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# The development of within-song type variation in song sparrows

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We investigated the development of within-song type variation in song sparrows, *Melospiza melodia*, with two experiments designed to determine how exposure to within-type variation influences the song-learning process and whether within-type variation itself is a learned trait. In the first experiment, we compared learning between two groups of males, one group tutored exclusively with song models presented with no variation, and the other group tutored exclusively with song models presented with a range of within-type variation that is normally produced by birds in the field. The two groups in this experiment did not differ significantly in any measure of how well they learned, suggesting that exposure to within-type variation has no measurable influence on the learning process overall. Nor did the groups differ in the expression of within-song type variation in their own adult songs, demonstrating that within-type variation is not a learned feature of song sparrow song. In the second experiment, we tutored a single group of birds with both invariant and variable models, allowing us to ask how within-type variability affects learning preferences. Young birds preferentially copied song type models presented with variation significantly more than invariant models. Taken together, these experiments provide insight into the evolution of within-song type variation in song sparrows, although the functional significance of this level of variation and learning preferences based on variation remain enigmatic.

The importance of bird song as a model system for the study of behavioural development (Konishi et al. 1989) can be attributed largely to the discovery that much of the structural detail of song is learned by imitation (Marler & Mundinger 1971; Catchpole & Slater 1995; Todt & Hultsch 1996). In this respect, the development of bird song resembles the development of human speech, and contrasts with the development of most other vertebrate vocal behaviours. Because of interest in imitation in the learning process, studies of song learning have focused primarily on features that are most obviously copied directly from models, such as syllable structure, syntax, song duration, sound frequency and rhythm (Baptista 1996). These aspects of song tend to vary little in successive renditions of a particular song type after development is complete, as implied by the term 'crystallization' given to the end-point of song development (Catchpole & Slater 1995). In contrast to such invariant song features, little attention has been given to the development of song variation, even though variation has become a primary focus for studies of song function (Searcy & Andersson 1986; Catchpole & Slater 1995).

The development of song variation is important to study for two reasons. First, insight into how variation influences learning and how learning influences variation may broaden our understanding of the general mechanisms that underlie song ontogeny, beyond what has been learned from studying how invariant features are copied. Second, knowledge of how variability develops may shed further light on the function of song variation. Accordingly, we here report on two experiments investigating the development of song variation in the song sparrow, *Melospiza melodia*, a species with highly variable singing behaviour.

To our knowledge, only two previous studies have addressed the development of song repertoire variation in songbirds. These studies both focused on a single aspect of song variation, the number of song types an adult male produces, but reached opposite conclusions. Brenowitz et al. (1995) demonstrated that marsh wrens, *Cistothorus palustris*, trained with more song types develop larger repertoires, whereas Kroodsma et al. (1997) found that the repertoire size of catbirds, *Dumetella carolinensis*, does not correspond to the number of song types heard during tutoring.

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In song sparrows, song varies within individuals at two levels. First, an individual male sings a repertoire of five to more than 15 song types, each of which is a highly distinctive version of the species song (Nice 1943; Searcy 1984). Second, renditions of one particular song type often vary from performance to performance (Borror 1965; Podos et al. 1992), producing what is termed ‘within-type variation’ (Kroodsma 1982). Within-type variation seems to be greater in song sparrows than in most species (Nowicki & Podos 1993), although quantitative comparisons between species have not yet been made. The similarity of any two songs produced by a male song sparrow can be measured as the proportion of notes shared between the two. Cluster analysis performed on such similarity measures demonstrates that song types are more distinctive than are variants of the same type, and that the two levels of variation can be separated objectively (Podos et al. 1992). Playback experiments have confirmed that song sparrows themselves judge song type differences to be more distinctive than differences among variants of the same type (Stoddard et al. 1992; Searcy et al. 1995).

Male song sparrows reared in isolation, with no opportunity to hear either live tutors or tape recordings, develop structurally simpler songs than males with normal experience (Mulligan 1966; Kroodsma 1977; Marler & Sherman 1985). Males exposed to conspecific song early in life develop typical song (Marler & Peters 1987, 1988; Beecher 1996), precisely copying the acoustic details of models they learn, even after exposure to as few as 30 repetitions of a song (Peters et al. 1992). The process of song learning is relatively well studied in song sparrows (e.g. Marler & Peters 1977, 1987, 1988; Beecher et al. 1994; Beecher 1996; Peters & Nowicki 1996), but as with birds in general, the development of song variation remains unexplored, despite the highly variable nature of this species’ songs. One relevant experiment is that of Marler & Sherman (1985), who showed that song sparrows reared in isolation produce song repertoires half the size of those found in nature. This result suggests that variation at the song type level, at least, may be influenced by learning.

