Syntactic rules predict song type matching in a songbird

William A. Searcy[1] · Lauren M. Chronister[2] · Stephen Nowicki[3]

Abstract

Song type matching has been hypothesized to be a graded signal of aggression; however, it is often the case that variation in matching behavior is unrelated to variation in aggressiveness. An alternative view is that whether an individual matches a song is determined mainly by syntactic rules governing how songs are sequenced. In song sparrows (*Melospiza melodia*), two such rules are the cycling rule, which directs that a bird cycles through its song types in close to the minimum number of bouts, and the bout length rule, which directs that a long bout of a song type is followed by a long interval before that song type is sung again. The effect of these rules on matching is confirmed here for a population of eastern song sparrows. Territorial males were challenged at the end of a recording session with playback of one of their own song types. Logistic regression showed that the probability of matching the playback song type increased with the length of the interval since the subject had last sung that song type, as predicted by the cycling rule. The probability of matching decreased as prior bout length increased, as predicted by the bout length rule. In a multivariate logistic regression, interval length and prior bout length were both associated with matching and together correctly predicted matching in 81.3% of cases. The results support the syntactic constraints hypothesis, which proposes that matching is a non-signaling by-product of internal rules governing the ordering of song type sequences.

Significance statement

Vocal matching has attracted widespread interest in large part because it seems an effective method of directing an aggressive message at a particular recipient. Here, we show that in an eastern population of song sparrows, decisions on whether to match another bird are largely determined by internal rules of syntax governing how a singer sequences its song types, rather than by variation in aggressiveness or other individual traits. These results support the view that vocal matching is an incidental byproduct of internal mechanisms controlling the ordering of vocalization types and so is not a signal at all. This hypothesis may be broadly applicable to vocal matching in other species.

Communicated by J. Podos

✉ William A. Searcy
  wsearcy@miami.edu

1 Department of Biology, University of Miami, Coral Gables, FL 33124, USA

2 Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA

3 Department of Biology, Duke University, Durham, NC, USA

Introduction

Song type matching occurs when one individual replies to another with the same song type the other has just sung. This form of vocal matching has been studied mainly in songbirds (Catchpole and Slater 2008; Searcy and Beecher 2009), although both song type matching and other forms of vocal matching have been found in a diverse array of additional taxa (Arak 1983; Sugiura 1998; Gerhardt et al. 2000; Janik 2000; Miller et al. 2004; Balsby and Bradbury 2009; Alves et al. 2014; King and McGregor 2016). It is possible for one songbird to reply to another with a similar song type just by chance, but in a number of songbird species song type matching has been shown to occur too frequently to be

accounted for by chance alone (e.g. Hinde 1958; Krebs et al. 1981; Schroeder and Wiley 1983; Falls 1985; Stoddard et al. 1992; Rogers 2004; Gammon et al. 2008; Yuan and Price 2011; Ansell et al. 2020). The most common functional interpretation of matching is that it serves as a graded signal of aggression, in the sense that a bird signals the likelihood of attacking a rival by the probability of matching the rival's song (Krebs et al. 1981). Here, we test an alternative interpretation of matching: whether a singer matches a rival's song type is determined chiefly by the singer's adherence to syntactic rules governing how its songs are sequenced (Hinde 1958; Falls 1985; Searcy et al. 2019). This "syntactic constraints" hypothesis competes with the aggressive signaling hypothesis in that the more strongly matching is determined by rules of syntax, the less this behavior can vary with and thus signal aggressiveness.

An aggressive signaling function of matching is supported for some populations of songbirds, including western populations of our study species, the song sparrow (*Melospiza melodia).* There is evidence, for example, that individuals are more likely to match rivals in more aggressive contexts than in less aggressive ones in western song sparrows (Stoddard et al. 1992; Beecher et al. 2000; Burt et al. 2001), great tits (*Parus major*) (Krebs et al. 1981), white-crowned scrub-wrens (*Sericornis frontalis*) (Ansell et al. 2020), and yellow-breasted boubous (*Laniarius atroflavus*) (Wheeldon et al. 2021). In addition, individuals that match show a stronger aggressive response than individuals that do not match in western song sparrows (Vehrencamp 2001; Akçay et al. 2013). In our study population of eastern song sparrows, however, a variety of evidence runs counter to the aggressive signaling hypothesis. In this population, type matching does not predict whether a singer will attack an intruder (Searcy et al. 2006), nor does it predict escalation to stronger forms of aggressive signaling (Searcy et al. 2013). Territory owners are not more aggressive towards song playback that matches them than towards non-matching playback (Anderson et al. 2008). Individuals in this population are consistent from playback trial to playback trial in aggressive responses such as approach and singing rate (Nowicki et al. 2002; Hyman et al. 2004; Searcy et al. 2013) but are not consistent in whether they match (Anderson et al. 2005; Searcy et al. 2013, 2019). Evidence countering the aggressive signaling hypothesis has also been found in other songbirds, such as western meadowlarks (*Sturnella neglecta*) (Falls 1985), great tits (Falls et al. 1982), and swamp sparrows (*Melospiza georgiana*) (Ballentine et al. 2008), in all of which matching behavior does not predict individual variation in aggressiveness.

