

## Discrimination of song types and variants in song sparrows

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**Abstract.** Male song sparrows, *Melospiza melodia*, sing highly variable songs. Traditionally, researchers have partitioned this variability by assigning songs to discrete categories termed 'song types', but researchers also have recognized that songs classified as the same song type are themselves variable. Territorial playbacks were used in a habituation/recovery design to investigate whether song sparrows perceive songs classified as separate song types to be more distinct from one another than songs classified as variants of the same song type. Cluster analysis was used to classify playback songs as song types or variants. Playbacks consisted of focal songs repeated for 1 h, followed by a switch to 6 min of either (1) a second variant of the focal song type from the same source male or (2) a second song type of the same source male. Twelve sets of playback tapes were used in a total of 96 trials. Subjects showed habituation in the response measure (distance to the speaker) during playback of the focal songs. Response recovered for between-song type switches, with mean distance to the speaker decreasing significantly between the last 3 min pre-switch and the first 3 min post-switch, and between the last 6 min pre-switch and the 6 min post-switch. For within-type switches, recovery was significant when comparing only the last and first 3 min. Recovery was significantly greater for between-type switches than for within-type switches on both measures. These results suggest that in the perception of male song sparrows, different song types are more distinct than are different variants of a single type.

The problem of how to categorize behaviour is a general one. Ideally, we would like categories that not only have clear and objective definitions, but that also mirror the way in which the behaviour patterns in question are categorized by the animals that use them. A good example of this problem is encountered in classifying the songs produced by male birds. In many species of songbirds, individual males sing variable songs, and it is customary for human observers to partition this variation by dividing songs into discrete categories termed 'song types' (Kroodsma 1982). Much research assumes the biological relevance of song-type classifications, for example, studies correlating the number of song types sung by males with their mating success (Howard 1974; Searcy 1984) or reproductive success (McGregor et al. 1981; Hiebert et al. 1989). Song-type classifications typically are arrived at by sorting spectrograms of songs according to relatively subjective criteria of similarity and dissimilarity. The end product of such procedures is a classification that accounts for much of the variation in

an individual's songs, but often there is still variation remaining within the resulting song-type categories (Kroodsma 1982). Song-type classifications, accordingly, are vulnerable to two criticisms: first, that a more objective classification of songs might produce different categories; and, second, that even if an objective classification did produce the same categories, the birds singing and responding to the songs might not recognize those categories, that is, they might not classify songs in the same way. The first criticism was addressed recently for our study species, the song sparrow, *Melospiza melodia*, by Podos et al. (1992). In the present paper, we address the second criticism, by investigating whether songs classified by us as separate song types are perceived by song sparrows as being more different from one another than are songs classified as variants of the same song type.

Early workers (Wheeler & Nichols 1924; Nice 1943) began the practice of classifying song sparrow songs into song types. Nice (1943), for example, described a sample of 40 males in her

Ohio study population as singing between six and 17 song types each. Nice (1943) also noted that there was some variation within her song-type categories. These early studies were limited to using handwritten notation to describe songs, but later studies based on spectrographic analysis generated similar song-type classifications and confirmed the presence of extensive within-type variation (Mulligan 1963, 1966; Borror 1965). Subsequent research on the function of song variation in song sparrows has neglected within-type variation, focusing instead on the between-song type level of variation. Functional studies have shown, for example, that female song sparrows are more stimulated in courtship by larger numbers of song types (Searcy & Marler 1981; Searcy 1984), and that there is a strong, positive correlation between repertoire size and reproductive success (Hiebert et al. 1989). Song-type number does not, however, correlate with male pairing success (Gilbert 1983; Searcy 1984) or with other measures of male quality (Searcy et al. 1985a). The interpretation of negative results is complicated by the possibility that the subjective classification of song types generated by the researchers does not fully capture the nature of the variation that is significant to the birds.

