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Selective attrition and individual song repertoire development in song sparrows

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We compared the songs of young male song sparrows, *Melospiza melodia*, in the early 'plastic' phase (while the songs may still be modified, or dropped altogether) and in the later 'crystallized' phase. Birds in this sample dropped 1–3 songs from their plastic repertoire on their way to a crystallized repertoire of 8–11 songs. Consistent with theory of selective attrition, the songs the young birds tended to drop were songs that matched fewer neighbours and matched them more poorly than the songs they retained. At the same time, however, the birds often modified the songs they retained so that these crystallized versions were less similar to the songs of their neighbours than the plastic versions had been. They were more likely to do this for songs they shared with more neighbours. Thus, the song learning process appears to consist of two opposing processes: a tendency to copy and retain the songs of the birds who will be the young bird's neighbours in the first breeding season; and a tendency to modify at least some of these songs so that they are more individually distinctive.

Keywords: *Melospiza melodia*; song learning; song sparrow; vocal communication

Songbirds learn their songs, but species vary widely in how they use this ability, ranging from those in which individuals slavishly copy the songs of their tutors to those in which individuals improvise or invent their songs (Catchpole & Slater 1995; Brainard & Doupe 2002; Beecher & Brenowitz 2005). Most songbirds fall in the middle ground, so that song learning usually results in area- or neighbourhood-wide song conformity, or 'dialects', but there are also clear differences between the song repertoires of different birds within the dialect group. Our study species, the song sparrow, *Melospiza melodia*, is one of the species from this middle ground. A male song sparrow develops a repertoire of 8–9 songs, which he typically shares with his neighbours, but which are distinctive enough to permit individual recognition (Stoddard et al. 1991; Wilson & Vehrencamp 2001).

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We previously showed that a young male song sparrow in our study population (and in western North American populations generally), learns the songs of a group of tutor-neighbours during his natal summer and autumn, and retains for his adult repertoire about 8 or 9 songs, most of which resemble the songs of those tutors that survived the winter (Nordby et al. 1999). By March or April, the beginning of their first breeding season, males produce fully formed or adult song and their repertoires do not change; that is, they 'crystallize' after that point (Nordby et al. 2002). We also showed that sharing songs with one's neighbours is advantageous (Beecher et al. 2000b; Wilson et al. 2000). Nevertheless, the bird's songs are not perfect copies of his tutors' songs but tend to differ in some ways that make them individually distinctive. In cultural transmission models of song learning, these small differences in the songs of tutor and tutee are often treated as 'errors' (Slater & Ince 1979; Goodfellow & Slater 1986; Payne et al. 1988; Lachlan & Feldman 2003).

Marler & Peters (1981, 1982) showed that a young songbird memorizes many more songs in the natal summer and autumn than he will keep for his final repertoire, which typically 'crystallizes' the following spring. The

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young bird will sing many of these songs in the plastic song stage of song development before dropping some of them on route to his final repertoire. Nelson & Marler (1994) proposed that this 'selective attrition' of the repertoire results from social interactions with the young bird's new neighbours in late winter or early spring, the young bird keeping the songs that best match the songs of these neighbours and dropping those that match them less well. Nelson (1992) provided direct evidence for the selective attrition hypothesis for a migratory population of field sparrows, *Spizella pusilla*. In this population, a young male returns from migration with several songs, and ultimately pares his repertoire down to one song that best matches the song of his most active neighbour.

In our resident population of song sparrows, we showed that young song sparrows retain more songs from those adults who survive the winter than from those who do not (Nordby et al. 1999). However, the adult birds whose songs the young bird memorizes in his natal summer and autumn typically overlap the neighbours with whom he will interact the next spring. Thus, while this finding is consistent with a selective attrition effect, it does not directly show it, for the similarity may be due to an early rather than a late effect: the young bird may have interacted more in the natal summer and autumn with (and learnt more songs from) those adults who ultimately survived the winter.

