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Song type variants and aggressive context

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Abstract We asked whether switching among song type variants functions as a graded signal of aggression in song sparrows (*Melospiza melodia*). Song type variants are different versions of a given song type and are defined by much smaller acoustic differences than those defining separate song types. The principal evidence that switching between song types functions as an aggressive signal, in song sparrows and other species, is that song type switching frequencies increase during aggressive contexts, for example during simulated territorial intrusions. We tested whether variant switching frequencies change in the same way, using playback of conspecific song to simulate intrusions. Male song sparrows showed a significant increase in variant switching frequencies during intrusion relative to before intrusion. After intrusions, variant switching frequencies returned to pre-intrusion levels. These results are consistent with the hypothesis that variant switching is a graded aggressive signal, but other interpretations are possible, for example, that variant switching is a signal of submission or represents simple production error.

Keywords Song sparrows · *Melospiza melodia* · Song variation

Introduction

Individual males in many songbird species sing repertoires of distinct song types, a behavior that has received widespread attention (Krebs and Kroodsma 1980; Kroodsma 1982; Catchpole and Slater 1995). Singing multiple song types allows a male to signal in ways not possible with a single, invariant song type for example by switching among types (Falls and D'Agincourt 1982; Kramer and Lemon 1983) or by matching types while countersinging (Lemon 1968; Krebs et al. 1981). Possession of a repertoire has been shown to be adaptive in both mate attraction (Catchpole et al. 1984; Searcy 1984; Hasselquist et al. 1996) and territory defense (Krebs et al. 1978; Yasukawa 1981). Much less attention, however, has been paid to another level of within-individual song variation, that occurring within song types. In at least some repertoire species, individuals sing multiple versions of each of their song types (Kroodsma 1982); these song type "variants" are defined by smaller differences than those defining separate song types. If differences among variants are discernible by listeners, then singing multiple variants could be used in some of the same signaling mechanisms as song types, notably in signaling via switching. Accordingly, we provide here a test of whether switching between variants changes with aggressive context in song sparrows (*Melospiza melodia*), using the same general approach that has been used to test for a signaling function of song type switching in this species (Kramer and Lemon 1983; Kramer et al. 1985).

The songs produced by a given male song sparrow can usually be sorted into 5–16 major categories by human observers (Borror 1965; Searcy 1984; Podos et al. 1992). Substantial additional variation occurs within each of these "song types," however (Borror 1965; Mulligan 1966). Differences between variants of a song type range from the minor, such as the addition or deletion of one or more terminal notes, to the relatively major, such as the addition or substitution of entire phrases (see Nowicki et al. 1994; Searcy and Nowicki 1999 for illustrations). The existence of considerable within-song type variation raises the question of whether song types are meaningful units (Wheeler and Nichols 1924; Stoddard et al. 1988). The validity of song types as functional categories is

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supported, however, by several lines of evidence. First, objective classification of song sparrow songs via cluster analysis produces major categories that map very closely to the song types produced by subjective classification (Podos et al. 1992). Second, operant conditioning methods show that song sparrows associate variants of the same song type with each other (Stoddard et al. 1992b). Finally, playback to male song sparrows using habituation/recovery designs demonstrates that males respond significantly more strongly to switches between song types than to switches between variants of a single type (Searcy et al. 1995, 1999).

Although song types appear to be fundamental categories in song sparrow song, male song sparrows nevertheless show greater response to playback of multiple variants than to playback of single variants (Stoddard et al. 1988), and show significant recovery in response to playback when variants are switched (Searcy et al. 1995). These results demonstrate that song sparrows perceive distinctions among variants, and thus raise the possibility that this level of variation has some signal function. As is true for many songbirds (Catchpole and Slater 1995), song sparrow song functions both in signaling to females during courtship (Searcy 1984) and in signaling to males during territorial defense (Nowicki et al. 1998). Tests for female response to within-type variation during courtship have thus far proved negative (Searcy and Nowicki 1999), suggesting communication between males is the more likely context for a signaling role of within-type variation.