While there is strong evidence against the aggressive signaling explanation of matching in eastern song sparrows, what is known about between-song syntax in this species supports the plausibility of an alternative "syntactic constraints" hypothesis, which holds that syntactic rules largely determine whether matching occurs (Searcy et al. 2019). Male song sparrows develop repertoires of five to 13 song types which they sing in an eventual variety pattern, meaning that they typically produce a "bout" of multiple repetitions of one song type before switching to another type (Saunders 1924; Nice 1943). For example, in a study carried out in Crawford County, Pennsylvania, Searcy et al. (2022) found that the mean bout length of 21 field-recorded males was 12.0 songs and that only 3% of bouts consisted of a single song. This same study found evidence for three syntactic rules that affect the ordering of song type bouts. The cycling rule dictates that a singer cycles through its repertoire efficiently, producing its entire repertoire of song types in close to the minimum number of bouts. In support of this rule, Searcy et al. (2022) found that cycle lengths—the number of bouts used to present all of a subject's repertoire—were always less than the values expected from random sequences and took the minimum possible value about 60% of the time. The adaptive value of this rule may be that cycling enables a singer to impress its complete repertoire on a listener more rapidly than if song type bouts were sequenced randomly. Song sparrows also follow a "bout length rule," balancing a long bout of a particular song type with a long "recursion interval" before that song type is produced again. Supporting this rule, 20 of 21 males in the Pennsylvania study showed a positive correlation between bout length and subsequent recursion interval, with a mean correlation that was significantly greater than 0 (Searcy et al. 2022). The benefit of the bout length rule may be that it tends to equalize the number of renditions of a male's song types that are produced. Despite this effect, song sparrows show evidence of a usage preference rule, whereby they consistently produce some of their song types more than others (see also Lapierre et al. 2011). Usage preferences, however, were only supported in 15 of 21 subjects and were driven more by variation in bout lengths, which does not reflect song type sequencing, than by the relative frequency of bouts of different types, which does reflect sequencing (Searcy et al. 2022).

Previous results supporting the syntactic constraints hypothesis come from studies of great tits. Krebs (1976) showed that these birds avoid singing bouts of the same song type close together in a sequence, which supports the occurrence of cycling. Krebs et al. (1981) showed that the probability of matching a playback song increased with increasing intervals since the birds had last sung that song type, with interval length measured by the numbers of song type switches. This result is consistent with an effect of cycling on matching, though confidence in the result is weakened by the use in the analysis of pooled data from just two birds (Machlis et al. 1985).

Searcy et al. (2019) carried out an experimental test of the effect of cycling on matching in eastern song sparrows.

Previously recorded territorial males were confronted with playback of one of their own song types following either a short interval or a long interval since they had last sung that type. Interval here was measured as the number of bouts of other song types produced since the last bout of the target song; this is just one less than the number of switches used to measure interval length by Krebs et al. (1981). This experimental design required real-time monitoring of song type production using spectrographs generated on a laptop computer in the field. The 22 subjects type-matched significantly more often than expected by chance for the long-delay treatment but not for the short-delay treatment; however, the difference in frequency of matching between the two treatments (36% vs 27%) was not significant. Regression analysis of the experimental results supported two relationships between matching and syntax: the probability of matching decreased strongly with prior bout length of the target song type and increased weakly with the frequency of the target song type in prior recordings.

Here, we present a second test of the syntactic constraints hypothesis for song sparrows, seeking a stronger test of the effect of cycling on matching and additional tests of the effects of prior bout length and song type preferences. Our previous test of the effect of cycling (Searcy et al. 2019) was weak in that only a limited portion of the range of possible interval values was employed, with one intervening bout used for the short delay treatment, and for the long delay treatment either three intervening bouts for individuals having repertoires of six types or four bouts for individuals having 7–12 song types. Thus, the long delays were at most only 0.57 (4/7) of the minimum cycle length and sometimes were as low as 0.33 (4/12) of the minimum cycle length. In the present study, we test for matching of a playback song type while starting playback at random points in the subject's cycle, allowing interval values ranging up to and (in one case) exceeding minimum cycle lengths. This approach also provides a stronger test in that it allows us to treat interval as a continuous rather than a dichotomous variable. Our approach further allows a test of the combined effects on matching of multiple syntactic rules.

