad (www.datadryad.org; doi:10.5061/dryad.cj27s).

3. RESULTS

At the species level, only CV_P ($\beta = 1.826 \pm 0.855$ s.e.) was positively related to $PC_{\text{complexity}}$ (final model, $\lambda = 0.611$, $F_{2,42} = 4.561$, $r^2 = 0.076$, $p = 0.016$; figure 2a). None of the predictor variables explained intraspecific song variation, but intraindividual song variation was positively related to precipitation seasonality ($\beta_{\text{precip}} = 0.025 \pm 0.009$ s.e.; figure 2b) and colour dimorphism ($\beta_{\text{dimorph}} = 0.111 \pm 0.038$ s.e.; final model, $\lambda = 0$, $F_{3,41} = 9.211$, $r^2 = 0.276$, $p < 0.001$; figure 2c). Neither complexity nor either measure of song variation was related to repertoire size (all $p > 0.23$, electronic supplementary material, figure S4).

4. DISCUSSION

Our results enhance knowledge of how the environment shapes song traits [3,5], but placed within a framework that also evaluates the relative role of sexual selection. Temporal and geographical variation in precipitation had more influence on song traits than temperature, perhaps owing to its importance in determining regional and temporal variation in vegetation density [12], a feature known to influence song traits [3]. We found that songs were more complex for species that experience different precipitation regimes across their ranges. A similar pattern was found in mockingbirds (family Mimidae) where song complexity is positively related to climatic variability, including variation in precipitation [9]. Environmental conditions that are limiting or variable may also lead to

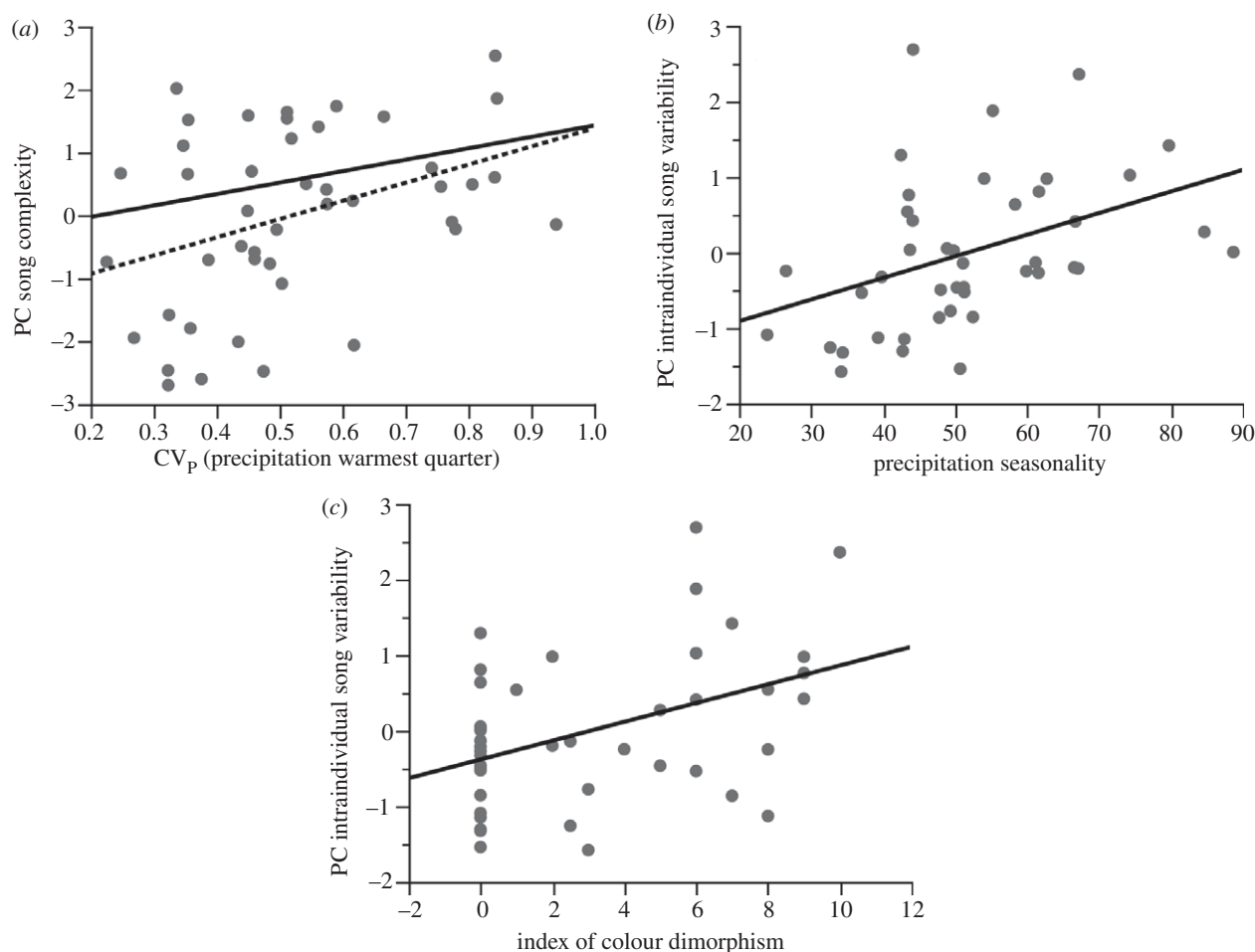


Figure 2. (a) Relationship between spatial variability in precipitation and song complexity. Solid and dashed lines represent regression slopes with ($\lambda = 0.547$) and without ($\lambda = 0$) phylogenetic correction, respectively. (b) Positive relationship between precipitation seasonality and intraindividual song variability. (c) Positive relationship between sexual dichromatism and intraindividual song variability.

intense sexual selection, favouring song elaboration [20]. However, because short-term song complexity and three sexual selection indexes (sexual dichromatism, latitude and migration) were unrelated; short-term song complexity in variable environments may not necessarily reflect a response to intense sexual selection. Alternatively, this may be a by-product of selection for innovation and cognition [9], but additional work is needed to clarify the precise sources of selection.

Despite considerable evidence for signal adaptation to different habitats as gauged through their averaged values [2,3], no variables explained intraspecific song variability that would reflect local adaptation to environmental conditions. In contrast, because environmental seasonality explained intraindividual song variation, selection may favour song variability to cope with different acoustic environments that an individual encounters throughout its life or even shorter timescales such as a single breeding season or day. Recent findings suggest that birds and frogs may adjust their signals immediately in response to increase in background noise or structural habitat changes, respectively [6,7]. Coupled with our results, these studies suggest that individual song variation, rather than a restricted set of traits, may be adaptive and represent a key aspect to understanding signal evolution in response to various sources of selection.

Acoustic adaptation may explain high intraindividual variability in more seasonal environments; however, the sensory drive hypothesis explicitly suggests that sexual selection should be the operating force favouring signals that transmit well for a variety of environments [1]. We found a significant relationship between one index of sexual selection intensity (sexual dichromatism) and intraindividual song variability. Importantly, sexual dichromatism and precipitation seasonality are unrelated ($\lambda = 0.738$, $p = 0.454$), suggesting that both high environmental variation and intense sexual selection favour increased intraindividual variability. Taken together, these results suggest that sensory drive may promote signal variation at the level of the individual.

These findings illustrate that acoustic adaptation to environmental heterogeneity is prevalent across taxonomically diverse songbirds and operates at different levels of variation: species-level song complexity and increased intraindividual variability. Moreover, we provide evidence that sensory drive may be important in maintaining song variability at the individual level, something often overlooked in this type of study, but a promising avenue for future investigations.

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