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Accounting for syntax in analyses of countersinging reveals hidden vocal dynamics in a songbird with a large repertoire

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Identifying the signalling strategies employed by animals during vocal interactions is a challenge, especially for species with large vocal repertoires. We propose that efforts to study such vocal dynamics can benefit by integrating models of syntax into their analyses. In this study, we conducted playback experiments on Cassin's vireo, *Vireo cassinii*, to examine the role of syntax, and more specifically, shared syntactic patterns, in countersinging. We presented 11 males with song sequences ordered according to population norms, and with sequences whose order deviated from population norms. We did not find evidence that individuals markedly altered their responses based on the syntax of the playback, either in their physical approach to the speaker or in the quantity of song they delivered in response. We did, however, find evidence that syntax was important in governing their choice of phrase types in response to the playbacks. Subjects did not match the playback phrase types. Instead, they engaged in a vocal behaviour referred to as song advancing, where they responded to a stimulus phrase type by singing the phrase type that most often followed the stimulus in their own normal song sequences. When playback sequences were ordered according to population norms, song advancing resulted in birds pre-empting the upcoming playback phrase type or delivering another of the prior playback phrase types (i.e. delayed matching) at higher rates than when playback sequences deviated from population norms. The detection of song advancing was only possible with the explicit inclusion of syntax in our analysis, suggesting that studies of the vocal interactions of species with repertoires of multiple vocalizations can benefit from consideration not only of a subject's repertoire, but also their syntax.

Countersinging interactions between neighbouring songbirds facilitate the establishment and maintenance of territory boundaries (Yasukawa, 1981). In species that possess repertoires of discrete song types, such interactions can involve complex dynamics and apparently sophisticated exchange of information (Burt, Bard, Campbell, & Beecher, 2002; Burt, Campbell, & Beecher, 2001; Molles, 2006; Searcy & Beecher, 2009). Many species have been shown to employ pattern-specific responses, meaning they adjust their song pattern in response to the song of their rival (Todt & Naguib, 2000). This can include subtly altering the acoustic structure of an individual song type (Vehrencamp, Yantachka, Hall, & de Kort, 2013), or altering their choice of song type altogether (Falls, 1985; Krebs, Ashcroft, & Orsdol, 1981; Stoddard, Beecher, Campbell, & Horning, 1992). Identifying and studying pattern-specific responses is fundamental to our understanding of the evolution of vocal complexity in birds. This is particularly true of species with large song repertoires, in which the dynamics of vocal interactions can be complex, and where the functional significance of large song repertoires remains a topic of debate (Byers & Kroodsma, 2009).

A central challenge in the study of pattern-specific responses is determining what factors lead a bird to deliver a particular song type at a particular time. This aim makes clear that if we seek to understand a singer's vocal behaviour, we should attempt to identify any and all influences on song choices, whether internal or external. It is well established that many, and probably all, songbirds abide by an internal syntax (Berwick, Okanoya, Beckers, & Bolhuis, 2011), meaning they arrange repertoire elements into nonrandom sequences characterized by frequent transitions between some pairs of elements and rare transitions between others. In light of this, the answer to the question may sometimes be as simple as to say that the bird delivered song type B at time t because he delivered song type A at time $t-1$, and typically

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transitions from A to B. Although this study focuses on a species in which syntax governs the order of song types (or phrase types) within a bout, the same reasoning can be applied to syllable types in species where syntax governs the ordering of syllables within a song.

When a bird interacts with a rival, it may abide by its internal syntax, or its song choices may be influenced by external factors such as the rival's song. In black-throated grey warblers, *Setophaga nigrescens*, for instance, the repertoire is partitioned into type I and II songs, and playback of any song lead males to respond with type I songs (Morrison & Hardy, 1983). In this case, the warbler's song sequence was disrupted by an external stimulus, leading the bird to deliver a type I song regardless of its prior singing behaviour. A similar behaviour is song type matching, where a bird repeats a perceived song type shortly after it was delivered by a rival (Falls, 1985; Krebs et al., 1981; Stoddard et al., 1992). Song type matching can be thought of as an interruption of a bird's normal song sequence.

