

## Research



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# Long-distance dependencies in birdsong syntax

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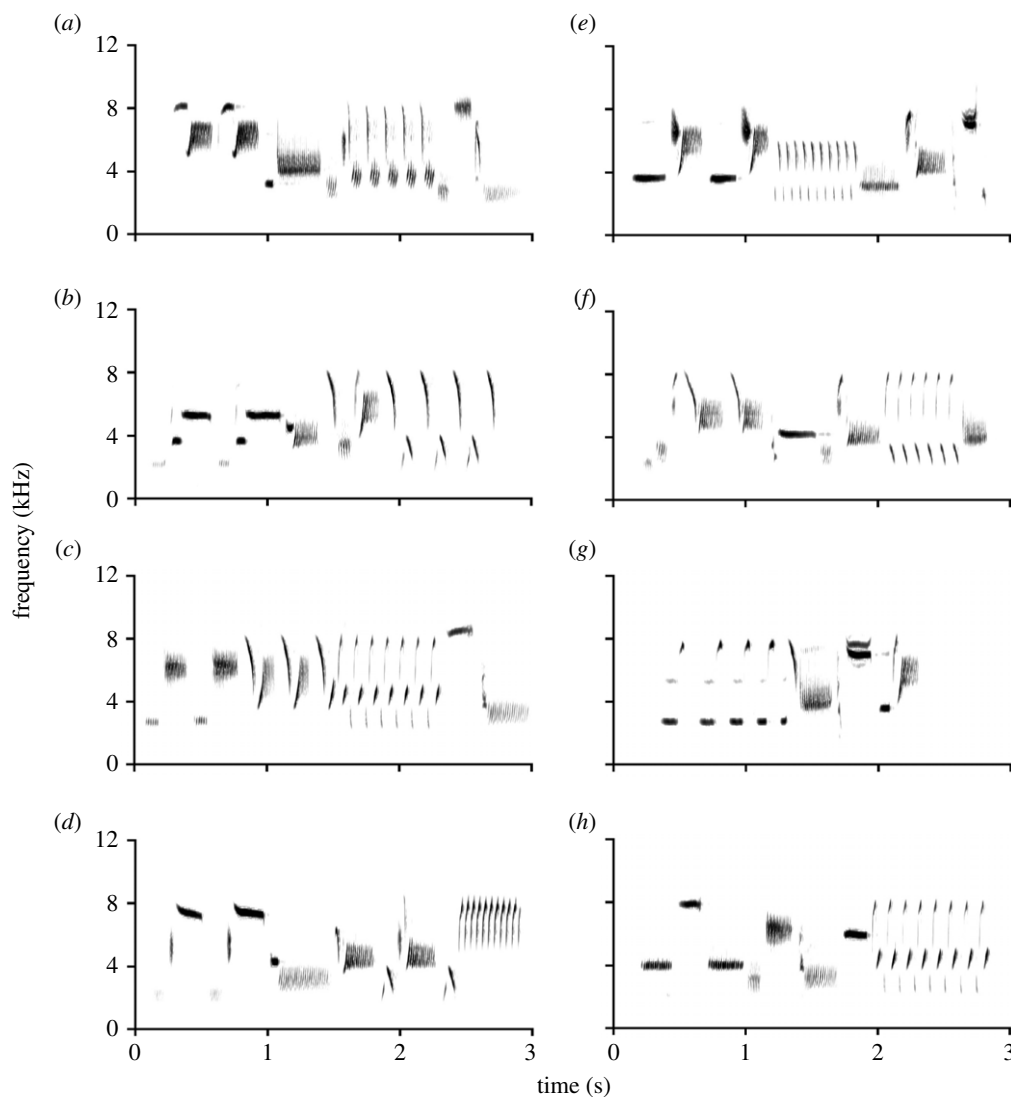
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Songbird syntax is generally thought to be simple, in particular lacking long-distance dependencies in which one element affects choice of another occurring considerably later in the sequence. Here, we test for long-distance dependencies in the sequences of songs produced by song sparrows (*Melospiza melodia*). Song sparrows sing with eventual variety, repeating each song type in a consecutive series termed a 'bout'. We show that in switching between song types, song sparrows follow a 'cycling rule', cycling through their repertoires in close to the minimum possible number of bouts. Song sparrows do not cycle in a set order but rather vary the order of song types from cycle to cycle. Cycling in a variable order strongly implies long-distance dependencies, in which choice of the next type depends on the song types sung over the past cycle, in the range of 9–10 bouts. Song sparrows also follow a 'bout length rule', whereby the number of repetitions of a song type in a bout is positively associated with the length of the interval until that type recurs. This rule requires even longer distance dependencies that cross one another; such dependencies are characteristic of more complex levels of syntax than previously attributed to non-human animals.