Methods

This study was performed in Crawford County, Pennsylvania, USA., on areas managed by Pennsylvania State Gamelands 213 and 214, Pymatuning State Park, and the University of Pittsburgh's Pymatuning Laboratory of Ecology. Data were obtained from 21 male song sparrows during May and June of 2019 and from an additional 11 males during May and June of 2021. These males defended territories mainly along woodland edges bordering old fields, reservoirs, waterways, and mowed areas. Most of the males were

unbanded, but they all could be individually identified from spectrograms of their songs, as song sharing is low in this population (Hughes et al. 1998; DuBois et al. 2016).

All subjects were first recorded to obtain their song repertoires and an estimate of their song type usages. We recorded males at a sample rate of 44.1 or 48 kHz using digital recorders (Marantz PMD 660 or 670) and cardioid microphones (Shure SM58) in parabolic reflectors (Sony PBR-330). In most cases, we stimulated singing by playing at the start of the session two songs of a single song sparrow song type, using songs that were unfamiliar to the subjects because they were recorded at least 2 km distant and 2–6 years earlier. No subsequent playback was used. Previous work with eastern song sparrows suggested that a sample of 300 songs is sufficient to capture complete repertoires (Searcy et al. 1985). In these first recording sessions, we recorded a mean of 355 songs per male (range 295–500).

We recorded each subject a second time after a mean interval of 11 days (range 4–18), using the same recording equipment and methods as in the first recording sessions. Recording was again preceded in most cases by playback of two songs of an unfamiliar song type. We again attempted to record 300 songs from a subject, after which, with the recorder still running, we began the playback trial testing for matching (see below). In these second sessions, we recorded a mean of 315 songs (range 288–383) before beginning playback. Playback was initiated without reference to which song type the male was currently singing, with the important exception that we did not start playback while the subject was singing the song type chosen for playback. To aid in identifying the playback song type, we carried a printed copy of that song's spectrogram in the field, which we compared by eye to the sound of the subject's songs.

Playback stimuli

Each subject was tested for matching with playback of one of its own songs, chosen from those recorded in session 1 based on recording quality. Songs with a strong (high amplitude) signal and little background noise were chosen. Song sparrows treat their own songs ("self songs") very similarly to stranger songs as measured by both matching (Stoddard et al. 1992) and other behavioral responses (Searcy et al. 1981; Akçay and Beecher 2020). Self songs have been used extensively in previous experiments on matching in song sparrows (Anderson et al. 2005; Akçay et al. 2011, 2013; Searcy et al. 2019) and other species (Hinde 1958; Krebs et al. 1981; Todt 1981; Templeton et al. 2013).