Our experiments focus on the influence of learning on the within-song type level of variation. Our first experiment addresses whether within-type variation itself is a learned characteristic; that is, do males tutored with variable songs produce more variation than males tutored with invariant songs? Our second experiment addresses whether within-type variation affects choice of song models; that is, do males prefer to learn models presented with variation over models presented invariantly?

These two experiments, taken together, have implications for understanding the evolution of song variation. Singing multiple song types appears to have a reproductive benefit for male song sparrows, in that female song sparrows perform courtship and copulatory behaviour more readily in response to multiple song types than in response to single song types (Searcy & Marler 1981; Searcy 1984), suggesting that song repertoires have evolved in response to sexual selection. Female song sparrows, however, do not show an analogous preference for multiple variants over single variants within song types (W. A. Searcy & S. Nowicki, unpublished data), reducing the likelihood that sexual selection is responsible for the evolution of within-type variation. An alternative explanation for the high degree of within-type variation found in song sparrows is that this level of variation has been favoured by cultural selection. Cultural selection requires that ‘memes’ (i.e. units of cultural selection) differ in their probability of transmission between generations because certain memes are learned preferentially (Lynch 1996). Cultural selection on bird song has been invoked, for example, to explain habitat matching: songs whose acoustic properties match the transmission properties of a particular habitat should be heard clearly at greater distances and therefore should be learned preferentially relative to songs more poorly matched to the habitat (Hansen 1979; Catchpole & Slater 1995). If cultural selection is to explain the evolution of within-type variability in an analogous way, it must be true both that males learn variable songs in preference to invariant songs, and that the learners subsequently reproduce the variable models with greater variability than they do the invariant models. Together, our experiments test both these conditions.

# METHODS

## Experimental Design

Subjects in our two experiments were male song sparrows collected as nestlings (3–5 days old) within an 80-km radius of Durham, North Carolina. We hand-fed the birds until they were approximately 4 weeks old, at which time they were feeding independently. Seed and water were supplied ad libitum after fledging. Birds were housed together as nestlings and for a brief period after fledging. During tutoring, each bird was housed individually in a sound attenuation chamber (Industrial Acoustics AC-1, $58 \times 40 \times 36$ cm) containing a loudspeaker (Realistic 40-1272). In both experiments we tutored birds with tape-recorded songs (Marantz PMD 221 tape recorder, Paso series 5000 amplifier). Tutoring was done for 12 weeks, until the subjects were about 100 days old. This tutoring period corresponds to the sensitive period for song acquisition for song sparrows raised in the laboratory (Marler & Peters 1987).

In experiment 1, we compared learning between two groups, one tutored exclusively with song models presented with no within-type variation (invariant models) and one tutored exclusively with models presented with variation (variable models). Fifteen young males from 10 nests were divided into two groups (individuals from the same nest were divided randomly between the two groups). The ‘Invariant’ group ($N$=7) was exposed to 16 different song sparrow song types, all presented without any within-type song variation. The ‘Variable’ group ($N$=8) was exposed to the same 16 song types, but in this case the song types were presented with variation that approximated the within-type variation heard in the wild (see below). Tutoring for the Invariant and Variable groups began at $17 \pm 4$ ($\bar{X} \pm$ SD) and $16 \pm 2$ days of age, respectively. By comparing these two groups with respect to how much the birds learned, we are able to examine the influence of variation of song types on song acquisition. By comparing the extent to which the birds in these two groups produced within-type variation in their crystallized adult repertoires, we are able to ask whether this level of song variation is a learned characteristic in song sparrows.

In experiment 2, we tutored a single group of birds with both invariant and variable song models. Seven males from six nests were tutored with a total of 16 models beginning at 19 ± 3 days of age. These song models were the same as those used in experiment 1, but eight were presented as invariant models (as to the invariant group in experiment 1) and the other eight as variable models (as to the variable group in experiment 1). By determining which models were selected and how much was learned from them, we are able to ask whether within-type variability affects learning preferences.

