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Examining song complexity of Australian pied butcherbirds

Jeffrey Xing (1), Tim Sainburg (1), Timothy Q. Gentner (1) and Hollis Taylor (2)

(1) Department of Psychology, University of California, UC San Diego, La Jolla, CA 92093, USA.
(2) Sydney Conservatorium of Music, University of Sydney, Sydney, NSW, Australia.

ABSTRACT

Songbird vocal communication signals (birdsongs) often evolve in secondary sexual selection contexts and are shaped by female preferences. Such female preferences to male songs are typically linked to information-theoretic features of song complexity such as repertoire size or syntax of discrete song elements. Recent discoveries of similar structures between birdsong and human music suggest, however, that musical features of song complexity may also be relevant to female preferences. Australian pied butcherbirds (*Cracticus nigrogularis*) exhibit songs with recombinatory syntax and structural similarities to human music, but the depth of their song complexity remains ill-defined. To holistically examine pied butcherbird song complexity, we characterized relevant features of song complexity through a combination of symbolic sequence and musical rhythm analysis. This integrated approach reveals long-range dependencies in pied butcherbird songs, in which song elements are dependent on song history, and strong categorical song rhythms, in which the temporal spacings between song element onsets occur at discretely organized intervals. As categorical song rhythms can facilitate song history encoding, it may be critical in enabling long-range dependencies in pied butcherbird songs. A systematic conception of song complexity that takes into account such potential interactions between song features stands to benefit songbird communication research.

1 INTRODUCTION

Animals utilize acoustic communication signals to influence the behaviors of their conspecifics. In particular, songbird vocal communication signals (birdsongs) are vital components of avian courtship, in which males produce songs that elicit mating behaviors in females according to female preferences (Collins, 2004). Female preferences are thought to be mediated by song complexity, where complexity is constituted by a collection of lower-level song features such as high repertoire size, long vocalization duration, or organized syntax of discrete song elements (Collins, 2004; Okanoya, 2004). One songbird species that exhibits vocalizations with great song complexity are the Australian pied butcherbirds (*Cracticus nigrogularis*); their syntax is not only highly recombinatory, but is also structured to create balance between repetitive elements and novel elements similarly to human music (Janney et al., 2016; Taylor, 2017). Although pied butcherbird songs are known to be complex, the extent of their complexities remain understudied.

Further inquiries into pied butcherbird song complexity can be made with an infomational-theoretic approach, in which the communication signal is parsed into a string of symbolic units that model information transmission (Lemon, 1977). This approach has a rich history of characterizing song features that contribute to complexity, and recent discoveries of novel infomational-theoretic song features continue to validate information theory as a dominant methodological framework for analyzing song complexity (Markowitz et al., 2013). Recent interest in examining birdsong as a musical signal, however, has also discovered novel musical features that contribute to song complexity, and are furthermore theorized to be functionally-relevant in mate attraction (Roeske et al., 2020; Rothenberg et al., 2014). As combining both approaches may offer complementary insights on how song features contribute to complexity, we attempt to further characterize pied butcherbird song features with both symbolic sequence and musical rhythm analyses. We reveal that pied butcherbird songs contain long-range dependencies, in which song elements are dependent on song history, and categorical rhythms, in which the temporal onset of song elements are discretely organized.

2 METHODS AND RESULTS

To examine if pied butcherbird songs exhibit long-range dependency, we first parsed manually segmented song units of a song bout into symbolic sequences, which are then attached with historical context of varying lengths. We also generated various synthetic models of the song sequences to create baselines to which we can compare the true song to. By calculating the normalized entropy for such sequences, we found that true pied butcherbird song sequences have more orderly transitions than their synthesized counterparts across all lengths of historical contexts; the normalized entropy of true pied butcherbird song sequences is consistently lower than that of synthetic models (Figure 1A). Particularly, true song sequences contain lower entropy than its first-order Markov

model, which assumes that probability of the current element is strictly dependent on the previous element. This reveals the presence of long-range dependent structures in pied butcherbird songs, in which song construction is dependent on historical contexts beyond the last adjacent element.

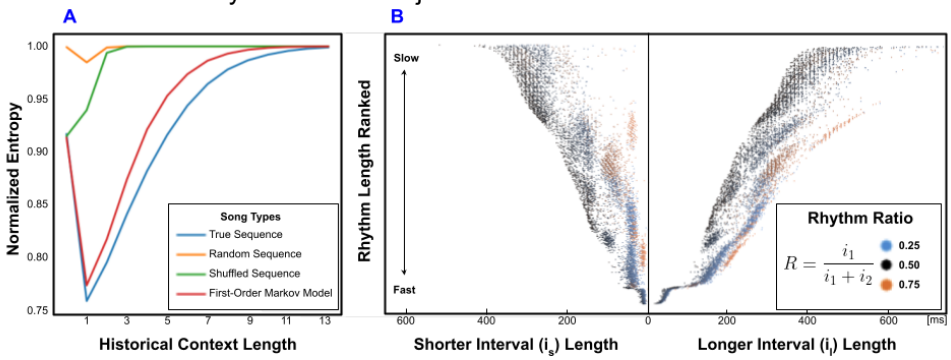

Figure 1: (A) Normalized entropy of pied butcherbird song sequences against synthetic models; (B) Rasterplots showing interval components of pied butcherbird rhythm ratios.

To investigate the musical rhythms of pied butcherbird songs, we analyzed the temporal placement of notes in relation to one another. We first manually extracted note onsets over the same song bout, calculated note spacings as the onset-to-onset intervals of neighboring notes, and then analyzed the ratio of each interval with its successive interval. Over the entire song bout, this analysis revealed that note onsets are temporally spaced in a discretized manner. By sorting each ratio by the length of its two interval components, and visualizing the interval components of each ratio in separate rastor plots, we found that the interval components roughly fall into data clusters that suggest categorical organization (Figure 1B). We also found strong quantitative evidence of rhythm clustering by calculating the Hopkins statistic of the rhythm ratios (H = 0.916), in which clustered data exhibit values close to 1, random data exhibit values close to 0.5, and uniform data exhibit values close to 0. This collectively supports that pied butcherbird songs are constructed with categorical rhythms.

3 DISCUSSION

We further characterized the relevant features of song complexity in pied butcherbird songs through a combined approach that incorporates both information and music theory. We found evidence that pied butcherbird songs contain more information-theoretic and musical features than previously described; pied butcherbird song exhibits long-range dependencies in its syntactic organization and exhibit categorical rhythms in its temporal organization. Both are plausible features that females may be sensitive to during mate selection (Okanoya, 2004; Roeske et al., 2020). Furthermore, as categorization in a communication signal improves encoding efficiency (Bradbury & Vehrencamp, 1998), categorical rhythms may be critical in enabling long-range dependencies within the song's syntax, which requires the singer to retain sung songs in memory. Future research in songbird communication research should be mindful of such potential interactions between song features in examining song complexity, and we argue that a systematic approach to song complexity that considers the relationship between song features will establish a better basis for examining songbird female preferences.

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