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Subspecies status and methods explain strength of response to local versus foreign song by oscine birds in meta-analysis

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To understand the implications of geographical variation in vocal culture in songbirds, researchers have often compared territorial responses to playback of local songs versus responses to playback of songs from 'foreign' conspecifics. This body of work has the potential to help us move towards a general understanding of factors driving divergence in signal recognition. We conducted a systematic review and meta-analysis of 57 playback studies to explain variation in strength of response to local versus foreign songs. Studies with incomplete reporting of results had elevated effects due to selective reporting. Studies that used small numbers of stimuli as exemplars (pseudoreplication) had more variable effects than studies without severe pseudoreplication. Whether or not we controlled for pseudoreplication, we found greater response to playback of local song than to foreign song. In investigating potential biological drivers of the variation in strength of experimental effects, we found that the difference in territorial response to local versus foreign song was stronger if the foreign song was recorded from another subspecies than if the foreign song was recorded from the same subspecies as the focal individuals. Indexes of risk of accidental response to heterospecific song did not coherently explain response to foreign conspecific songs, nor did factors expected to influence individual experience with foreign conspecific songs. Thus, although oscine songbirds clearly react more aggressively to local song than to foreign song and variation in the strength of this effect is influenced by methodological choices and subspecies status, considerable variation in the strength of response to local versus foreign song playback remains to be explained.

Understanding the factors influencing receiver response to conspecific signals has long been a major part of behavioural research (Wiley, 1983). Response to conspecific signals is especially interesting when these signals differ geographically (e.g. Danner et al., 2011; Searcy & Andersson, 1986). Geographical variation in vocal signals is common and is often particularly striking in the oscine songbirds thanks to learning from local conspecifics (Beecher & Brenowitz, 2005). In songbirds, receiver responses to geographically variable vocal signals have been studied for decades with song playback experiments in which focal territorial individuals are played either local or foreign song. In such playback experiments, it seems that the most common result is for the territorial individual to respond more strongly to playback of the local song than to playback of the foreign song (e.g. Bradley, Molles, & Waas, 2013; Lemon, 1967; McGregor, 1983; Podos, 2007), although this has never been quantified. However, these playback experiments (Appendix, Table A1) reveal substantial variability in response to foreign and local song as measured in hundreds of statistical tests from dozens of species and populations studied around the world (Parker, Greig, Nakagawa, Parra, & Dalisio, 2018). Thus, these experiments are an excellent resource for seeking to understand variability in response to geographically divergent signals. Explanations for this variability might plausibly come from a combination of evolutionary and developmental processes and from methodological differences among studies.

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One possible explanation for variable response to foreign playback is rooted in signalling theory, which predicts that receivers should evolve to respond to signallers with whom they interact and whose signals convey relevant information while simultaneously avoiding response to irrelevant signallers with whom they do not interact (Wiley, 1994). Relevant interactions often involve mate attraction or competition with conspecifics, so an important axis of discrimination will be between conspecifics and heterospecifics (Amézquita, Flechas, Lima, Gasser, & Hödl, 2011). Any receiver can be imagined to have a degree of permissiveness for what it will consider relevant in any given context, and with respect to recognizing mates and competitors we can think of this permissiveness as a 'window of recognition' (Hudson & Price, 2014). The boundaries of the window of recognition for conspecifics should depend in part on the acoustic environment created by the singing of heterospecifics. Most songbirds probably face selection to avoid responding to heterospecific songs without reducing response to conspecifics (e.g. Shizuka, 2014) as appears to be the case in other taxa (Amézquita et al., 2011; Symes, 2014). This selection may be stronger in the presence of more species or of more closely related species (Hamao, 2016). Thus, selection to discriminate between conspecific and heterospecific song might plausibly narrow the window of conspecific recognition and thus as a by-product reduce response to foreign conspecific song.

Although this variation in the signalling environment may drive the evolution of divergent patterns of discrimination against foreign conspecific song, variation in song discrimination could also emerge as a plastic developmental response to individual experience. For instance, interaction with individuals from other conspecific vocal cultures could serve to broaden what is recognized as a conspecific song (Wright & Dorin, 2001). Such interactions could occur in any number of scenarios, but might be more likely in migratory populations or in populations in which individuals often disperse across cultural boundaries or gradients (Colbeck, Sillett, & Webster, 2010).