Recently, Podos et al. (1992) have provided a technique for classifying song sparrow songs that is more objective than the traditional method of visually sorting sonagrams. Podos et al. (1992) illustrated the new technique by classifying the songs of 12 males. All 'minimal units of production', or 'MUPs', were identified in a large sample of songs for each male. A MUP is usually a single note, but it may also be a group of notes that always occur together and in sequence. Pair-wise similarities were calculated between all songs produced by individuals, based on the proportion of MUPs shared between songs. Cluster analyses were then performed on these sets of pair-wise similarities. The resulting classification of songs to song types closely resembled a classification produced independently by the traditional method. The two classification methods produced similar numbers of song types per male, and on average disagreed on the classification of only 3.5% of each male's songs. The cluster analysis shows that a statistical description of song variation in song sparrow repertoires yields song-type categories similar to those produced by the traditional method. The cluster analysis does not, however,

address the issue of whether the resulting categories are meaningful to song sparrows themselves.

A study by Stoddard et al. (1988) served to highlight the question of how song sparrows classify songs. Stoddard et al. (1988) presented to territorial males playbacks of (1) single variants of single song types, (2) single variants of three different song types and (3) six different variants of a single song type. Response to all three sets of stimuli was similar during playback, but responses declined faster after playback for single variants of single song types than for either the multiple types or multiple variants. Response to multiple types and multiple variants was similar both during and after playback, suggesting that song sparrows regard variants of the same song type as being equally as distinctive as different song types.

In a second study, Stoddard et al. (1992) approached more directly the question of how song sparrows classify songs. Two male song sparrows were taught to respond (by pecking a key) to one group of song types (GO), and not to respond to a second group (NOGO). The subjects were then tested with new variants not used in training. The subjects responded to a high proportion of variants of GO song types, and failed to respond to a high proportion of NOGO variants, indicating that they lumped these variants in the same song types as did the experimenters.

In the present study, we take another approach to the discrimination of song types and variants by song sparrows, using a habituation/recovery paradigm, with free-living territorial males as subjects. Previous work with other species has shown that aggressive responses of territorial males habituate during continued playback of the same song, and recover when the song is switched (e.g. Petrionovich & Patterson 1979; Yasukawa 1981). In our experiments, we present a single variant of a song type repeatedly to a male on his territory, sustaining playback long enough so that the subject's response habituates. We then switch the playback to a second song that is either (1) a variant of the song type used in the habituation part of the playback, or (2) a second song type of the same source male. We then measure the subject's response recovery. All playback songs are from recordings made distant from the playback sites, so the subjects could have had no prior experience with them. We predict that if male song sparrows regard two song types as being

more distinctive than two variants of the same song type, they should show greater response recovery for switches between song types than for switches between variants.

## METHODS

Subjects were male song sparrows holding territories within 10 km of the Pymatuning Laboratory of Ecology in Crawford County, Pennsylvania. Experiments were performed between 0600 and 1200 hours between 2 June and 11 July 1992 and between 1 and 13 May 1993.

The playback experiments used a single speaker design modified from Peters et al. (1980). The speaker was placed face-up on the ground, well within the boundaries of the subject's territory. The observer(s) stood 20–25 m away from the speaker. We used distance between subject and speaker as the sole response measure. Observers noted distance in five categories: 0–2 m, 2–4 m, 4–8 m, 8–16 m and greater than 16 m. Before playback started, we placed poles at measured distances of 4 and 8 m from the speaker as an aid to judging distance categories. Trials were timed with a stopwatch starting with the first playback song, and distances were recorded on flow charts divided into 5-s blocks. In calculating mean distances to the speaker, we assumed that a bird in the 0–2 m range was on average 1 m from speaker, in the 2–4 m range 3 m, in the 4–8 m range 6 m, in the 8–16 m range 12 m, and in the greater than 16 m range 24 m. We chose 24 m for the greater than 16 m range based on previous estimates of the sizes of song sparrow territories and on our experience with the behaviour of males during playback (Peters et al. 1980; Searcy et al. 1985b).