Songs chosen for playback were copied from the original recordings in either Audacity (https://audacityteam.org/) or RavenPro 1.4 (Cornell Lab of Ornithology). Songs were band-pass filtered in RavenPro, removing sounds below 1500 Hz and above 18 kHz. Filtered songs were saved as
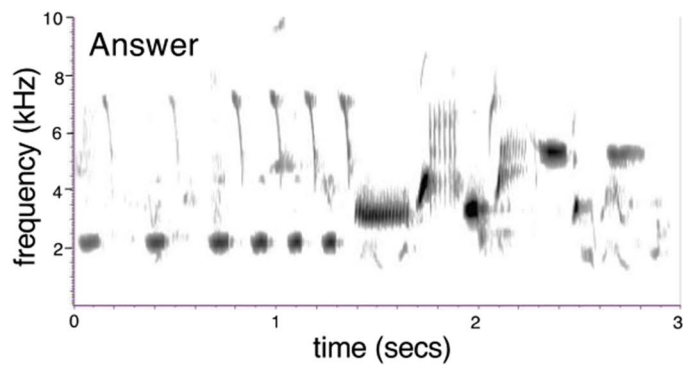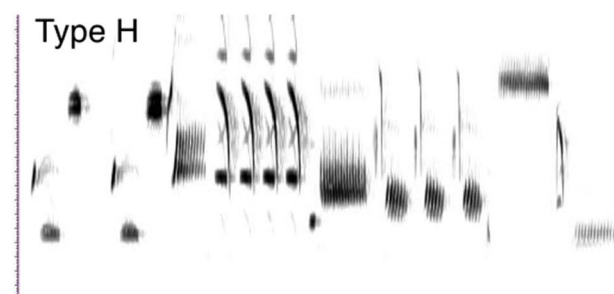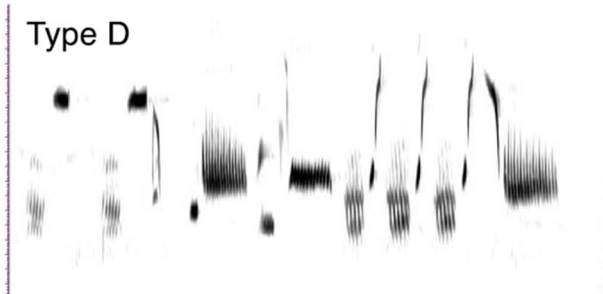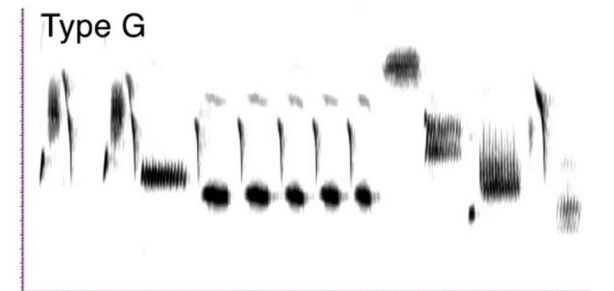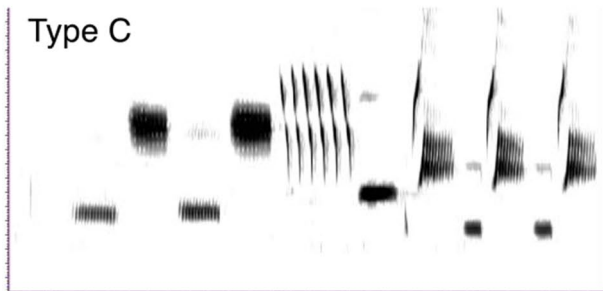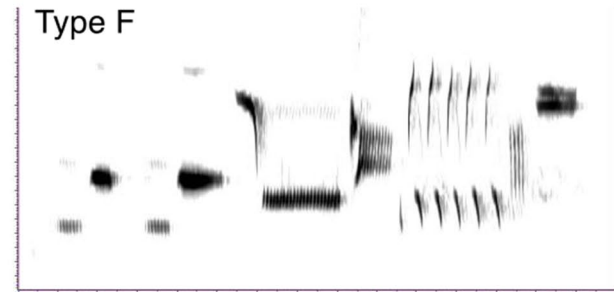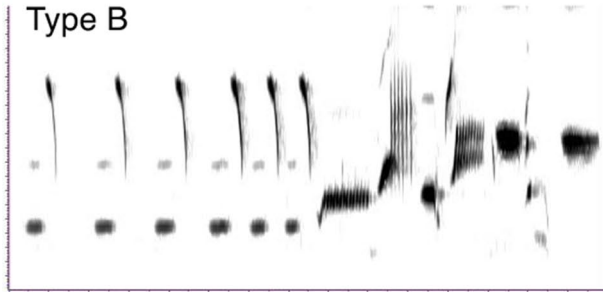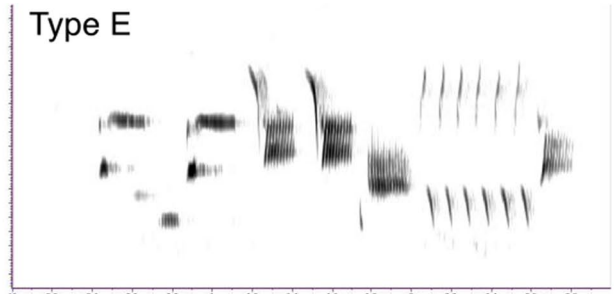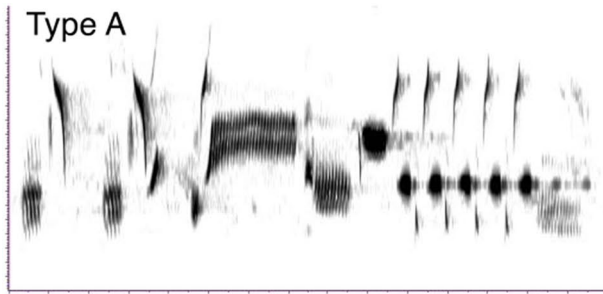
◀**Fig. 1** Spectrograms of the 8 songs (song types A-H) in the repertoire of one study male (male 1902) plus the answer song from this male's playback trial. The playback song used in the trial was type B. The answer song was also classified as type B so the male was counted as having matched. Spectrograms were made in Raven Pro 1.4 with a Hann window and a 256-point FFT

16-bit Wav files. The songs were then normalized in Audacity to either −1 dB (2019) or to −7 dB (2021). Silence was added after the song to produce a 10-s segment, and that segment was repeated 17 times to produce a 3-min recording containing 18 repetitions of the song. Both a song rate of 1 song/10 s and a bout length of 18 are well within normal limits for song sparrows (Nowicki et al. 1994).