In the present study, we asked two general questions. First, given that there is a delay between when the bird memorizes song models (beginning in his natal summer) and when he crystallizes his final repertoire (9–10 months later at the beginning of his first breeding season), does the bird modify his song repertoire to better match the songs of his neighbours of his first breeding season? We examined this question by comparing their plastic song repertoires recorded in the field in late winter to their crystallized repertoires several months later to see if, as predicted, they had kept songs more similar to and dropped songs less similar to those of their spring neighbours. In addition, we asked whether males modify the songs they retain to more closely match their neighbours' song types? Song sparrows have the ability to vary their song types (Stoddard et al. 1988; Podos et al. 1992), and thus in theory shaping of this sort would be quite feasible. We also considered the alternative hypothesis that 'fine tuning' of the song features might proceed in the opposite direction, to move the song away from those of close neighbours. We long noted these small differences between the bird's songs and those of his tutors and neighbours and wondered whether they were truly errors in transmission, or whether they have been introduced by the bird to individualize his song repertoire. Again, comparison of plastic and crystallized versions of a song can definitively establish whether the song has become more or less similar to that of a neighbour or model song.

METHODS

Study Population and Subjects

Our study site is an undeveloped 200-ha park along Puget Sound in Seattle, Washington, U.S.A. The sparrow habitat is a mixed coniferous and deciduous woodland with a dense understory interspersed with open meadows. The song sparrow population there is nonmigratory and birds remain on, and defend, their territories year-round. In any given year there are 120–150 males occupying breeding territories and the average territory tenure is three years. This site has been part of a long-term study for nearly 20 years, and during the years of the present study, all males were uniquely banded (with three plastic colour leg bands and one U.S. Geological Survey aluminium band) and their song repertoires were recorded.

Subjects for the present study were 12 young male song sparrows less than a year old (but in their second calendar year and thus identified as a 'second-year' or 'SY' bird) that we banded and recorded between 1993 and 2000. We identified these subjects as SY males by the nonstereotyped, plastic quality of their song in January and February of the year we first recorded them; although adult song is slightly less stereotyped at this time of the year than it is later in the spring, it is clearly distinguishable from the song of SY males. All subjects were territorial and paired with a female by March of their first breeding season.

Song Repertoire Recording

Plastic song repertoire

The precrystallized, plastic song repertoire of each subject was recorded during one to four recording sessions representing two or more hours of singing in January or February just before their first breeding season. No data are available to indicate how much recording is required to get the entire plastic repertoire, but our results suggest that we recorded most of the plastic repertoire (see below). All recordings were made using Sony TC-D5M or Marantz PMD221 cassette recorders and Sennheiser ME67 or ME88 directional microphones. We analysed all recordings using the real-time spectrographic software program Syrinx (J. M. Burt; http://syrinxpc.com/) and sonagrams of all significant variations of every song type each male produced were printed out for visual comparison to sonagrams of those in that male's crystallized repertoire.

Crystallized song repertoire

Each adult male song sparrow in our study population has 6–11 distinct song types in his crystallized song repertoire. A male will produce each song type with some, but limited, variation such that a sonagram of one song type is easily distinguished by eye from that of another song type (Stoddard et al. 1988; Podos et al. 1992). Males produce their song types with eventual variety, meaning they sing bouts of one song type before moving on to a bout of the next song type (i.e. AAA…, BBB…). In our study population, males cycle through their repertoire of N song types, on average, in $N+2$ song bouts and thus, for most purposes, we estimate that we identified all song types in a male's repertoire after recording 16 consecutive song bouts (Wilkerson, C. R., Nordby, J. C. & Beecher, M. D., unpublished data). For the present study, however, we doubled that criterion. Not only did we want to be sure that we had recorded all song types in each subject's repertoire, but we wanted to identify all significant variations of each song type as well. We recorded each subject on two to four separate occasions for a total of 34–76 song type bouts per male. To ensure that we were recording crystallized repertoires, all adult song recordings were made after March of each subject's first spring. Songs were recorded and analysed using the same methods described above.

Selective Attrition Analysis

We took a two-step approach to examine the selective attrition process. The first step was to determine whether song attrition had occurred between the plastic and crystallized stages of song development. If so, the second step was to determine whether the song attrition process was selective and aimed at producing a repertoire that better matched the song repertoires of each subject's neighbours in their first spring.

To examine whether subjects had dropped song types that were included in their plastic repertoires, three independent judges (authors J.C.N., S.E.C. and M.D.B.) visually compared sonagrams of song types in each male's plastic repertoire to sonagrams of those in his crystallized repertoire. We were specifically looking for entire song types that had been dropped and not necessarily trying to identify changes in variations within song types.