Male song sparrows signal to other males using both song type matching (a male replies to another with the same song type) and repertoire matching (a male replies to another with any shared song type) (Stoddard et al. 1992a; Beecher et al. 1996). Either form of matching would be possible using song type variants rather than song types, but both kinds of variant matching might be difficult to detect, either by researchers or by the birds themselves. A more likely use of song type variants in signaling between males is in switching. Kramer and Lemon (1983) showed that male song sparrows switch song types infrequently when singing undisturbed, and switch more and more frequently as they enter into increasingly aggressive situations. Kramer et al. (1985) experimentally manipulated aggressive context using playback of song sparrow song or playback paired with a taxidermic mount, and argued that switching rates were higher the more aggressive the context (but see Discussion). Nielsen and Vehrencamp (1995) showed that male song sparrows respond more strongly to playback with switching between song types than to playback with no switching. Switching between song types also increases in aggressive contexts in other species of songbird (Falls and D'Agincourt 1982; D'Agincourt and Falls 1983; Simpson 1985). These patterns are usually interpreted to mean that males use switching rates to signal their level of aggressive motivation (Kramer et al. 1985).

We tested whether frequency of switching between variants of song types changes with aggressive context. Following Kramer et al. (1985), we used playback to simulate intrusion on our subjects' territories. We then examined how frequently our subjects switched between variants during simulated intrusions compared to before and after. We also examined how simulated intrusions affect song rates and song type switching frequencies, for comparison to earlier results (Kramer and Lemon 1983; Kramer et al. 1985).

Methods

Simulated intrusions

We used 2 min of playback of conspecific songs to simulate relatively brief intrusions onto the territories of male song sparrows. Trials were performed between 4 and 9 July 1997, in the vicinity of the Pymatuning Laboratory of Ecology, Crawford County, Penn., USA. Trials were run in the morning, between 0600 and 1200 hours. Subjects were not individually marked, but we feel confident that we avoided testing the same subjects twice by using each territory only once and completing the trials in a sufficiently short time span (6 days) that movement of male territory owners between territories was highly unlikely.

After locating a male song sparrow singing on his territory, we first installed the playback equipment, with a Nagra DSM loudspeaker set near the center of the male's territory, connected by 16 m of speaker cord to a Marantz PMD 221 tape recorder. We placed the speaker on the ground, face up, near one or more bushes that could be used as cover by the subject when approaching the speaker. Then, without starting playback, we tape-recorded the male for 10 min. If the subject failed to sing at least 15 songs during this "preintrusion" period, we aborted the trial. If the subject sang 15 or more songs, we then initiated playback. The lag between the end of the pre-intrusion period and the broadcast of the first song, which marked the onset of the intrusion period for analysis, was the order of 1 min.

Playback consisted of 13 songs spaced at 10-s intervals. The total duration of the playback period was therefore 2 min plus the length of the 13th song (song sparrow songs are usually 2–3 s in length). For calculating song rates, we rounded the length of this "intrusion" period to 2 min. Songs were broadcast at approximately 85 dB sound pressure level (measured at 1 m). We tape-recorded the subject through the intrusion period and continued recording without any break for a 10-min "post-intrusion" period. We continued the trial through the intrusion and post-intrusion periods regardless of the number of songs sung during those periods, i.e., we used no criteria for minimum song number.

We recorded the subjects using either a Sony TCM D5M or a Sony TCM 500 tape recorder with either a Sennheiser ME88 shotgun microphone or a Sony ECM-170 microphone in a Sony PBR-330 parabola.

Playback songs had been recorded previously in Crawford County, using the same equipment. We used 12 playback tapes, each containing a different song sparrow song type, and we presented each tape to two different males. In the analysis we use as the sample size the number of males (24) rather than the number of stimuli (12), as we are not comparing the response to different classes of stimuli.