Given that syntax is likely to play such a large role in determining song type choices, and that pattern-specific responses constitute disruptions to a bird's normal song sequences, it is surprising that few studies have assessed the role of syntax in countersinging interactions. Those that have done so have occasionally documented additional behaviours. For example, Verner (1975) noted that western marsh wrens, *Cistothorus palustris*, deliver their songs by cycling through their large song repertoires in nearly stereotyped orders, and that the sequences employed by neighbouring males are similar. When Verner (1975) broadcast a sequence to a bird, 'the subject *anticipated* each song type to be played next by the recorder' (emphasis his, page 283). The birds, he proposed, cued in on the previous playback song, which led them to jump ahead in a shared sequence. Similar observations have been made in wood thrush, *Hylocichla mustelina* (Whitney, 1985), and nightingales, *Luscinia megarhynchos* (Todt, 1971). We henceforth refer to this behaviour as 'song advancing', defined as responding to a perceived song with the song type that typically follows it in one's own preferred song sequences. Song advancing would seem to be challenging, if not impossible, to detect and study without prior knowledge of an individual bird's syntax. The integration of syntactic models into analyses of vocal interactions is therefore warranted, and may even be necessary if we wish to identify an exhaustive list of the vocal behaviours of any species, not only because syntax itself may guide a bird's song choices, but also because some pattern-specific responses may be syntactic in nature, as in the case of song advancing.

We sought to take such an approach using playback experiments to examine the countersinging dynamics of Cassin's vireo, *Vireo cassinii*. Males of this species possess repertoires of ~50 phrase types (equivalent to song types in other species) and sing according to a structured syntax, wherein the identity of upcoming phrase types can be predicted with >55% accuracy if the previous phrase type is known (Hedley, 2016a). Song sequences in this species show two additional phenomena. First, phrase types are arranged into clusters that consistently appear together in sequences (Fig. 1a). These clusters have been shown to be stable over time with respect to the phrase types contained therein, and the song sequences can be well described using Markov models (Hedley, 2016a). Second, cluster composition is often shared between individuals (Fig. 1b). That is, not only do neighbours overlap in their song repertoires (Hedley, 2016b), their syntax appears to be shared to an extent as well.

Our experiments examined the role of shared song syntax in countersinging interactions. Observations of natural countersinging interactions, such as the interaction depicted in Fig. 1c, suggest that birds interact nonrandomly using phrase types that are shared between the two participants. To test the role of syntax in these interactions, we presented each bird with a playback trial containing phrase types that normally occurred adjacently in sequences ('typical' trials) and one containing phrase types that rarely occurred adjacently in sequences ('atypical' trials), and examined the dynamics of each bird's response to the playbacks.

Our statistical approach to analyse vocal responses was motivated by the work of Kroodsma (1975), who proposed that the probability of matching in response to a phrase type depends on four factors: (1) the frequency of occurrence of that phrase type overall; (2) the transition probability from the bird's most recent phrase type to the playback phrase type; (3) the amount of time since the bird most recently sang the phrase type in question; and (4) the vocal behaviour of other males within earshot. We employed a model that incorporated properties of syntax from the songs of the subjects, and thereby effectively controlled for (1), (2) and (3). The influence of other males (4) is precisely what we hope to understand with playback experiments, and while it is possible that songs from distant background males may affect the subject, such effects are likely to be minimal relative to the effect of a playback speaker positioned within the territory to simulate a territorial intrusion. Although Kroodsma (1975) referred only to song type matching, our model was flexible enough to be applied to song advancing as well. We used this approach to show that Cassin's vireos engage in song advancing at levels exceeding the rate expected by chance.

METHODS

Study Site and Species

Research was conducted in a 1 km^2 valley of mixed conifer–deciduous forest near Volcano, CA, U.S.A. (UTM: 10 S 706584 4262742, datum WGS 84). Experiments were approved by the Animal Research Committee at the University of California Los Angeles (ARC number 2013-041-03A) and conducted under U.S. Fish and Wildlife Service bird banding permit number 23809 and California Scientific Collecting Permit number 12750. Prior to the initiation of this study, 11 male Cassin's Vireos were colour banded for individual identification. These 11 birds were all of the males present at our study site in 2015.

Males in our study population possess repertoires composed of an average of 51 phrase types (range 31–60), which they deliver in structured sequences with immediate variety, meaning phrase types are rarely repeated consecutively (Hedley, 2016b). Phrase types are short (<0.7 s long), highly stereotyped, and can be readily identified by a trained observer with >99% accuracy (Hedley, 2016a). Phrase types are widely shared in this population, such that the repertoires of any two males tend to overlap by about 50% (Hedley, 2016b). Details regarding the singing style of this species are examined in more detail elsewhere (Hedley, 2016a, 2016b).

Nonexperimental Recording Sets

We constructed a set of recordings of each of the 11 individuals made under nonexperimental conditions. In general, these recordings were made when birds were singing individually on their territory and not interacting closely with another bird. The nonexperimental recording sets contained a total of 62 395 phrases (mean = 5672 phrases per bird, range 1498–14 101) and 300 recordings (mean = 27 recordings per bird, range 9–60). The nonexperimental recording sets of five individuals spanned 3 years, those of two individuals spanned 2 years and those of four individuals included only recordings from 2015.