To examine whether the attrition process was selective, the judges visually compared sonagrams of all songs (including dropped song types and the plastic and crystallized versions of retained song types) for each subject to sonagrams of those in the repertoires of each subject's adjacent neighbours. We looked for the best matching variations of songs and then rated how well they matched using a four-point scale: 0 = no match, 1 = at least 50% of the song matched (i.e. half of the elements, or notes, were the same and occurred in the same order), 2 = at least 75% of the song matched, and 3 = all or most of the song matched. We devalued matches if the elements occurred in a different order.

RESULTS

Selective Song Attrition

Subjects had an average of 10.2 song types in their plastic repertoires and 9.3 song types in their crystallized repertoires. It is likely we missed a few songs in the plastic repertoire, since we discovered six songs in the crystallized repertoires of the 12 birds that we had not found in the plastic repertoire. The 12 birds dropped 16 songs from their plastic repertoires. Nine subjects dropped one song type each, two subjects dropped two song types each and one subject dropped three song types.

Subjects had between three and six adjacent male territorial neighbours (mean = 4.7 neighbours) in their first breeding season. The song types that subjects dropped from their repertoires were shared by significantly fewer neighbours than were the plastic versions or crystallized versions of the songs they retained ($N = 12$, means = 1.14 versus 1.82 versus 1.71 neighbours per song, respectively, paired t test: dropped versus plastic: $t = 2.82$, $P = 0.015$; dropped versus crystallized: $t = 2.78$, $P = 0.017$; Fig. 1).

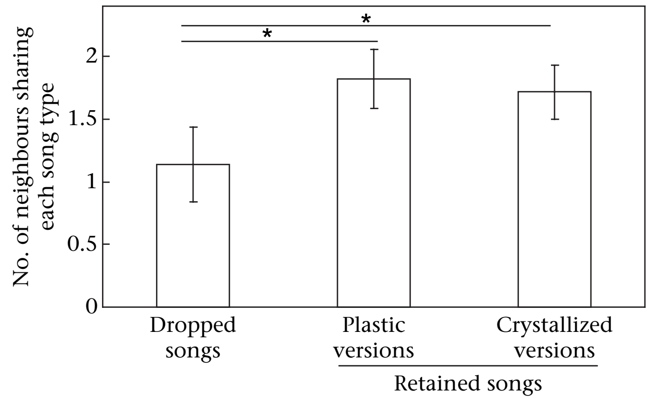

Figure 1. Number of neighbours (mean ± SE) that shared the songs that each subject dropped from their song repertoire or retained (plastic and crystallized versions). Paired t test: $^*P < 0.05$.

Given that the song types subjects dropped were shared by fewer neighbours, we then examined whether those dropped songs were also poorer matches to the neighbours' songs than were the retained songs. For this analysis, we compared each of the subject's song types with the one neighbour song that had the highest matching score (scale of 0–3, 3 being complete match) and compared the dropped songs to the plastic and crystallized versions of retained songs (Fig. 2). Both plastic and crystallized versions of the retained songs matched the neighbours' songs better than did the dropped songs, but the difference was significant only for the plastic versions ($N = 12$, means = 2.43 versus 1.69 rating, plastic retained versus dropped; paired t test: $t = 2.45$, $P = 0.031$, means = 2.20 versus 1.69 rating, crystallized retained versus dropped; paired t test: $t = 1.64$, $P = 0.09$; Fig. 2). In other words, subjects' plastic versions of retained songs were significantly better matches to neighbour songs than were the crystallized versions of these same songs ($N = 12$, means = 2.43 versus 2.20 rating, respectively, paired t test: $t = 2.50$, $P = 0.028$; Fig. 2).