## 1. Introduction

Although there have been claims that songbirds can be taught to recognize complex syntactical patterns in artificial sequences [1,2], it is generally agreed that natural song produced by the birds themselves exhibits relatively simple syntax [3,4]. An important aspect of this simplicity is a lack of long-distance dependencies [5], meaning that the next element produced in a sequence does not depend on elements earlier than the last one or two. Indeed, syntax in a number of songbird species has been characterized as specifying just first- or second-order Markov transitions [6–10] although longer dependencies have been suggested [11,12]. A Markov model of song type transitions constitutes a weak generative grammar, meaning a set of rules sufficient to produce sequences but not sufficient to serve as natural descriptions of sequence structure [13]. Here, we describe for song sparrows (*Melospiza melodia*) a strong generative grammar, one that provides a description of sequences that is 'natural' in the sense of being general, simple and economical [4]. We also demonstrate that sequences of song produced by song sparrows show long-distance dependencies of impressive length. This feature of song sparrow singing behaviour indicates a more complex level of syntax than previously attributed to non-human animals.

In the study of birdsong, syntax can refer to regularities either in how notes or syllables are assembled to produce songs [14,15] or in how songs are assembled into sequences [6,16]. Here, we focus on the songs-into-sequences aspects of syntax. Song sequences are of interest in those songbirds in which individuals sing multiple song types, as in song sparrows. In this species, individual males possess repertoires of six to 12 song types (figure 1). Although song sparrows vary renditions of the same song type [17], within-song type differences are smaller than between-song type differences [18] and elicit a lower dishabituation response from receivers [19,20]. Songs can be produced



**Figure 1.** Spectrograms of the eight song types (*a–h*) in the repertoire of male song sparrow 14.

in any sequence, and because no absolute limit can be assigned to sequence length, the variety of potential sequences is infinite.

Here, we test a set of six syntactical rules hypothesized to govern song sequencing in song sparrows. Below we describe the six rules, explain their sources and state the predictions derived from each that can be used to test them.

- (i) **Eventual variety rule:** a singer repeats a song type multiple times before switching to another song type. This pattern contrasts with immediate variety, in which a singer switches song types after every song [21]. The eventual variety pattern has long been attributed to song sparrows [22,23] and is also known to characterize many other songbird species [24]. The rule predicts that bouts consisting of a single song should be much rarer than bouts of multiple songs, where a bout is a series of consecutive repetitions of a song type.
- (ii) **Cycling rule:** a singer cycles through its repertoire in close to the minimum number of bouts. Regular cycling has been suggested for song sparrows previously [23,25], but we know of no previous statistical test for cycling in this species. The rule has been supported in other songbirds with evidence of significant avoidance of low recurrence intervals between bouts of the same

type [6,26]. We test the prediction that observed cycle lengths are shorter than cycle lengths found in random sequences.

- (iii) **Bout length rule:** the more repetitions of a song type in a bout, the longer the delay until the singer returns to that type. The bout length rule is expected as a consequence of two internal mechanisms proposed by Hinde [27] and Falls [28] to underlie cycling: first, a buildup of inhibition for a song type as it is repeated in a bout, and second, a gradual waning of that inhibition once production of the song type has ceased. Indirect support for the bout length rule in song sparrows comes from evidence that males are less likely to match a song type after they have sung a long bout of that type [29]. The rule predicts that bout length will be positively correlated with subsequent recurrence interval.
- (iv) **Psycho-hydraulic rule:** the longer a singer goes without singing a particular song type, the longer the next bout of that song type will be. This rule is derived from Lorenz's 'psycho-hydraulic model' [30], which posits that 'action specific energy' for a behaviour builds up gradually over time whenever a behaviour is not performed and that the more such energy has accumulated, the more intense the behaviour will be when eventually triggered. Previous tests of the

model on syntax of songbirds and mammals have been negative [31]. This rule predicts that recurrence interval will be positively correlated with subsequent bout length.