## Song Type Models

We used 16 different song sparrow song types as model songs, selected from the repertoires of three wild adult males recorded in the laboratory. We chose song types that were as distinct as possible so that later identification of models selected for learning could be as unambiguous as possible.

We digitized each of the 16 song types (SIGNAL software, Engineering Design 1996), and modified each of them in seven different ways. By inspecting songs recorded in the wild, we used naturally occurring variations of song types (i.e. typical patterns of note additions and deletions) to suggest the construction of the experimental variants (Podos et al. 1992; Nowicki et al. 1994). Thus, including the original form of the song type, each model song type had eight variants (e.g. Fig. 1). We varied all 16 types in a similar manner, so that the within-type variation for each song type was roughly equivalent. All songs used on training tapes were recorded from these digital models.

Tutoring tapes contained a sequence of bouts, each bout being 24 songs of one song type, recorded at one song per 10 s, for a total of 4 min. A bout of an invariant model type contained 24 repetitions of a single variant of one song type. A bout of a variable model type contained all eight variants of one song type, with the eight variants arranged randomly in three consecutive sequences. For each experiment, bouts of different song types were arranged randomly on the tutoring tape, with successive bouts separated by 1 min of silence. In experiment 1, the birds in the invariant group heard bouts of 16 invariant model types. The variant group heard the same 16 model types, in the same bout order, but presented with eight variants of each type. In experiment 2, in which birds heard eight bouts of invariant model types and eight bouts of variable model types, we arranged the invariant and variable song type bouts randomly on the tape.

## Song Analysis

We recorded all males when they were about one year old, after their adult repertoires had crystallized (Marantz PMD 221, Realistic Omni-directional microphone, Digitech RDS 1900 digital delay to facilitate automatic recording). We analysed about 300 songs from each individual, which was sufficient to ensure a complete sample of each bird's song type repertoire (Searcy et al. 1985; Podos et al. 1992). We determined the adult repertoire of each male by visually inspecting the spectrograms of their crystallized songs (Kay Elemetrics DSP 5500 Sona-graph, 16-kHz analysis range, 300-Hz frequency resolution). We defined spectrogram traces separated by at least 8 ms of silence as 'notes', which are the smallest units in a song (Podos et al. 1992).

Song sparrows in the laboratory may learn portions of song models (usually sequences of adjacent notes) rather than entire songs (Marler & Peters 1987, 1988; Beecher 1996), and develop note repertoires composed of notes that can be matched to model notes (copies) as well as notes that cannot be attributed to particular models. To determine which model types had been selected for learning and what proportion of a bird's note repertoire was learned, we visually compared the notes in each male's repertoire to the notes comprising the 16 model song types (as in Marler & Peters 1988). We used spectrographic similarity of student notes to model notes, using parameters such as frequency range, frequency and amplitude modulation, and duration, for identifying copies of models. Notes that we could not match to any model were considered 'inventions' (Marler & Peters 1982). After copies were identified, we could evaluate the song learning performance of the birds using two measures: (1) the proportion of copied notes in each male's note repertoire, and (2) the number and form (variable or invariant) of model song types selected by each male for learning.

We used the methods outlined by Podos et al. (1992) to define song types and song type variants and to measure within-type variation. In addition to assigning song variants to song types and determining the number of song types for each bird, this method also quantitatively describes the amount of variation with which each song type in a bird's repertoire is produced. Briefly, after describing the sequence of notes for each song in a bird's recorded sample using visual inspection of sonagrams (RTS software, Engineering Design 1996), we identified all 'minimal units of production' (MUPs) by visual inspection of spectrograms. A MUP is the smallest unit of song that is always produced intact throughout each bird's recorded sample; MUPs are often single notes but may be groups of notes that always occur together and in sequence. Each song composed of a unique sequence of MUPs is considered a 'variant'. We calculated pairwise similarities for all variants in a bird's repertoire based on the proportion of MUPs they shared, and performed a cluster analysis on these similarities to group variants according to song type (unweighted pair-group method, Sneath & Sokal 1973, with moat analysis used to determine the optimal level of grouping; Wirth et al. 1966).