Analysis

We tape-recorded a total of 1,958 songs from the subjects during the trials. All songs were spectrographed using Canary software (Charif et al. 1995), at a frequency resolution of 43 Hz and a time resolution of 5.8 ms. Hard copies were printed and saved of each song considered to be a new song type or variant.

Song sparrow song consists of two phrase categories: trills (successive repetitions of a specific series of notes, i.e., a syllable)

Table 1 Means±SE for song rates, type switching frequencies, and variant switching frequencies across the three experimental periods. Sample sizes in *parentheses*

	Before playback	During playback	After playback
Song rate	3.0±0.2 (24)	3.5±0.4 (24)	4.4±0.3 (24)
Type switching frequency	0.09±009 (24)	0.31±0.06 (20)	0.06±0.006 (24)
Variant switching frequency	0.66±0.04 (24)	0.83±0.06 (20)	0.68±0.03 (24)

and note complexes (unrepeated sequences of notes) (Mulligan 1966). Songs typically contain two to five such phrases. We considered two successive songs to be of the same song type if they shared at least two major phrases. Two trills were considered to be shared if they contained the same syllable, without reference to the number of repetitions of that syllable. Two note complexes were considered to be shared if at least half the notes were the same in both (Hughes et al. 1998). In the great majority of cases, two successive songs either shared all their phrases or shared no phrases, so judgments about when song types had switched were usually easy.

Two successive songs of the same song type were judged to be different variants if any notes or syllables were added or subtracted. Changes in the number of syllables in trills were used to discriminate successive variants as long as the trills were slow enough that we could count syllables. Note durations were not used to define variants.

To measure switching, we use switching frequencies, defined as the number of observed switches divided by the number of opportunities to switch (Searcy and Yasukawa 1990). Kramer and Lemon (1983) measured song type switching in song sparrows using bout lengths, defined as the number of renditions of a given song type sung in succession. If a male sings N songs in x bouts in a fixed time period, then mean bout length is N/x. Song type switching frequency, as we define it, would be $(x—1)/(N–1)$ for the same period. The two measures are thus fairly equivalent, though inverses. We prefer switching frequency to bout length, first for the minor reason that it directly rather than inversely measures the parameter of interest, and second because it is not biased, as is bout length, by the unavoidable truncation of the first and last bouts sung during any period over which song is analyzed (Searcy and Yasukawa 1990).

For variant switching, if a male sings a bout of n songs of one song type, he has $n–1$ opportunities to switch variants, and the total opportunities to switch is found by summing over the various song type bouts sung in a given period. A complication occurs if a recording of a given song is too poor to determine its variant and type; this occurred for 13 of the 1,958 songs (0.7%) in our sample. For such instances, we stopped the summing of switches and opportunities to switch before the unanalyzed song and started summing again after it; thus the song following the unanalyzed song was counted neither as a switch nor as an opportunity to switch.

Note that judgments about whether non-successive songs are the same type or variant do not enter into our estimates of switching frequencies. Suppose, for example, that a bird sings a series of songs of type A, a series of type B, and then one song of type X. Switching frequency will be the same whether we judge X to be another instance of song type A or a new song type C.

In four trials, neither type switching frequency nor variant switching frequency could be calculated for the intrusion period: twice because the subject sang no songs, once because the subject sang only one song (allowing no opportunities to switch), and once because the only two songs sung were not analyzable. Differences in song rates, type switching frequencies, and variant switching frequencies were assessed using ANOVA. The arc sine square root transformation was applied to both sets of switching frequencies to normalize those data. Post hoc pairwise comparisons were made using Fisher's least-significant-difference tests (Sokal and Rohlf 1995). For the latter tests, the P-values were Bonferroni adjusted for multiple comparisons.

Results

Song rates

Song rates varied significantly across the three time periods (F=5.21, df=2, 69, P=0.008). There is an upward bias in our estimate of song rate for the pre-intrusion period, due to our using a minimum criterion for number of songs in this period and no such criterion for the intrusion and post-intrusion periods. Despite this bias, song rates were lowest pre-intrusion (Table 1), significantly lower than post-intrusion (Fisher's LSD, P=0.006). Song rates did not differ significantly between the pre-intrusion and intrusion periods (P>0.10), or between the intrusion and post-intrusion periods (P>0.10).