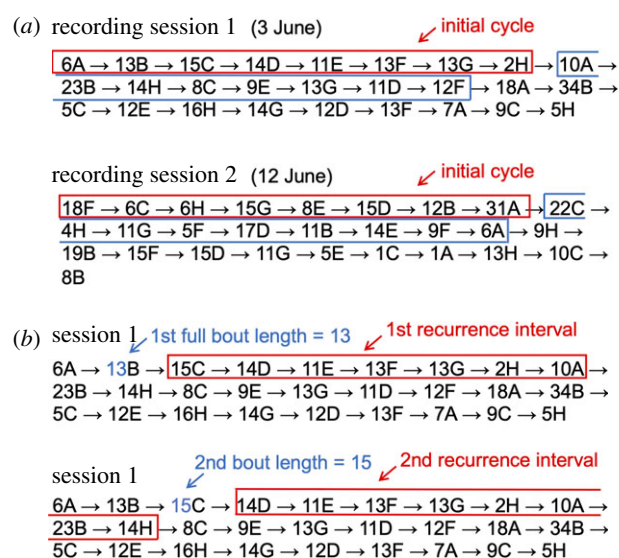
- (v) Song type usage preferences: individuals sing certain of their song types more than others. Evidence for preferential use of particular song types has been found previously in other songbirds [16,32–34]. Some authors have claimed such preferences exist in song sparrows [35], while others have denied them [23]. Lapiere *et al.* [36] found that song type usage differs significantly from uniform in most song sparrows but did not test observed usage against random usage. We test the prediction that if males have stable usage preferences, their usage frequencies in two independent samples should be positively correlated.
- (vi) Transition preferences: singers prefer to switch from one particular song type to another specific song type, for example from type X to type Y. Among songbirds, strong transition preferences have been found in some immediate variety singers [37–39] and weaker ones in eventual variety singers [7,32,40]. Robust first-order transition preferences could produce cycling without longer distance dependencies. Hedley *et al.* [41] provide a statistical test for consistency in transition preferences between individuals that can be adapted for testing consistency in transition preferences between recording sessions within individuals.

Certain of these syntactical rules have implications for the existence of long-distance dependencies and therefore bear importantly on the complexity of song sparrow syntax. Cycling through the repertoire in a set order can be accomplished with only first-order transition preferences, whereas cycling in a variable order implies that the order of song types over the past cycle influences choice of the next song type to be sung. The bout length rule, if supported, would imply that the lengths of song bouts over the past cycle affect choice of the next song type. We test all six rules using song sequences recorded in the field from territorial male song sparrows.

## 2. Methods

Fieldwork for this study was conducted in southwestern Crawford County, Pennsylvania, USA (41.6° N, 80.4° W) during May and June of 2019. Adult male song sparrows were recorded on their territories in old fields and forest clearings and along the shores of lakes and waterways. Each subject was recorded on two mornings (6.00–11.00) with a mean of 9.5 days (range 5–14) between recording sessions. Males were not banded prior to the study, but because of the low degree of song type sharing in the population [42,43] all could be easily identified from their recorded songs together with their locations. Recordings were made using digital recorders (Marantz PMD 660 or 670) and cardioid microphones (Shure SM58) in parabolic reflectors (Sony PBR-330) at a sampling rate of 44.1 or 48 kHz.

We initiated recording with 33 males and obtained samples that we judged to be sufficient for 21 of these. Though we aimed for 300 songs in each recording session, we retained one male in the analysis with 295 songs for his first session and two males with 288 songs for their second sessions. Samples of 300 songs virtually always capture the complete repertoire



**Figure 2.** (a) The sequence of songs sung by male 14 during two recording sessions. The initial cycle through the repertoire is delineated in the first box for each session, and the second cycle in the second box. (b) The sequence of songs sung by male 14 during his first recording session shown twice, first with the first full bout and first recurrence interval indicated and second with the second bout length and second recurrence interval indicated. (Online version in colour.)

of a song sparrow [44], especially if the recordings are continuous [45]. All our recordings were continuous, so that we could document the sequence in which song types were sung. In all cases, all the song types recorded in the first session were recorded in the second session and vice versa, so all recording sessions were adequate to capture full repertoires and one or more full cycles.

To obtain more in-depth data on short-term repertoire usage, we recorded five additional males for all daylight hours in a 24 h period using an Autonomous Recording Unit or ARU (Song Meter SM4, Wildlife Acoustics). These recordings were made in southwestern Crawford County between 14 May 2021 and 23 May 2021, each from the middle of one morning to the middle of the next. The five males were first recorded in person as above to allow identification of each subject's repertoire of song types (see the electronic supplementary material).