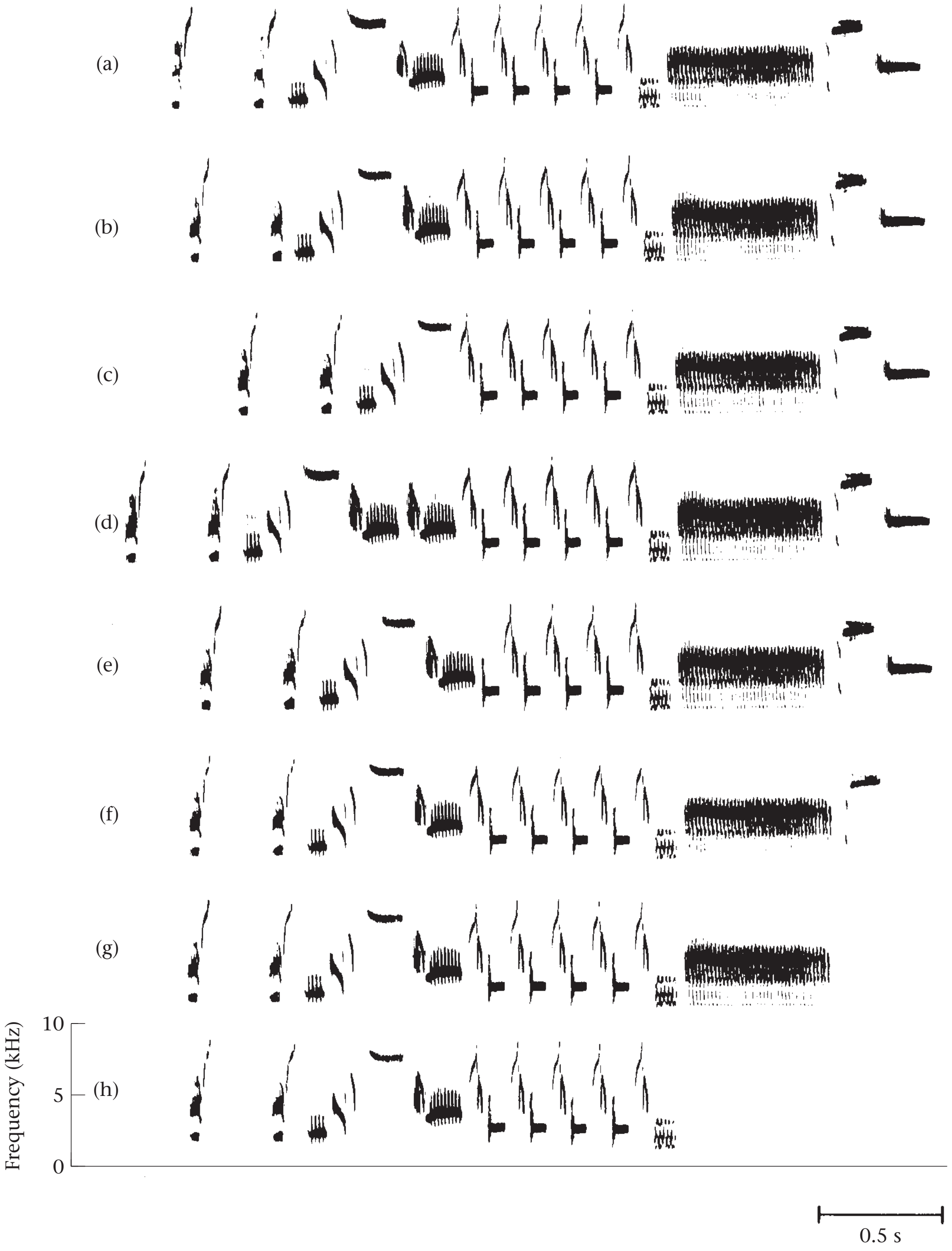

**Figure 1.** Example of the eight variants of one model song type used to tutor young males. In this example, song (a) is the original form of song type, and songs (b–h) are modifications of this song. Song (b) was made by removing the last note of the final syllable of the first trill of (a). Song (c) removes two notes in the first note complex of (a). Song (d) repeats the same two notes defined in (b) so that these notes in the first note complex of (a) become a two-syllable trill. Song (e) removes the first two notes of the first syllable of the second trill of (a). Songs (f), (g) and (h) remove different combinations of notes from the final note complex of (a) (the final note, the final three notes, and the final four notes, respectively). In general, we used these same seven types of changes to create variants for each of the 16 model song types. Sonagrams here were produced on a Kay Elemetrics DSP 5500 Sonagraph, 16-kHz analysis range, 300-Hz frequency resolution.