Playback procedures

Songs were played to subjects from an iPod Touch connected to an Anchor Audio AN-Mini/MiniVox speaker. Amplitude levels on the iPod and speaker were adjusted for each 3-min playback segment to produce songs in the range of 84–88 dB SPL at 1 m (B&K Precision 32A sound level meter, A weighting).

Playbacks were conducted with the speaker placed on the ground near an edge of the subject's territory. The playback equipment was set up in advance of the second recording session, and playback was triggered once the observer making the recordings was confident that 300 songs had been recorded and that the subject was not singing the song type chosen for playback. The observer continued to record the subject's songs through the 3-min playback and beyond until confident that the subject had switched song types at least once after playback started.

Analysis

We consider matching to have occurred if the subject switched to the same song type used for playback in the first song-type switch made after playback started (Anderson et al. 2005; Searcy et al. 2019). With this criterion, matching by the subject is not possible if the subject is already singing the target song type when playback commences (hence, the care we took was not to start playback when the subject was singing the playback song type). We examined spectrograms of all songs recorded from the subject in the second (playback) session to identify the first song produced at the first song-type switch after playback started, which we designate as the "answer song" (Fig. 1). We then visually compared the spectrogram of this answer song to spectrograms of all the song types in the subject's repertoire to classify the answer song to song type and thus determine whether matching occurred. Our

original assessments of the dependent variable (matching/non-matching) were not made blind to the independent variables; however, we subsequently had our classification of answer songs to song type repeated by another experienced observer who was blind to the independent variables, blind to our original classifications of the answer songs, and blind to the identity of the playback songs. The independent observer agreed with our classifications for 32 of 32 answer songs.

We used bivariate logistic regression to test the association of matching (yes/no) with three independent variables, which we designate as "interval length," "prior bout length," and "type frequency." Interval length describes the interval since the subject last sang the playback song type and is measured as the number of bouts the subject sang in this period divided by its repertoire size. This calculation gives the proportion of a minimum cycle that has passed since the male last sang the playback song type and thus is a measure of how much the subject is due to sing it again according to the cycling rule. Prior bout length is the length (in the number of songs) of the last bout of the playback song type that was produced by the subject. The bout length rule predicts that the greater the length of the most recent bout of a song type, the less willing the subject should be to switch to that type. Type frequency is the usage frequency of the playback song type, measured by the relative frequency of that song type in the subject's first recording session, calculated as the number of songs of the playback type that were recorded divided by the total number of songs recorded. The usage preference rule predicts that song types with high usage should be matched more often.

We ran three univariate logistic regression models, one for each of the three independent variables listed above. We then ran one multivariate logistic regression model incorporating the two independent variables that showed significant relationships with matching in the univariate models. In the interest of avoiding over-parameterization, we did not incorporate additional independent variables, covariates, or interaction terms in the models. Logistic regression analyses were run in SPSS Statistics v 26. We checked for outliers in the independent variables by converting the data to Z-scores. Only one value for one variable (type frequency) exceeded the usual criterion for outliers that $|Z| > 3$. Because the Z-score, in this case, was only marginally greater than 3 ($Z = 3.056$) and because eliminating the case did not change the significance of the regression, we retained the case in the analysis. We also confirmed that the two independent variables used in the multivariate logistic regression showed low collinearity ($r = -0.091$). The sample size in all statistical tests is the number of subjects (32). All probability levels are two-tailed.

Results

The 32 song sparrows in this study had a mean repertoire size of 8.2 song types (range 5 – 12). These males therefore had a mean of 7.2 song types to choose from when they switched away from the song type they were singing prior to playback, giving them a $1/7.2 = 0.139$ probability of matching the playback by chance. Nineteen of 32 males, or 0.594, matched the playback song type during their single playback trials. The observed incidence of matching was significantly greater than the chance expectation by a chi-square test ($X^2 = 56.1$, $P < 0.00001$).

A bar plot of standardized interval lengths for matchers and non-matchers (Fig. 2a) suggests that males with long intervals since last singing the playback song type were more likely to match that type. Confirming this suggestion, the univariate logistic regression with interval length as the sole independent variable was significant ($X^2 = 5.840$, df =1, $P = 0.016$). The coefficient relating interval length to matching was positive ($B = 3.773$) and significant (Wald $X^2 = 4.533$, $P = 0.033$). The pseudo-R^2 for this model (Nagelkerke R^2) was 0.225. The model successfully classified individuals as matchers or non-matchers in 68.8% of cases, compared to 59.4% correctly classified by a null model assuming that all individuals perform the more common behavior (i.e., matching).