We assigned recorded songs to song types using spectrograms made with AUDACITY software using a 256-point fast Fourier transform and a Hanning window. We classified two songs as the same song type if they shared the same introductory phrase and half or more of all phrases [29]. Spectrograms of one or more renditions of each song type were printed (using RAVEN PRO software) to aid in classification. In previous work in this study population, observers blindly classifying songs to song types agreed on the correct classification in 97.7% of cases [29].

To test the bout length rule, we counted the consecutive renditions of each song type in each recording in the 2019 sample. To test the cycling rule, we determined for each sample of songs the initial cycle length, where cycle length is defined as the number of song type bouts used to present all the song types in an individual's repertoire (figure 2a). The minimum possible cycle length is equal to an individual's repertoire size. To estimate expected cycle lengths, we generated 10 000 random sequences for each repertoire size, sampling with replacement and stipulating that no song type could immediately succeed itself. The expected cycle length was then estimated as the mean of the initial cycle lengths in the 10 000 sequences for each repertoire size. We compared observed cycle lengths in the 2019 sample to expected cycle lengths using sign tests [46], with sample sizes equal to the number of subjects.

The bout length rule predicts that bout length will be positively correlated with subsequent recurrence interval, and the psycho-hydraulic rule predicts that recurrence interval will be positively correlated with subsequent bout length. Here, we measure recurrence interval [9,47] as the number of bouts of other song types that occur between two bouts of a focal song type (figure 2*b*). Bout lengths are measured for the first full bout of each song type in each recording session, ignoring the first bout, which usually will not have been fully captured. Data are combined for the two recording sessions for individuals in the 2019 sample, and a single Pearson's correlation coefficient is calculated for the test of the bout length rule (bout length versus subsequent recurrence interval) and another for the test of the psycho-hydraulic rule (recurrence interval versus subsequent bout length). Separately for each rule, we test whether the mean correlation coefficient is different from 0 with a two-tailed one-sample *t*-test.

Usage refers to the number of renditions of each song type that a subject produces. Our test for usage preferences starts by correlating each individual's observed usage in one continuous recording with its observed usage in a second continuous recording made 5 to 14 days later. We then test whether the mean correlation coefficient for the sample of males is different from 0 with a two-tailed one-sample *t*-test. A mean significantly greater than 0 is expected only if males possess usage preferences that are stable over several days.

We test for transition preferences using a procedure based on one formulated by Hedley *et al.* [41] for testing for sharing of transition preferences between individuals. In the modified procedure: (i) transition matrices are constructed for transitions between-song types; (ii) one-tailed Fisher's exact tests are used to determine whether the count in any one cell of the transition matrix exceeds random expectation; and (iii) a second one-tailed Fisher's exact test is used to test whether the number of preferred transitions shared between the two samples for one male is greater than expected by chance. We term a transition preferred in both samples of a single male a 'consistently preferred transition'.

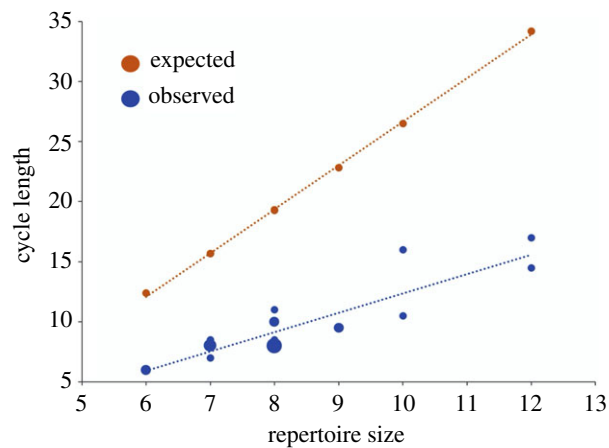
To assess the consistency of the order in which song types are sung, we use the Jaccard index to measure the proportional sharing of transitions between the initial cycles in the first and second recording sessions and between the first and second cycles within each recording session. The general definition of the Jaccard index is the intersection of two sets divided by the union of the two sets; in this case, that definition translates to  $c/(a + b + c)$ , where  $c$  is the number of transitions shared by two cycles,  $a$  is the number of transitions unique to cycle 1 and  $b$  is the number unique to cycle 2 [48].

After obtaining transition probability matrices for each bird, we used these to generate 10 000 sequences for a simulation test of whether observed cycle lengths could be explained by observed transition probabilities alone.