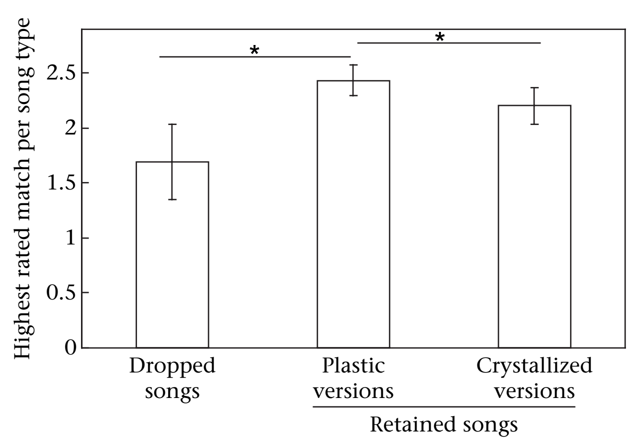

Figure 2. Highest rated neighbour-matching song (mean ± SE, scale 0–3) for songs that each subject dropped from their song repertoire or retained (plastic and crystallized versions). Paired t test: $^*P < 0.05$.

Song Type Shaping

We were intrigued by the finding that the plastic versions of some of the songs the birds retained were better matches to their neighbours' songs than were the crystallized versions, suggesting that in these cases the bird had modified its song in the direction away from the presumptive model. Because our analysis had compared the subjects' songs to the best matching neighbour song, we wondered whether the young males had perhaps altered their songs so that they matched the songs of more neighbours. That is, perhaps they averaged the differences between neighbour songs. In this way, a song would have been modified 'away' from the best matching neighbour song, but 'towards' the songs of other neighbours. To test this hypothesis we focused only on those songs that had different matching scores in plastic versus crystallized form (i.e. those that had been modified in some way) and compared the average matching score for all neighbours that shared each song.

All 12 subjects had at least one song type that had been modified in some way between plastic and crystallized song (mean = 2.8 songs, range 1–5 songs). Of the 112 subjects' song types, 30% had been modified in some way, so most songs, in fact, did not change much between plastic and crystallized song. Of the 34 songs that were modified, 26 (76%) were altered such that the crystallized versions were poorer matches to all neighbours' songs, not just to the best matching neighbour song as we had already observed. For example, Fig. 3 shows subject GEMO's plastic and crystallized versions of a song that he shared with his neighbour. The plastic version was a good match to his neighbour's song (match rating = 3), but in the crystallized version he had changed the order of the song elements and altered the trill (match rating = 2). An example of more drastic song modifying is given in Fig. 4. Subject YBPM had a song in his plastic repertoire that was a good match to one of his neighbours songs (match rating = 3), but he also sang a variation of that song type that was quite different. In his crystallized repertoire he had altered the nonmatching variation even more and never produced the matching version such that this crystallized song type was not considered a shared song (match rating = 0). The new crystallized version of that song did not match any other neighbour's songs either.

Looking at all modified songs together, the mean neighbour-matching score was higher for the plastic versions than for the crystallized versions of songs but the difference was only marginally significant ($N = 12$, means = 2.24 versus 1.77 rating, respectively, paired t test: $t = 2.07$, $P = 0.063$).

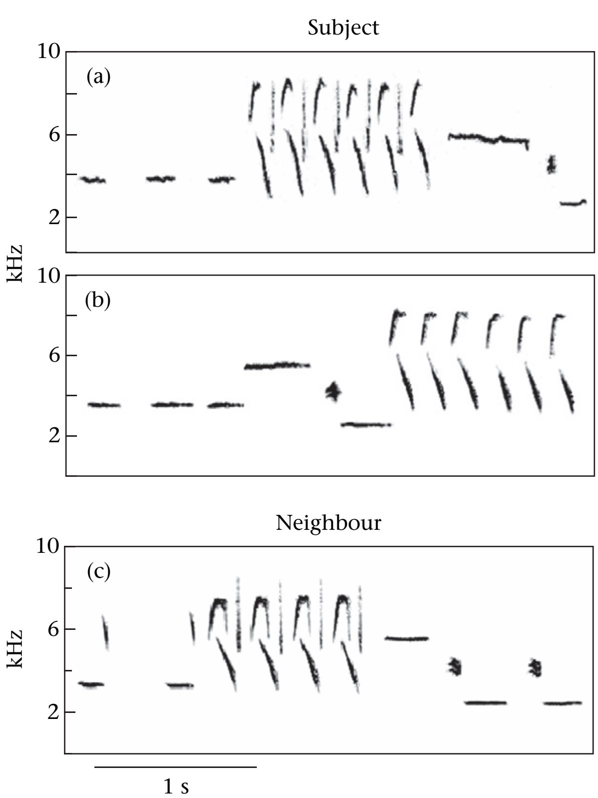

Figure 3. Plastic version (a) and crystallized version (b) of a song type that subject GEMO shared with his neighbour (c). Plastic version match rating = 3, crystallized version match rating = 2 (scale 0–3).