Another possibility is that evolutionary divergence of populations leads to divergent signals and divergent signal recognition. This hypothesis seems likely to be true especially given that even naïve juveniles may preferentially learn songs of their own subspecies over conspecific song from other subspecies (Nelson, 2000). Stronger response to song from the local subspecies has received some support (Alström & Olsson, 1999; Petrinovich, 1981; Turcokova, Pavel, Chutny, Petrusek, & Petruskova, 2011), but is sometimes contradicted (Tietze, Wassmann, & Martens, 2012). However, divergence of response to song has itself been used as evidence of evolutionary divergence (Freeman & Montgomery, 2017; Randler et al., 2012).

Although biological hypotheses may explain variability in response to foreign and local songs, it is also likely that various methodological differences among playback studies have influenced the distribution of published effects. Of particular interest in playback studies is the effect of pseudoreplication of song stimuli, in which a relatively small number of distinct stimuli are used in a larger number of trials. When the number of stimuli is smaller than that number of otherwise independent trials, trials with the same stimulus are not true independent replicates (Kroodsma, 1989). This form of pseudoreplication has become less common since it was first identified in the song playback literature (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001), but it characterizes nearly all of the early song playback literature and some more recent papers as well (Supplementary Fig. S1). One way to think about the problem with this sort of pseudoreplication is that as the number of stimuli declines, the probability that the chosen stimuli reliably represent the distribution of stimuli in the population from which they are drawn also declines. In the extreme case, it is easy to see that a single recording of a single individual might tend to induce a weaker or a stronger response in playback trials than the average response from a series of stimuli recorded from multiple individuals. In other words, pseudoreplicated studies should produce more variable and thus less reliable results than those from studies in which different stimuli were used for each trial. However, this hypothesis has never been tested empirically.

We used meta-analysis of published studies (Appendix, Table A1) of response to playback by oscine birds to assess several hypotheses about the determinants of signal recognition. Before testing our primary biological hypotheses, we tested several hypotheses that might explain variation in effect size as a function of the methods of the original study, including whether or not the original study suffered from pseudoreplication. We explored three potential biological explanations for variation in effect size. Our first such hypothesis was that the risk of accidentally responding to heterospecifics drives increased discrimination against foreign conspecifics. If this mechanism were operating, then we expected greater difference in response (i.e. reduced response to foreign song relative to local song) at sites with congeners or confamilials present, or at sites expected to have higher songbird species diversity overall. Our second biological hypothesis was that individual experience drives discrimination, either due to direct experience with particular songs or experience with a diversity of conspecific song types. If this mechanism were operating, then we expected birds that move longer distances during their lifetime to be more likely to respond to foreign songs than more sedentary birds, birds being played foreign songs from nearby dialects to respond more strongly to those songs than those hearing songs recorded at much greater distances, and birds that are physically isolated from the foreign song by geographical barriers to respond less strongly to foreign songs than birds separated from foreign song by occupied habitat. Our final hypothesis was that evolutionary divergence drives song discrimination. In this scenario we expected stronger differences in response between foreign song from different subspecies and local song than between foreign song from within the same subspecies and local song.

METHODS

Locating and Screening Primary Studies

We conducted a systematic review of studies in which the response of wild territorial oscine birds to playback of recorded song on their territory was assessed using the playback of local songs and the playback of foreign songs. To locate studies, we searched the complete Web of Science database (year 1900 to present) with the following search terms (play*back* (song* or sing*)) on 20 September 2016, which produced 1521 records, and on 27 September 2016 (dialect recogn* bird*), which produced 78 records, (geograph* recogn* vocal*), which produced 127 records, (dialect* (song* or sing*) foreign*), which produced 26 records, and (dialect* (song* or sing*) local), which produced 145 records, for a total of 1748 unique records (Supplementary Fig. S2). We examined each title and rejected all papers that were obviously not applicable, for instance because the study subject was not an oscine songbird or because the stated topic differed dramatically from playback of song in the wild. At this first stage, we read the abstracts of all papers not rejected based on their title and again filtered out papers that were obviously unsuitable. This left us with 128 studies. We then examined the full text versions of papers themselves to determine suitability for our analysis. Finally, for each of the 44 papers that were judged suitable for our analysis, we read its literature cited and identified any potentially relevant papers that had not been identified in our Web of Science search. This