### 3. Results

#### (a) Eventual variety rule

Figure 2*a* shows the sequences of songs produced by one male (designated male 14), chosen for illustration because he has the modal repertoire size (eight song types) and is close to the average in the number of bouts and songs recorded. This male follows the eventual variety rule, almost always singing multiple repetitions of a song type before switching to another. Disregarding the first and last bouts (both of which are probably not recorded in full), the average bout length is 12.0 songs. This example is representative of the 21 subjects in the 2019 sample: across all subjects, the mean bout length was



**Figure 3.** Observed and expected cycle lengths graphed against repertoire sizes. Circle size indicates the number of individuals (1–4) at a point. Observed cycle lengths are the means of the initial cycle lengths from each individual's two recording sessions. Expected cycle lengths are means from 10 000 random sequences for each repertoire size. (Online version in colour.)

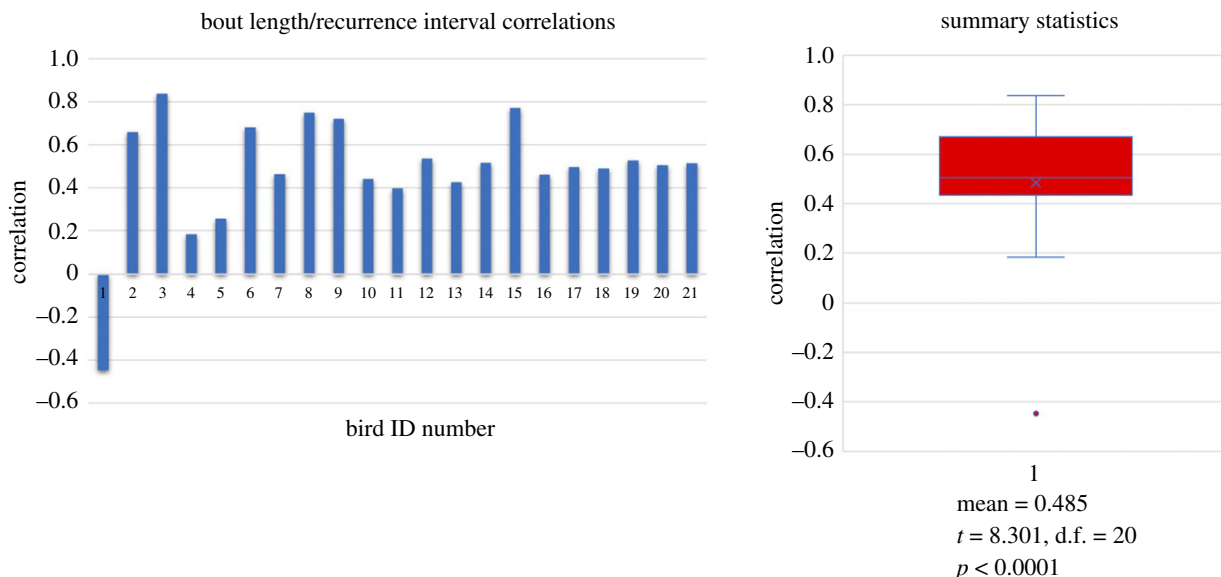
14.0 repetitions, with individual means ranging from 5.9 to 26.8. Only a mean of 3% of bouts consisted of a single song (range 0–10%). Only 0.3% of songs occurred in bouts of one song (range 0–1.7%). Thus, the eventual variety pattern is indeed the rule and immediate variety a rare exception.

#### (b) Cycling rule

The initial cycle lengths for male 14 are delineated for the two recording sessions in figure 2*a*. These initial cycle lengths are both eight songs, which is the minimum possible given this male's repertoire of eight song types. Minimum possible cycle lengths of course increase with repertoire size, as do the mean cycle lengths in random sequences (figure 3). For all 21 males in the 2019 sample, mean initial cycle length (averaged over the two recording sessions per individual) was lower than the expected mean from random sequences (figure 3). This result is significantly different from chance by a two-tailed sign test ( $z = 4.583$ ,  $n = 21$ ,  $p < 0.00001$ ). Initial cycle lengths took their minimum possible values in 26 of 42 recordings (62%). The cycling rule is thus followed with good but not perfect fidelity.

#### (c) Bout length rule

This rule predicts that the length of a bout of a particular song type should be positively associated with the length of the subsequent recurrence interval, defined as the number of bouts of other song types produced between two bouts of a focal song type. Figure 2*b* shows how the data used to test this rule are compiled for male 14. Again, the first bouts of recording sessions are ignored because they are unlikely to have been fully recorded. Bout lengths and recurrence intervals are determined for the first full bout of each song type in both recording sessions. Using these data, the correlation between bout length and recurrence interval was 0.516 for male 14. The correlation between bout length and recurrence interval was positive for 20 of 21 subjects (figure 4). The mean correlation was 0.485 ( $\pm 0.058$ ), which is significantly greater than 0 by a two-tailed one-sample *t*-test ( $t = 8.301$ , d.f. = 20,  $p < 0.00001$ ). The bout length rule thus is strongly supported.