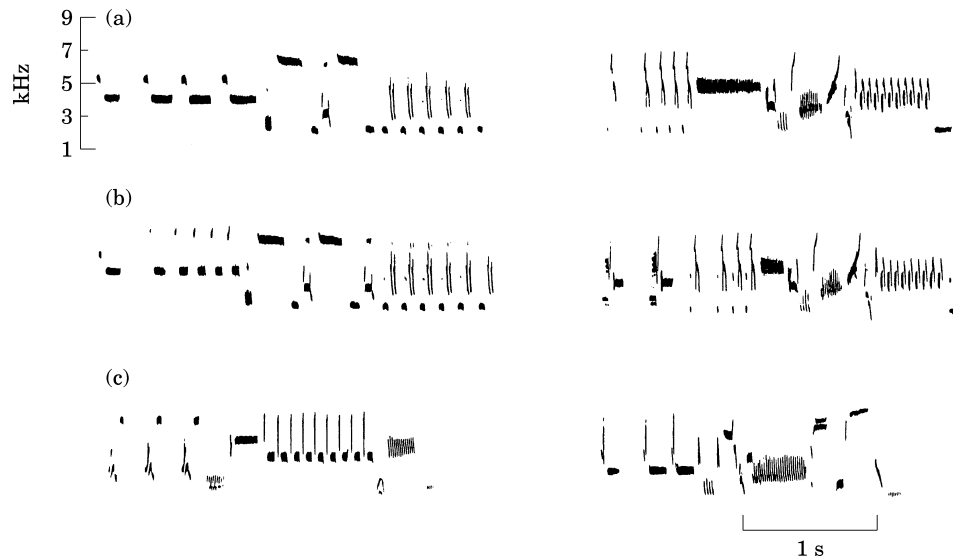
In pilot experiments performed during June and July of 1991, we sought a protocol under which subjects would reliably habituate to playback. In the first pilot experiment, we presented 2-min periods of playback of a single song (6 songs/min) alternating with 2-min silent periods, repeating this sequence six times. In a second pilot experiment, we presented 15 repetitions of the 2-min playback and 2-min silent period alternation. Subjects did not show significant habituation in either case. In a third pilot experiment, we presented 60 min of continuous playback (6 songs/min), and analysed the data by averaging distances over 3-min blocks. As in the earlier pilot experiments,

we found that response increased (i.e. mean distance decreased) between the first and second playback blocks. Response thereafter gradually decreased (mean distance increased), from a mean ( $\pm$  SE) of  $2.8 \pm 0.6$  m during the second 3-min block to a mean of  $6.1 \pm 1.5$  m during the 20th block. This increase in mean distance to the speaker between periods 2 and 20 was significant (Wilcoxon  $T=0$ ,  $N=10$ ,  $P<0.01$ ).

The design of our main experiment was modelled on the third pilot experiment. Playback started with 60 min of a focal song, presented at six songs/min. Playback then switched to either (1) 6 min of a variant of the focal song type (a within-type switch) or (2) 6 min of a second song type from the same male (a between-type switch). We again analysed the data by averaging distance to the speaker over 3-min blocks. Two measures of habituation were planned: (1) a comparison of mean distance in the second and 20th time blocks, using a Wilcoxon matched-pairs signed-ranks test and (2) a linear regression of mean distance against time period for time blocks 2–20. We also planned two measures of recovery, both using Wilcoxon tests: (1) a comparison of mean distance to the speaker in time blocks 20 (last pre-switch) and 21 (first post-switch), and (2) a comparison of mean distance to the speaker in time blocks 19 and 20 combined (last two pre-switch) and blocks 21 and 22 combined (two post-switch). Finally, we planned comparisons of both recovery measures for within-type switches versus between-type switches, using Wilcoxon tests.

We used 12 sets of playback tapes, two of which are illustrated in Fig. 1. Each set consisted of one tape with a within-type switch and one with a between-type switch, both using the same focal song type. We presented each tape to four subjects. Results were averaged over the four subjects, and the Wilcoxon tests were performed on those averages. Thus, the sample size in most of the statistical tests is the number of tape sets (12 pairs) rather than numbers of subjects, as recommended by Kroodsma (1989). The exceptions (with regard to sample sizes) are the linear regressions, in which we averaged distances for each time period over all tapes and regressed these averages against time period; here the sample size for each regression is the number of time periods in the analysis (19).