A bar plot of prior bout length for matchers and non-matchers (Fig. 2b) suggests that males with high prior bout lengths were less likely to match. Confirming this suggestion, the univariate logistic regression model with prior bout length as the sole independent variable was significant ($X^2 = 6.402$, d.f. = 1, $P = 0.011$). The coefficient relating prior bout length to matching was negative ($B = -0.158$) and significant (Wald $X^2 = 4.439$, $P = 0.035$). The pseudo-R^2 for this model (Nagelkerke R^2) was 0.245. The percentage of cases correctly classified by this model (62.5%) was barely higher than for the null model.

A bar plot of frequency of usage of the playback song type for matchers and non-matchers (Fig. 2c) suggests little relationship between usage frequency and matching. In agreement with this inference, the univariate logistic regression model with matching as the dependent variable and type frequency as the sole independent variable was not significant overall ($X^2 = 0.546$, df = 1, $P = 0.460$). The pseudo-R^2 for this model was very low (Nagelkerke $R^2 = 0.023$), and the percentage of cases correctly predicted (62.5%) was barely higher than for the null model

A multivariate logistic regression model was fitted with prior bout length and interval length as the two independent variables. This model was strongly statistically significant ($X^2 = 11.947$, df = 2, $P = 0.003$) with a substantially higher pseudo R^2 (0.420) than for any of the univariate models. Regression coefficients for both prior bout length ($B = -0.169$) and interval length ($B = 4.12$) were significant ($P = 0.047$ and $P = 0.040$ respectively). The model containing prior bout length and interval length (plus a constant) successfully predicted matching/non-matching for 81.3% of cases.

Discussion

Our results demonstrate that two previously established syntactic rules affect the probability of song type matching in an eastern population of song sparrows. The cycling rule states that individuals cycle through their repertoires in close to the minimum number of song type bouts (Searcy et al. 2022). In the context of matching, the cycling rule predicts that an individual should be more likely to match a song type it shares with a rival male the longer the interval has been since that individual last sang that type. In accordance with this prediction, we found a significant positive relationship between the probability of matching playback of a self song type and the length of the interval since the subject had sung that type. The bout length rule states that individuals follow longer bouts of a song type with longer intervals until that song type is sung again (Searcy et al. 2022). As predicted by this rule, we found that the probability of matching a song type decreases as the length of the prior bout of that song type increases. An effect on matching of a third aspect of syntax, song type usage preferences, was not supported.

Together, the cycling and bout length rules explained much of the variation in matching behavior, correctly predicting matching versus non-matching for just over 80% of individuals. A fuller understanding of the rules of song sparrow syntax might show that matching is even more tightly constrained by syntax. This accounting leaves little room for matching to vary with aggressiveness, and thus makes aggressive signaling via matching unlikely. Information on aggressiveness could still be conveyed by matching if receivers were able to adjust their response to matching based on memory of the past song sequence of the singer. Thus, for example, a singer who matched a particular song type despite having recently sung a long bout of that song type could be judged as being particularly aggressive. We have no evidence, however, that songbirds keep track of and remember the song sequences of rivals in the context of matching, and such a mechanism would certainly be demanding in terms of attention and memory. Furthermore, it would be impossible under this adjustment hypothesis for a bird to signal aggression if challenged by a shared song type that it had not sung recently or for which the most recent bout had been short. It is more parsimonious to assume that song sparrows do not attempt such adjustment and hence that aggressive