**Figure 4.** Per-individual Pearson correlations between bout lengths and recurrence intervals. The results support the bout length rule, which states that longer bouts of a song type should be followed by longer delays before that song type is sung again. (Online version in colour.)

#### (d) Psycho-hydraulic rule

Applied to song sequences, this rule predicts that the longer the recurrence interval between two bouts of a song type, the longer the second bout of that type will be. Contrary to this prediction, we found the mean correlation between recurrence interval and subsequent bout length to be no different from 0 (mean  $r = 0.042 \pm 0.060$ ,  $t = 0.705$ ,  $p = 0.489$ ). Combining this result with the results on the bout length rule (above), the lengths of recurrence intervals are positively correlated with prior bout length but not with subsequent bout length.

#### (e) Usage preference rule

A positive correlation between frequency of song type usage in recording session 1 and frequency of usage in session 2 is evidence of usage preferences that are consistent over periods of at least the 5–14 days separating recording sessions. For male 14 (figure 2a), the correlation between usage frequencies in sessions 1 and 2 was 0.605. Correlations in usage between recording sessions were similarly positive for 15 of 21 individuals in the 2019 sample (figure 5), and the mean correlation ( $0.312 \pm 0.087$ ) was significantly greater than 0 by a two-tailed one-sample  $t$ -test ( $t_{20} = 3.595$ ,  $p = 0.002$ ). Thus, the usage preference rule is followed but not as consistently as the bout length and cycling rules. Variation in usage was driven more by variation in bout length than by variation in number of bouts (electronic supplementary material, table S1).

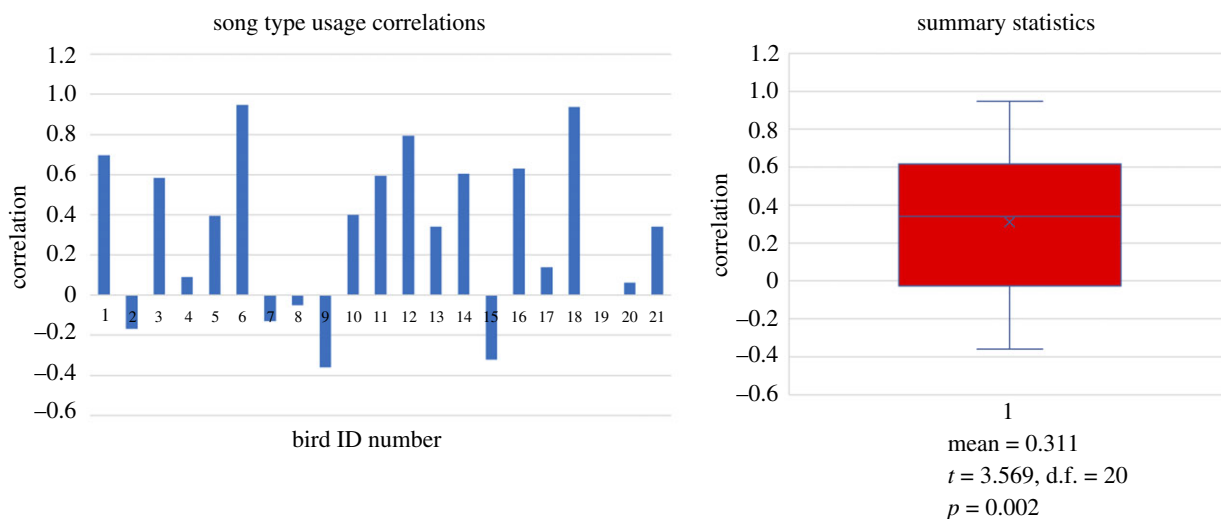
#### (f) Transition preference rule

Although our subjects tended to cycle through their repertoires efficiently, they did so without using a fixed order. Male 14, for example, produced his repertoire of eight song types in just eight bouts in both recording periods (figure 2a), but with no overlap in the first-order transitions used in these two initial cycles (Jaccard similarity = 0). The similarity between the first and second cycles within both recording sessions was also quite low for this male (mean similarity = 0.14). This pattern is representative of the subjects as a

whole: across the 21 subjects in the 2019 sample, the mean Jaccard similarity in transition usage comparing the initial cycles of the two recording sessions was 0.13 and comparing the first and second cycles within recording sessions was 0.11.