Type switching

Type switching frequencies varied significantly across the three experimental periods (F=8.48, df=2, 65, P=0.0005). Type switching frequencies were highest during intrusion (Table 1), significantly higher than before (P=0.005) or after (P=0.0006). Switching frequencies were no different after intrusion than before (P>0.10).

To examine more closely the time course of changes in type switching frequencies, we analyzed these frequencies in seven-song blocks, seven being the mean number of songs given during playback. Mean type switching frequencies were calculated for three such blocks stretching backwards in time from the end of the pre-intrusion period and forwards from the start of the post-intrusion period. The results (Fig. 1) show that type switching frequencies returned rapidly to pre-intrusion levels immediately after intrusions ended, with a suggestion of a continued decline through the rest of the post-intrusion period.

Variant switching

Variant switching frequencies also showed significant differences across the three experimental periods (F=10.27, df=2, 65, P=0.0001). As with type switching, variant switching frequencies were highest during intrusions, significantly higher than either pre-intrusion (P=0.0003) or post-intrusion (P=0.0006). Variant switching frequencies were no different after intrusion than before (P>0.10).

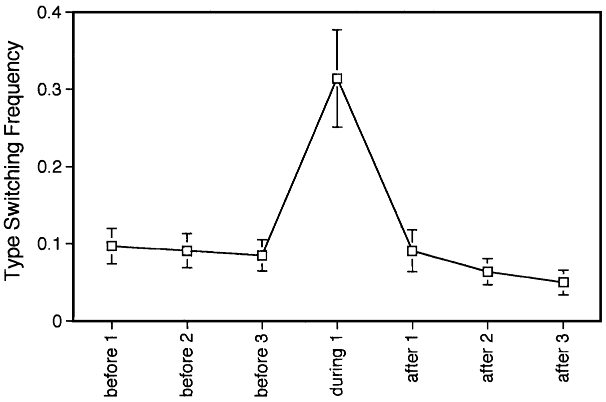

Fig. 1 Frequency of song type switching during the playback period and for the three seven-song blocks immediately before and after playback. Note that 21 songs often does not include the entire before or after periods

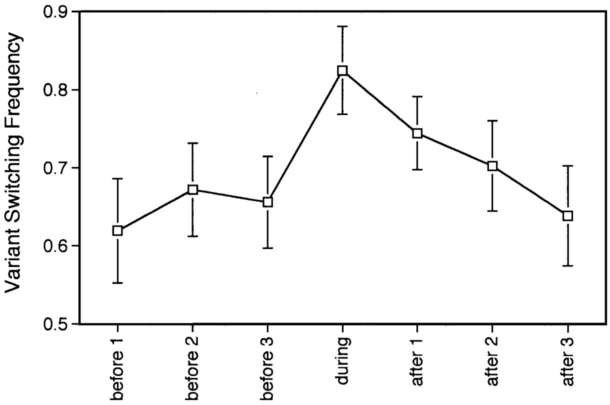

Fig. 2 Frequency of variant switching during the playback period and for the three seven-song blocks immediately before and after playback. Note that 21 songs often does not include the entire before or after periods

At the finer scale of seven-song blocks, variant switching (Fig. 2) showed a somewhat different pattern than type switching. Rather than decreasing abruptly after intrusion ended, variant switching frequencies declined more gradually, only reaching pre-intrusion levels in the third seven-song block post-intrusion.

Discussion

Song rates in our experiments exhibited a pattern similar to that found by Peters et al. (1980) in song sparrows: no significant increase during playback of conspecific song compared to before, and a large, significant increase after playback. By contrast, Kramer et al. (1985) observed a significant increase in song rates during as well as after playback. The difference in these results may be explained by the greater duration of playback in the Kramer et al. (1985) experiments (9 min) than in ours (2 min) or those of Peters et al. (1980) (3 min), as it is our impression that song sparrows increase song rates only gradually after playback commences.