We ran all eight trials with one tape set (four within-type trials and four between-type trials) before moving on to the next set. On the first trial



**Figure 1.** Sound spectrograms illustrating two sets of the playback songs. Songs on the left and the right are from two different males and were used in different tape sets. (a) The two songs used as focal (habituation) songs; (b) variants of the song types in (a) according to MUP cluster analysis, which were used as recovery songs in the within-type trials; (c) different song types than (a) and (b) (but from the same males), which were used as recovery songs in the between-type trials. Spectrograms were made using a Kay Elemetrics DSP Sona-graph model 5500 (300 Hz frequency resolution, 4.8 ms time resolution).

with a given set, we chose the tape to be presented (within-type or between-type) by coin toss, after the subject had been chosen and the equipment had been set up. On the second trial, we presented the other tape in the set, on the third trial we chose randomly again, and so forth. All 96 trials were done on different theories, at 15 different sites. Males were not individually marked, so it is conceivable that we tested the same male twice if he moved between territories over the period of testing. Male song sparrows generally are site faithful (Nice 1937, 1943), so such duplication is unlikely. If the subject disappeared while we were setting up the playback equipment, and did not reappear during the first 3 min of playback, we terminated the trial. Approximately 45 trials (or one in three) were terminated before completion, most for the above reason, but we also terminated trials and discarded the data if we found we had set the speaker out on a boundary between two territories, if there was an equipment failure, if we lost track of the subject, or if rain started during the trial. Tapes were played from a Marantz PMD 221 cassette-tape recorder over a Nagra DSM speaker-amplifier. Playback amplitudes were approximately 90–95 dB SPL measured at 1 m.

Playback songs were recorded in Dutchess County, New York, approximately 600 km east of the playback sites; thus none of the subjects could have had prior experience with these songs. Previous work showed that males from the study area respond as strongly to Dutchess County songs as to local songs (Searcy et al. 1985a). Songs used for playback were recorded from six individuals; four males each contributed the songs used in two playback sets, one male contributed the songs for three sets, and one male contributed songs to a single set. For each set, a focal (habituation) song was chosen haphazardly. Then two other (recovery) songs were taken from the same male's repertoire, one that had been classified as another song type, and a second that had been classified as a variant of the same song type as the focal song. Classifications were made a priori by Podos et al. (1992).

Songs were digitized at 25 kpt/s (Data Translation DT-2128G board) using 'SIGNAL' digital processing software (Beeman 1992) on a 486-based microprocessor. During acquisition, all songs were high-pass filtered (Krohn-Hite model 3500 filter, 1 kHz corner frequency, 24 dB/octave) to reduce environmental noise and low-pass

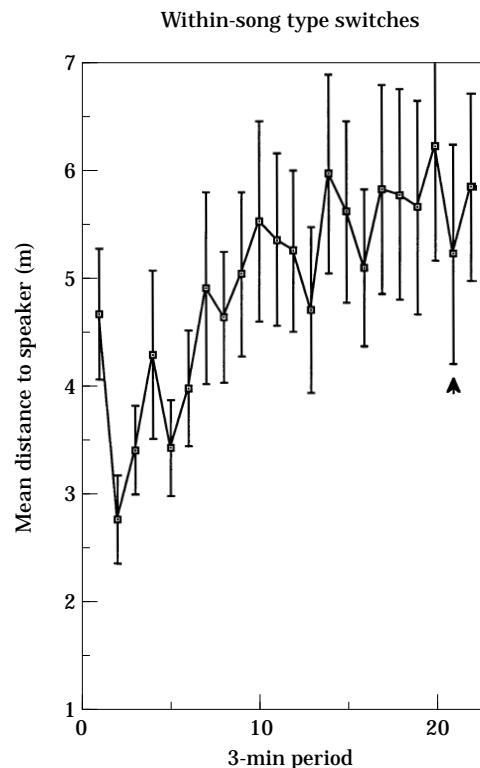
filtered (Stanford Research Systems model SR640, 10 kHz corner frequency, 115 dB/octave) to prevent aliasing. Digitized songs were then recorded directly onto a Marantz PMD 221, using SIGNAL functions to control the repetition rate (6 songs/min) and the total number of song repetitions (360 for the habituation stimulus and 36 for the recovery stimulus).