The most common transition in the first recording session for male 14 was  $A \rightarrow B$ , which occurred a total of three times in that session, more than expected by chance ( $p < 0.01$  by a Fisher's exact test). This  $A \rightarrow B$  transition did not, however, occur at all in the second recording session (figure 2a). Four other transitions were more common than expected by chance ( $p < 0.05$ ) in the first recording session, but none of these were over-represented in the second session. In the entire 2019 sample, only 2 of 21 birds showed one or more specific song type transitions that were significantly more common than expected in both of their recording sessions (electronic supplementary material, table S2). The number of consistently preferred transitions exceeded random expectation at the 0.05 level for only one of these two individuals (electronic supplementary material, table S2). When we used the observed transition frequencies compiled across the two recording sessions to generate simulated sequences for each subject, the initial cycle lengths in these sequences were similar to those in random sequences (electronic supplementary material, table S3). Observed cycle lengths in the field recordings were significantly shorter than the expected cycle lengths derived from these simulated sequences ( $p < 0.00001$ ).

The rarity of transitions that are consistently preferred across recording sessions is consistent with weak transition preferences but could also reflect strong first-order transition preferences that change between recording periods (i.e. are not time homogeneous). Because a mean of only 25 transitions were sampled per recording session in 2019, only a narrow range of first-order transition types were observed in many cases, which allows the possibility of strong transition preferences within days. The larger sample sizes provided by the 2021 ARU recordings (mean of 184 transitions) allow rejection of this alternative. Among the five males in this sample, three males with repertoire sizes of seven song types used respectively 41, 42 and 42 of 42 possible transition types (98–100%) within 24 h. The two males



**Figure 5.** Per-individual Pearson correlations between-song type usage frequency in recording session 1 and usage of the same song types in recording session 2 (5–14 days later). The results support within-male preferences for singing certain song types more than others. (Online version in colour.)

with larger repertoires (of 10 and 11 song types) each used a greater number of transition types though a smaller percentage of the total possible: 63 of 90 (70%) and 90 of 110 (82%), respectively (electronic supplementary material, table S4). Simulations run with transition matrices based on these 2021 ARU data produce cycle lengths similar to random sequences and much longer than observed (electronic supplementary material, table S4).

## 4. Discussion

### (a) Long-distance dependencies

These results provide support for both long-distance dependencies and a strong generative grammar in the syntax of song sparrow song sequences, a combination that, to our knowledge, has not previously been described in any animal signalling system. Evidence for long-distance dependencies comes in part from the cycling rule results. These data show that song sparrows cycle through their repertoires significantly more efficiently than would be expected from random sequencing, using the minimum possible cycle length in the majority of cases. Such cycling could be accomplished with strong first-order transition preferences, but the simulations show that observed transition preferences are not strong enough to produce efficient cycling. Another possibility is that cycling is produced by second-order Markov preferences. We are sceptical that second-order transition models can explain the observed combination of efficient cycling, weak first-order preferences and rapidly varying sequence order, but we do not at present have sufficient data to test such models. A third explanation, which we favour, is that song sparrows cycle by making the choice of each song type dependent on the order of song types over the entire preceding cycle. Since average cycle lengths varied from 6 to 17 bouts (mean = 9.5), this reasoning implies dependencies of equivalent length.

More direct evidence for long-distance dependencies comes from our results on the bout length rule, showing that bout lengths are consistently positively correlated with recurrence intervals. Thus, the decision whether to sing a particular song type next depends on the length of the last bout

of that song type produced on average one cycle ago. This dependency is also supported by previous results showing that the decision whether to match playback of a particular song type depends on the length of the last bout of that type [29]. Given that the mean cycle length is 9.5 bouts and the mean bout length is 14 songs, following the bout length rule requires dependencies that extend on the order of 130 songs. At typical singing rates of about four to six songs per minute, the time over which these dependencies stretch is on the order of 20–30 min. Furthermore, the dependencies implied by the bout length rule are often cross-serial, in the sense that arrows indicating the dependencies on a timeline representing the song sequence must cross over each other.