Within-song type variation was quantified by averaging the linkage similarity values (i.e. the cluster analysis branch lengths) of adjacent variants classified as a particular song type by the cluster analysis. Our measure of mean within-song type variation for an individual was calculated by averaging all within-type song variation values for that individual. In a wild population, this score typically ranges between 0.8 and 1.0 (Podos et al. 1992). In experiment 1, the average within-type similarity score was 0.91 ± 0.05 for all model song types used in the variable group, and 1.00 for the invariant group. The average within-type similarity score for experiment 2,

**Table 1.** Comparison of song repertoire characteristics and measures of song learning between the invariant and variable groups in experiment 1 (means and standard deviations are shown)

| | Invariant group | Variable group | *P* |
|---|---|---|---|
| Total number of notes | 80±12 | 81±17 | 0.87 |
| Total number of MUPs | 61±10 | 60±9 | 0.76 |
| Total number of song types | 9.7±3.7 | 9.9±1.1 | 0.81 |
| Number of copied notes | 40±19 | 44±31 | 0.79 |
| Proportion of model copied | 0.46±0.12 | 0.48±0.15 | 0.60* |
| Size of 'chunk' copied (*n* notes) | 3.4±1.2 | 3.3±0.8 | 0.83 |
| Number of models copied | 6.6±2.9 | 5.9±2.9 | 0.65 |
| Within-type variation | 0.92±0.04 | 0.91±0.03 | 0.70 |

*Mann–Whitney *U* test.

with eight variable song types and eight invariant types, was intermediate (0.96 ± 0.06).

Data were checked for normality by the Lilliefors test. Unless otherwise noted, statistical comparisons were made using *t* tests.

## RESULTS

### Experiment 1

Song repertoire characteristics and measures of song learning for the invariant and variable groups are compared in Table 1. The mean size of the note repertoire did not differ between the two groups, nor did the number of MUPs per male or the number of song types per male. Measures of song learning also were very similar between the two groups: the number of copied notes per male did not differ between the invariant group and the variable group, and once a male in either group chose a model, he learned about half of the notes in that model. The number of notes per sequence of adjacent notes copied from models was virtually identical for the two groups, indicating that one group did not learn larger intact 'chunks' of the models. There also was no significant difference in the number of song type models selected for learning between the groups.

Finally, the level of within-song type variation was no different between the group tutored with invariant models and those tutored with variable models. The mean within-type variation was 0.92 ± 0.04 for the former group and 0.91 ± 0.03 for the latter. The level of within-type variation produced by both groups was similar to the level in the variable tutor model songs (0.91), even though the birds in the invariant group were never exposed to variable songs.

### Experiment 2

The birds in this experiment were exposed to equal numbers of variable and invariant song types, but learned significantly more of the variable songs than of the invariant songs (*P*=0.011; Fig. 2). Furthermore, every male in the sample chose variable model types more often than invariant model types (sign test: *P*=0.008). Although the subjects copied more of the variable models than of the invariant models, the proportion they copied per variable model (0.42 ± 0.14) was no higher than the proportion they copied per invariant model (0.41 ± 0.27; Mann–Whitney *U* test: *P*=0.90).

As a control for whether the preference for learning variable song models in experiment 2 was due to some acoustic feature other than variability, we examined the learning preferences of the birds in experiment 1. All the model types presented to birds in experiment 2 were presented to the subjects of both treatment groups in experiment 1, either without variation (to the invariant group) or with variation (to the variable group). In neither group was there a significant preference for the models that were presented with variation in experiment 2 over the invariant models (*P*>0.20 for both groups). In other words, when presented with equal variability in experiment 1 (i.e. all types being variable as presented to one group, or all types being invariant as presented to the other group), no preference was shown for these particular song types, but when presented with a contrast in variability (in experiment 2), a significant preference was shown for the variable models.