## RESULTS

Response to within-song type switches is shown in Fig. 2. We found habituation on both our measures during playback of the focal song type. Mean ( $\pm$  SE) distance of the subjects to the speaker increased significantly from  $2.8 \pm 0.4$  m in the second playback period to  $6.2 \pm 1.1$  m in the 20th period (Wilcoxon  $T=0$ ,  $z=3.06$ ,  $P<0.01$ ). Regression analysis showed a significant increase in mean distance to the speaker over periods 2–20; the regression equation was  $Y=3.3+0.15X$ , where  $Y$  is the distance and  $X$  is the period number ( $r^2=0.77$ ,  $P<0.01$ ). We also found habituation to the focal song for the tapes with between-type switches (Fig. 3). Mean distance to the speaker increased significantly from  $2.8 \pm 0.3$  m during period 2 to  $5.0 \pm 0.9$  m during period 20 ( $T=5$ ,  $z=2.67$ ,  $P<0.01$ ). Regression analysis showed a significant increase in distance between periods 2 and 20 ( $Y=2.85+0.13X$ ,  $r^2=0.87$ ,  $P<0.01$ ). Comparing response to the within-type tapes and the between-type tapes for the first 60 min, no significant differences were found for any time period ( $P>0.05$  in each case according to Wilcoxon tests). This was expected, because within-type tapes and between-type tapes were identical (within sets) for the 60 min of the focal song playbacks.

We found significant recovery for within-type switches (Fig. 2) on one measure but not the other. Mean distance to the speaker decreased significantly between periods 20 (last pre-switch) and 21 (first post-switch) from  $6.2 \pm 1.1$  m to  $5.2 \pm 1.0$  m ( $T=14$ ,  $z=1.96$ ,  $P=0.05$ ). Mean distance decreased between periods 19 and 20 combined (last two pre-switch) and periods 21 and 22 combined (first two post-switch) from  $6.0 \pm 1.0$  m to  $5.6 \pm 0.9$  m, but this decrease was not significant ( $T=24.5$ ,  $z=0.76$ ,  $P>0.10$ ).

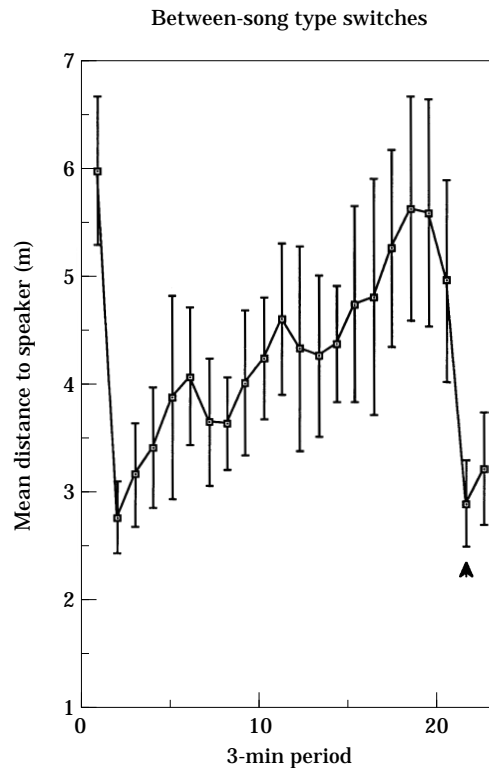
We found significant recovery for between-type switches (Fig. 3) on both measures. Mean distance to the speaker decreased significantly between