Previous studies of syntax in other songbirds have mainly looked for and found only short-distance dependencies, in which the next song type sung depends only on the last one or two previous songs [6,8,10,38]. Short-distance dependencies seem to be adequate to allow some species to cycle through quite large song repertoires, for example of around 36 song types in grey-crowned warblers (*Seicercus tephrocephalus*) [39] and of over 100 song types in marsh wrens (*Cistothorus palustris*) [41]. In such a system, the order of songs must be repeated fairly faithfully from cycle to cycle, which is what is observed in grey-crowned warblers and marsh wrens, but which is not what we observe in song sparrows. To our knowledge, the longest distance dependencies that have been previously shown in songbirds are from domestic canaries of the Belgian waterslager strain (*Serinus canaria*), which sing long songs consisting of a series of phrases each of about 1 s duration. Here, the choice of the next phrase can depend on as many as the past three to six phrases, though most choices seem to depend on only the last phrase [11]. Note that syntax in this case is within-song rather than between-songs. The longest distance dependencies known in canaries extend about 5–10 s, compared to 20–30 min in song sparrows.

### (b) Strong versus weak generative grammar

Most studies of birdsong syntax have examined transition probabilities between one element and the next or between sets of prior elements and the next [3,9,49]. Such transition probabilities can be considered aspects of weak generative

grammar, as they are sufficient to generate strings of elements but do not provide satisfying structural descriptions of such sequences. Less attention has been given to general, descriptive rules of birdsong syntax that might be considered aspects of strong generative grammar. An exception is the eventual variety/immediate variety distinction, which has been applied to many songbird species [21,24] and which simply and economically describes a major aspect of sequence structure.

Here, we provide evidence from song sparrows supporting eventual variety and a set of additional rules that are sufficiently general and economical to be considered aspects of a strong generative grammar. Together, these rules give a convincing general description of the species' song sequences: a singer repeats a song type multiple times before switching to the next, cycles through his repertoire in varying order but in close to the minimum number of bouts, balances a long bout of a song type with a long delay until that song is sung again and prefers singing some of his song types more than others. Presumably, other general rules remain to be discovered in song sparrows; for example, we are interested in the possibility that there are general rules determining which song types are preferred, based perhaps on song structure or on sharing with neighbouring males [36]. Presumably also, many other general rules may be discoverable in some of the other 4000 or so species of songbirds.

### (c) Syntax complexity

Given that song sparrows do not follow first-order Markov transitions consistently, the syntax of their song sequences cannot be placed in the first-order Markov category as defined by Hurford [4] in his description of the formal language hierarchy. The presence of long-distance cross-serial dependencies argues that song sparrow syntax also cannot be categorized at the state chain level, that is syntax that entails unidirectional transitions between a finite set of states and no memory of prior parts of the sequence [4]. Instead, song sparrow syntax appears to fall into the context free category, in which the effect of the present state on choice of the next element is augmented by a potentially unlimited auxiliary memory [3]. Although song sparrows could achieve this level of syntax complexity by maintaining explicit memory of all songs produced over the past cycle, simpler mechanisms would also suffice. As proposed by Hinde [27] and Falls [28], inhibition of a song type might build up gradually as a male repeats a song type in a bout, eventually

causing the singer to switch away from that type. Inhibition of this song type might then dissipate gradually, as the male sings other types. Following Slater [50], an element of competition must be added to this model, whereby song types compete for production based on which is least inhibited. The buildup and waning of inhibition fulfills the definition of memory as a 'process that allows animals to base their behaviour on information from individual past experience' [51, p. 256] making the model compatible with the stipulation that memory of earlier parts of the sequence can affect choice of the next element.

Some instances have recently been found in songbirds in which the syntax of calls (not songs) affects meaning [52–54]. These cases involve calls that refer to things or events external to the signaller. Songs are not known to be referential in this sense, so direct effects of song order on meaning are perhaps unlikely. Indirect effects on meaning are nevertheless possible. In song sparrows, for example, obedience to syntactical rules has been shown to constrain the ability of males to match the song types of rivals [29], a behaviour thought to have an especially aggressive meaning [55]. Studies of the effects of the syntax of song sequences on the response of conspecifics of both sexes might help illuminate the function of syntactical rules, but comparative studies of syntactical patterns across a range of songbird species might be even more illuminating.

**Data accessibility.** Data and computer code are available from the Dryad Digital Depository: <https://doi.org/10.5061/dryad.j6q573nfw> [56].

**Authors' contributions.** W.A.S.: conceptualization, data curation, formal analysis, investigation, methodology, supervision, validation, visualization, writing—original draft; J.S.: conceptualization, data curation, formal analysis, methodology, visualization, writing—review and editing; S.P.: conceptualization, data curation, methodology, project administration, validation, visualization, writing—review and editing; S.N.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

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