Fig. 2 Bar plots of the number of trials in which males matched (cyan) or did not match (red) as a function of **a** the length of the interval since the subject had last sung the playback song type. Interval length is measured as the number of bouts of other song types given since the subject last sung the playback song type divided by the male's minimum cycle length. **b** The length (in the number of songs) of the subject's prior bout of the playback song type. **c** The frequency of usage of the playback song type in the first recording session for each male. Usage frequency is measured as the number of songs of the playback type that were recorded divided by the total number of songs recorded
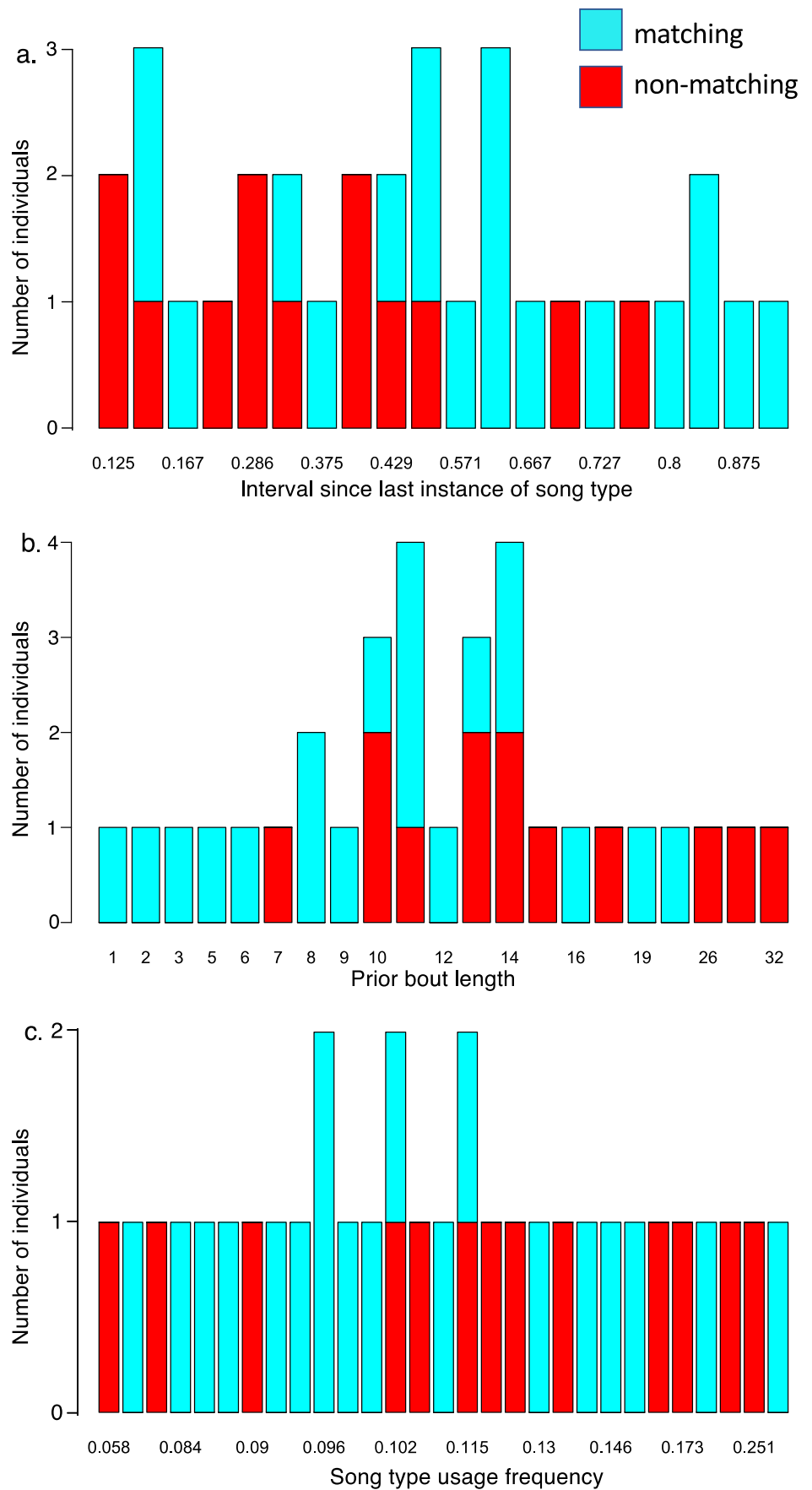
signaling via matching is not workable, at least not in our study population.

Results on aggressive signaling via matching differ substantially between our eastern population of song sparrows and western populations of the same species (Akçay et al. 2013; Searcy et al. 2014). Male song sparrows respond with greater aggression to playback of songs that type-match them than to control songs in a Washington state population (Burt et al. 2001) but not in our Pennsylvania population (Anderson et al. 2008). Type matching predicts whether male song sparrows will attack a taxidermic mount in Washington (Ackay et al. 2013) but does not have the same predictive power in Pennsylvania (Searcy et al. 2006). Matching at the territory boundary predicts subsequent escalation to more intense aggressive displays at the territory center in Washington (Akçay et al. 2013) but, again, this pattern does not hold in Pennsylvania (Searcy et al. 2013). Individuals in the Pennsylvania population are consistent from trial to trial in their aggressiveness (Nowicki et al. 2002; Hyman et al. 2004; Searcy et al. 2013) but not in whether they match (Anderson et al. 2005; Searcy et al. 2013, 2019). The overall evidence thus supports the use of matching as an aggressive signal in Washington but not in Pennsylvania. This difference in the use of matching as a signal may be explained, at least in part, by differing levels of song-sharing between neighbors in the two populations. Sharing of whole songs averages 24–26% per dyad of neighbors in the focal Washington population (Hill et al. 1999) compared to only 3–8% in the Pennsylvania population (Hughes et al. 1998; DuBois et al. 2016). Substantial levels of song-sharing may be necessary for reliance on matching as a signal, but it should be noted that song sparrows show matching of partially shared songs as well as of whole songs in both western and eastern populations (Burt et al. 2002; Anderson et al. 2005). The difference in song-sharing levels may in turn be explained by a propensity of western song sparrows to copy whole songs from older males (Beecher et al. 1994; Nordby et al. 1999) compared to a propensity of eastern birds to copy only parts of songs such as single phrases or syllables (Marler and Peters 1987, 1988). Why such a difference in song learning exists is unknown. That matching varies with aggressiveness in Washington suggests that the performance of matching is less constrained by syntax in this population than in Pennsylvania. A test of this prediction would be a valuable contribution.