**Figure 2.** Response of male song sparrows to playback of 60 min of one song followed by 6 min of a second variant of the same song type. Response is measured as mean ( $\pm$  SE) distance to the speaker during 3-min periods. The arrow indicates the first 3-min period after the switch. Mean distance increased between the second and the last (20th) period of playback of the initial song, showing habituation. Mean distance decreased when the variant was switched, showing recovery. The decrease was significant on one measure (comparing the last pre-switch and first post-switch periods) but not on a second (comparing the last two pre-switch periods and the first two post-switch periods).

periods 20 and 21, from  $5.0 \pm 0.9$  m to  $2.9 \pm 0.4$  m ( $T=3$ ,  $z=2.67$ ,  $P<0.01$ ). Mean distance also decreased significantly between periods 19 and 20 combined and periods 21 and 22 combined, from  $5.3 \pm 1.0$  m to  $3.1 \pm 0.5$  m ( $T=0$ ,  $z=2.94$ ,  $P<0.01$ ).

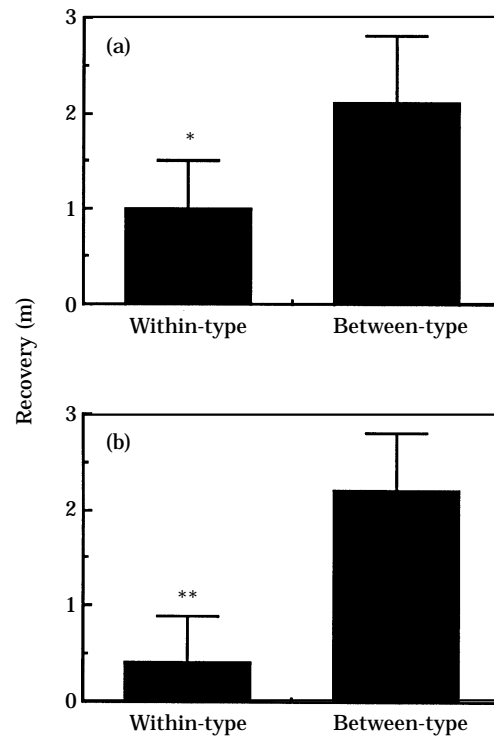
We did not perform a control to test whether recovery would occur after 60 min of playback without any switch in stimulus. We did, however, examine both the within-type and between-type results for periods 2–20, to see whether a significant recovery ever occurred between successive 3-min periods before the end of the first 60 min,



**Figure 3.** Response of male song sparrows to playback of 60 min of one song type followed by 6 min of a second song type of the same male. Response is measured as mean ( $\pm$  SE) distance to the speaker during 3-min periods. The arrow indicates the first 3-min period after the switch. Mean distance increased between the second and the last (20th) period of playback of the initial song, showing habituation. Mean distance decreased when the song type was switched, showing recovery. The decrease was significant both when comparing the last pre-switch and first post-switch periods and when comparing the last two pre-switch periods and the first two post-switch periods.

that is, during playback of the focal song. For both experiments combined, there was a total of 36 such comparisons, and in none of these was there a significant decrease in mean distance to the speaker ( $P > 0.05$  by Wilcoxon tests for each comparison). It seems extremely unlikely, then, that there would have been significant decreases between periods 20 and 21 without a switch in stimulus.

Recovery was significantly greater for between-type switches than for within-type switches on both measures (Fig. 4). Recovery between the



**Figure 4.** Recovery measured as a decrease in mean distance of the subject to the speaker (a) between the last 3-min pre-switch and the first 3-min post-switch and (b) between the last 6-min pre-switch and the first 6-min post-switch. Values are means  $\pm$  SE. \*Indicates a significant difference between the two time blocks at  $P < 0.05$ ; \*\* $P < 0.01$ .

last pre-switch and the first post-switch period averaged  $1.0 \pm 0.5$  m for within-type switches compared with  $2.1 \pm 0.7$  m for between-type switches ( $T = 13$ ,  $z = 2.04$ ,  $P < 0.05$ ). Recovery between the last two pre-switch and the first two post-switch periods was  $0.4 \pm 0.5$  m for within-type switches and  $2.2 \pm 0.6$  m for between-type switches ( $T = 4$ ,  $z = 2.75$ ,  $P < 0.01$ ).