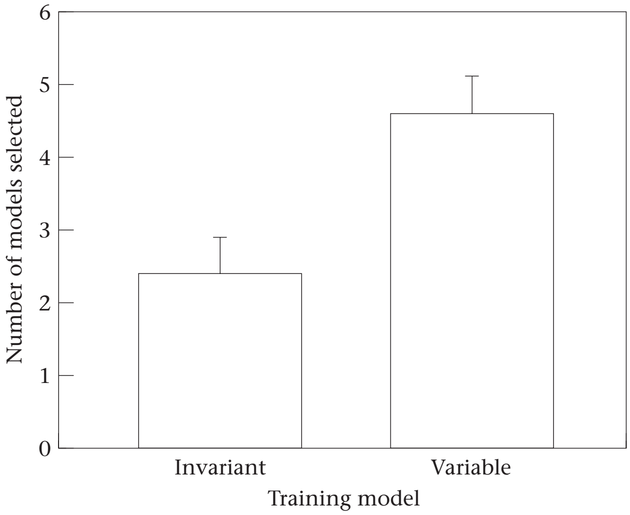

**Figure 2.** Mean (±SE) number of model song types copied by males in experiment 2. Variable model types were selected significantly more often than invariant model types.

## DISCUSSION

The results of experiment 1 indicate that song sparrows do not require exposure to within-type variation in order to produce such variation (Table 1). Birds tutored with completely invariant song types produced songs with just as much within-type variability as did birds tutored with variable song types. Both groups of subjects, whether tutored with variable or invariant songs, produced levels of within-type variation squarely within the range produced by male song sparrows in nature. Similarly, we found no evidence in experiment 2 that song material learned from variable song types was subsequently produced with greater variation than material learned from invariant song types. We can conclude, then, that within-type variation is not a learned feature of song sparrow song.

When presented with both variable and invariant song types as potential models in experiment 2, young male song sparrows preferred to copy the variable types (Fig. 2). The variable types in our experiments were presented with species-typical levels of within-type variation, whereas the invariant song types were presented with no variation, which is abnormal for song sparrow song. Thus, the preference for variable songs might be interpreted as a preference for learning conspecific song patterns, analogous to the preferences for conspecific note structure, syllable structure and temporal patterning previously demonstrated for song sparrows (Marler & Peters 1977, 1988). Alternatively, the preference we have shown could reflect the outcome of an adaptive mechanism related to the function (if any) of within-song type variation in this species. Finally, learning preferences for variable song may reflect a nonadaptive mechanism whereby attention is drawn to variable stimuli even when such selectivity brings no particular benefit. We consider each of these possibilities in turn.

In general, learning preferences for conspecific features of song should be favoured by natural selection because they promote copying of conspecific over heterospecific song, and conspecific song functions better during adulthood in attracting females and defending a territory. Preference for a certain level of song variation, however, seems unlikely to be a particularly efficient mechanism for species recognition, and other species identifying cues are certainly available (Marler & Peters 1977; Peters et al. 1980). Previous studies using tutor songs presented with no within-type variation have found song sparrows quite capable of choosing and accurately learning conspecific song (Marler & Peters 1977, 1988; Peters et al. 1992). In our experiment 1, song sparrows selected the same number of models for learning and produced an equal number of copied notes whether tutored with invariant songs or solely with variable songs. These results demonstrate that within-type variation is not a necessary cue for recognition of conspecific song. We think it unlikely that variation is even a subsidiary cue for species recognition, but we cannot disprove this possibility.

Natural selection might favour a preference for learning variable songs if the preference confers some other selective advantage to the young birds copying these more variable songs. We do not see an obvious adaptive advantage here, especially given that within-type variation itself is not a learned trait, as demonstrated by experiment 1. In general, our attempts to demonstrate an adaptive function for within-song type variation in song sparrows have met with negative results (reviewed in Searcy & Nowicki, in press). One possibility, however, is raised by recent work on song sparrows in a New York population showing that within-song type variation increases prior to aggressive encounters, such as territory incursions (J. Bower, personal communication). This observation suggests that within-type variation could signal level of aggressiveness (although this inference needs to be tested experimentally). If so, the preference for learning more variable songs might represent a mechanism whereby young birds learn preferentially from aggressive males, as has been suggested for indigo buntings, *Passerina cyanea*, and zebra finches, *Taeniopygia guttata* (Payne 1981; Clayton 1987).