Hinde (1958) proposed that the eventual variety pattern of singing, in which the singer produces a bout of multiple repetitions of a song type before switching to another type, could be explained on a mechanistic level by facilitation: producing or hearing a particular song type facilitates further production of that song type so that a bout of such songs results. Hinde (1958) further suggested that the production of a song type simultaneously produced inhibition that would gradually build up until a switch away from that type was triggered. As noted by Hinde (1958), Bertram (1970), and Falls (1985), facilitation, if it worked through hearing, could also explain matching: hearing a particular song type from an external source might facilitate the production of that type by a listener. Under this hypothesis, the auditory stimulus of a bird hearing an external song substitutes for the auditory stimulus of the bird hearing itself produce that song in prompting the choice of the next song to sing. Matching then can be viewed as "essentially a side effect of the mechanism of ordering a bird's own call types" or song types (Bertram 1970, p. 189).

The idea that matching is an unintended byproduct of mechanisms that underlie the sequencing of a bird's own song production is compatible with matching having no signaling function at all. On the other hand, it is possible for variation in matching to be partially accounted for by syntactic constraints and yet at the same time to be, in part, a free strategic choice signal (Hurd and Enquist 2005) of some parameter such as aggressiveness. This mixed view of matching was advocated by two pioneers in the study of song matching, John Krebs and J. Bruce Falls, with respect to their main study species, great tits and western meadowlarks (Krebs et al. 1981; Falls 1985). In these two species, however, individual variation in matching behavior shows no relationship with individual variation in aggressive response (Falls et al. 1982; Falls 1985), which undermines the aggressive signaling hypothesis. Great tits and western meadowlarks exhibit song sequencing patterns similar to those of song sparrows: males possess song repertoires of moderate size, sing with eventual variety, and show evidence of cycling (Falls and Krebs 1975; Krebs 1976). In both species, it seems plausible that a cycling rule exists and that it affects the occurrence of song type matching as suggested by Krebs et al. (1981) and Falls (1985). Whether these or any other species beyond song sparrows follow a bout length rule has not, to our knowledge, been investigated.

Syntax may also affect matching behavior in species having syntactic rules that differ from those of song sparrows. Songbirds that sing with immediate variety, for example, often cycle, though usually in a stereotyped order rather than a highly variable one as in song sparrows. Such cycling occurs in both immediate variety species with small repertoires, such as wood thrushes (*Hylocichla mustelina*) (Whitney 1985) and fox sparrows (*Passerella iliaca*) (Martin 1990), and in immediate variety singers with large repertoires, such as marsh wrens (*Telmatodytes palustris*) (Verner 1975) and Cassin's vireos (*Vireo cassinii*) (Hedley et al. 2017). The syntactic constraints hypothesis predicts that these immediate variety species, which rarely repeat a song type twice in succession, will respond to playback of a shared song type, not by matching it, but by singing the next song in the stereotyped sequence (Whitney 1985). Such song

advancing has been demonstrated in marsh wrens (Verner 1975), wood thrushes (Whitney 1985), and Cassin's vireos (Hedley et al. 2017).

For the great majority of songbird species, the syntactic rules governing song sequences have not been investigated; it follows that the effect of such rules on song matching and advancing has also not been studied in most species. This gap in research is especially pronounced for tropical species. To test the generality of the syntactic constraints hypothesis, further research is needed on a range of songbird species examining the syntax of song sequences and the effects of whatever syntactic rules are found on countersinging behaviors such as matching and advancing.

Declarations

Ethical approval All procedures used in this study were approved by the Institutional Animal Care and Use Committees of the University of Miami (protocols #14-049 and #20-055-LF), Duke University (protocols #A004-17-01 and #A260-19-12) and the University of Pittsburgh (protocols #18052783 and #21059264). All applicable national and institutional guidelines for the ethical treatment of animals were followed. The research was conducted with free-living birds that were not captured or otherwise handled for this study.

Conflict of interest The authors declare no competing interests.

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