## DISCUSSION

Male song sparrows showed greater recovery in response for switches between two song types than for switches between two variants of the same song type. The song types and variants used in the experiments were ones defined by a cluster analysis based on the sharing of acoustic elements

(MUPs) between songs (Podos et al. 1992). The MUP cluster analysis method in general produced categories very similar to those produced by visual sorting of spectrograms by human observers, and the assignments of the particular songs used in the present experiments as variants or separate song types agreed exactly with a previous subjective analysis of sonagrams (Podos et al. 1992). Our results indicate that male song sparrows distinguish between two levels of variation in their song repertoires: song types are responded to as being more distinct from one another than are within-type variants. These results accord well with those of Stoddard et al. (1992), who used an operant conditioning procedure in the laboratory to show that male song sparrows tend to associate variants of the same song type with each other. The results of the MUP cluster analysis (Podos et al. 1992), of the operant conditioning association tests (Stoddard et al. 1992) and of our discrimination experiments, taken together, provide considerable support for the conclusion that song-type classifications are biologically meaningful, in the sense that they reflect how song sparrows themselves categorize songs.

How well this conclusion generalizes to other species is an open question. We know of no other species for which experiments have been carried out testing the perceived distinctiveness of song types and variants, as in this study. Nor do we know of other studies testing whether variants of song types are associated with one another, as in Stoddard et al. (1992). Species with multiple song types often show some degree of within-type variability. Although quantitative comparisons have not been made, we suspect that the degree of within-type variability exhibited by song sparrows is relatively high. Even so, it is likely that there are species that produce song types that are as variable as those of song sparrows, and it is possible in any such case that the species categorizes its songs differently than we might.

The extent to which within-song type variation is expressed by song sparrows, and the way it is expressed by the deletion, addition and rearrangement of small units (MUPs) that are shared among many different song types (Podos et al. 1992), suggests that within-type variation is not simply the result of production errors, but instead is functional. The fact that song sparrows perceive and respond to within-type variation is also in accord with the hypothesis that such variation is

functional. Perception of within-type variation is indicated in our experiments by the significant recovery to switches between variants on one of two measures. Stoddard et al. (1988) also found that male song sparrows perceive and respond to within-song type variation, using an experimental design that was rather different from ours but which also employed territorial playback in the field. Neither study, however, directly demonstrates a function of within-type variation. Territorial playbacks test how effective particular songs or patterns of singing behaviour are in eliciting aggressive responses from a territory owner, but eliciting aggressive responses cannot be considered a function of song (Searcy 1992). Instead, the functions of song are to deter intrusion onto a territory and to attract and stimulate females. These two functions can be tested with speaker occupation experiments (e.g. Krebs et al. 1978; Yasukawa 1981) and solicitation display assays (e.g. Catchpole et al. 1984; Searcy 1984), respectively. Demonstrating that song sparrows perceive within-song type variation implies that this level of variation might be functional, but a clear demonstration of function must await the use of one or both of these other experimental designs.

One consequence of the way in which song sparrows assemble their song types from a discrete number of MUPs is that song types within the repertoire of a male resemble each other to varying degrees (Podos et al. 1992; Nowicki & Podos 1993). Repertoire size appears to be positively correlated with between-song type similarity (Podos et al. 1992), meaning that the larger a male's repertoire is, the more similar his song types are. Results from other species suggest that birds are more responsive to switches between dissimilar than between similar songs (Horn & Falls 1988; Falls et al. 1990). If song sparrows are also sensitive to between-song type similarities, then it may be that repertoire size alone is not an adequate measure of overall song variation, but instead more sophisticated measures will have to be developed that incorporate between-song type similarity.

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