Hartshorne (1956) proposed habituation avoidance as a primary function for repertoires of redundant song types. In a similar vein, within-song type variation may have the effect of reducing habituation to repetitions of the same song type. Thus, we cannot rule out the possibility that learning preferences for variable song are simply the outcome of a fundamental perceptual mechanism whereby attention is drawn to variable stimuli even when such selectivity itself has no particular adaptive benefit (Searcy 1992). Learning theorists also point out that animals presented with multiple exemplars of a stimulus class may take longer to learn them, but form a stronger general representation of the stimulus than when presented with only a single exemplar (Wasserman 1995). If the preference we have shown stems from increased attention or greater efficacy of a general learning mechanism, then we would expect a preference for learning from more variable songs to be a widespread, if not universal phenomenon, but we are not aware of any other work that would allow us to examine this prediction.

Do our results shed light on the evolution of within-song type variation? From the perspective of an adult male singer, the learning preference we have demonstrated could suggest an adaptive function of within-type variation only if adult males benefit by having their songs more likely to be copied. This would be the case, for example, if having one's songs more prevalent in the population somehow made those songs more attractive to females or more effective in male–male interactions. We do not know any mechanism by which the former could occur. It is conceivable that older males benefit from having younger males copy their songs, in that this copying might eventually increase the proportion of males in the population the older male is able to match. Song type matching has been proposed as a mechanism for directing song at a particular competing male (Brémond 1968). If being copied gives an older male a competitive advantage, however, selection might then act against the copying preference on the part of young birds.

An alternative explanation for the evolution of the production of within-type variation is that this level of variation has been favoured by cultural selection. Our learning results do not support this hypothesis. As stated previously, the cultural selection hypothesis requires that males learn variable songs in preference to invariant songs, and that the learners subsequently reproduce the variable models with greater variability than they do the invariant models. The first condition is supported by the results of experiment 2, but the second condition is negated by the results of experiment 1: males tutored with variable songs did not produce them with greater within-type variability than males tutored with invariant songs. Thus the preference for learning variable songs should not lead to any tendency for within-type variability to increase over generations. In light of this negative evidence for cultural evolution, and in the absence of concrete evidence for an adaptive function, we are left with the possibility that within-type variation represents production error, occurring because selection against variation is not sufficiently strong to eliminate it (Searcy & Nowicki, in press).

Our experiments did not directly test whether learning influences the development of between-type variation, that is of song type repertoires, but some of our results address this issue. Marler & Sherman (1985) found that male song sparrows reared in isolation develop a mean of five song types. Males in our experiment 1, whether or not they were exposed to within-type variation, developed a mean of about 10 song types (Table 1). Males in nature also develop a mean of about 10 song types (Podos et al. 1992). Subjects in both treatment groups in experiment 1 were tutored with only eight song types, whereas most free-living males are probably exposed to far larger numbers of song types (Beecher et al. 1994). We might infer from these facts that exposure to a few conspecific song types facilitates the development of a normal repertoire, but beyond this, the number of song types heard during learning has little effect on the numbers of song types developed by an individual. If this inference is true, then we would be left with the conclusion that learning plays little or no role in the development of within-male song type variation on any level, at least not in song sparrows.

This conclusion is the same as that reached for catbirds by Kroodsma et al. (1997), who found that the lack of early exposure to song models did not influence the size of a male's repertoire. But it differs from the findings of Brenowitz et al. (1995) working with marsh wrens, who found a relationship between the number of song types heard early in life and the size of adult males repertoires, with birds exposed to relatively fewer songs developing smaller repertoires than are normally observed in the wild. The contrasting results between catbirds and marsh wrens might be accounted for by the fact that catbird vocal development appears to be less dependent on imitation (Kroodsma et al. 1997), whereas marsh wrens rely heavily on imitation to acquire new songs (Kroodsma & Verner 1978). Our data confound this neat contrast, given that song sparrows rely on imitation to acquire song material (Marler & Peters 1987, 1988; Beecher et al. 1994), but we do not find evidence that the number of tutor songs strongly influences adult repertoire size. Clearly, more work needs to be done to clarify this issue. An interesting experiment would be to examine repertoire development in male song sparrows tutored with a single song type each.

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