Our results on song type switching frequencies confirm the results of Kramer and Lemon (1983): in song sparrows, song type switching frequencies increase (and thus bout lengths decrease) in aggressive contexts such as simulated intrusions. Comparing our results with those of Kramer et al. (1985) is problematic, because these authors measured switching using the number of switches observed over a time period. This measure is sensitive to changes in song rate as well as to switching rate, and we have seen that song rates can change over playback periods.

Type switching frequencies have been found to increase in aggressive contexts in species other than song sparrows, for example, eastern meadowlarks (*Sturnella magna*) (D'Agincourt and Falls 1983), western meadowlarks (*S. neglecta*) (Falls and D'Agincourt 1982), and Carolina wrens (*Thryothorus ludovicianus*) (Simpson 1985). The opposite pattern, that is a decrease in type switching frequencies in aggressive contexts, has been found in at least one species, red-winged blackbirds (*Agelaius phoeniceus*) (Searcy and Yasukawa 1990). Taken together, these results suggest that type switching is a conventional signal, in the sense of a signal whose message is arbitrary (Guilford and Dawkins 1995). Use of the same signal with opposite meanings in different species is strong evidence that the message is indeed arbitrary (Vehrencamp, in press).

We found that variant switching frequencies increased during simulated intrusions and decreased again after playback. This is the first evidence we know of for any species that use of song type variants changes with context. The changes in variant switching paralleled changes in type switching, except that variant switching declined gradually after playback, whereas type switching apparently declined abruptly to baseline as soon as playback stopped. Aggressive motivation may have remained somewhat elevated after playback, as suggested by the high song rates observed after playback, so variant switching may be a more finely tuned signal of aggressive motivation than is type switching.

The changes in variant switching that we observed are consistent with variant switching serving as an aggressive signal, but other interpretations are possible. One alternative is that high variant switching is a signal of submissiveness rather than aggressiveness; under this hypothesis, switching increases during intrusions because some subjects are intimidated by the intrusion. A second alternative is that song type variants are not a signal at all, but simply represent production error (Searcy and Nowicki 1999). Under this hypothesis, males increase variant switching during intrusions because they are more distracted and thus more inclined to make errors.

All three hypotheses – signal of aggression, signal of submission, and production error – are consistent with other experimental results on song variants in song sparrows. Stoddard et al. (1988) showed that song sparrow males respond more aggressively to playback of songs that switched between variants than to playback of a single variant. This result is consistent with variant switching being an aggressive signal if we assume that male song sparrows respond more aggressively to more aggressive signals from other males, a pattern that has been demonstrated in some songbird species (Nelson and Croner 1991). The result is consistent with variant switching being a submissive signal if we assume that male song sparrows respond more aggressively to less aggressive signals, a pattern that also has been found in some species (Järvi et al. 1980; Catchpole 1983). Finally, the result is consistent with variants representing production error if we assume that increased aggressiveness toward multiple variants is the product of simple dishabituation of aggressive response when variants switch. Dishabituation for switches in variants has been demonstrated for song sparrows by Searcy et al. (1995, 1999).

If the evidence that variant switching serves as an aggressive signal is ambiguous, so too is the evidence that type switching is an aggressive signal. Our knowledge about type switching in song sparrows closely parallels our knowledge for variant switching: territorial males respond more strongly to playback with increased switching rates [Stoddard et al. (1988) for variant switching; Nielsen and Vehrencamp (1995) for type switching], and switching rates increase in aggressive contexts [this paper for variant switching; Kramer and Lemon (1983) and this paper for type switching]. Again, neither evidence that a signal elicits aggression nor evidence that a signal is given in aggressive contexts conclusively demonstrates that the signal itself is aggressive, in the sense of signaling increased aggressive motivation. Better evidence would be to show that the signal predicts future aggression on the part of the signaler. Experiments are needed to test whether either type or variant switching predicts future aggression in song sparrows and other songbirds.

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