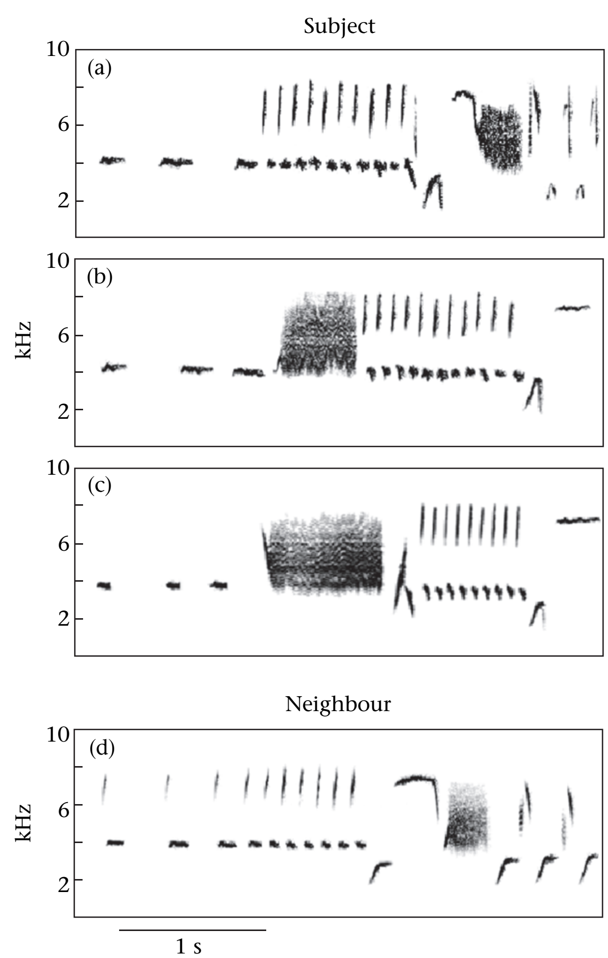

Figure 4. Plastic song variation A (a), plastic song variation B (b) and crystallized version (c) of a song type that subject YBPM shared with his neighbour (d). Plastic song variation A match rating = 3, crystallized version match rating = 0 (scale 0–3). Subject dropped plastic song variation A (a) from his repertoire.

We identified a clear predictor of which songs would be modified away from the same song type of the bird's neighbours: the modified songs were shared with more neighbours on average than were nonmodified songs ($N = 26$ and 72, means = 2.58 versus 1.58; $t = 3.85$, $P = 0.0002$).

DISCUSSION

Our comparison of a young males' plastic song repertoires recorded in January and February with their crystallized song repertoires recorded in April or later reveals that song attrition does occur in song sparrows. Moreover, an important feature of this attrition is the young male's tendency to drop song types that are shared by fewer neighbours and that match the neighbours' songs less well. Thus, these results are consistent with the Nelson–Marler theory that young songbirds fine-tune their song repertoires by preferentially retaining those song types that best match those of their neighbours of their first breeding season.

Our results are consistent with other results obtained for our and other populations of western song sparrows that suggest that sharing songs with neighbours is advantageous. Most relevant are the following findings. (1) Field and laboratory studies both indicate that young sparrows preferentially learn or retain tutor- or neighbour-shared songs (Nordby et al. 1999, 2000, 2001). (2) Birds who share more songs with their neighbours hold their territories for more breeding seasons than do those sharing fewer songs (Beecher et al. 2000b; Wilson et al. 2000). (3) Neighbours sharing more songs have fewer aggressive interactions than those sharing fewer songs (Wilson & Vehrencamp 2001). (4) Neighbours preferentially use their shared songs in countersinging interactions (Beecher et al. 2000a; Burt et al. 2001; Beecher & Campbell 2005).

On the other hand, our failure to find that young song sparrows modify the song types they retain to more closely match their neighbours' song types is contrary to the larger theory. As observed earlier, this form of shaping is certainly within the capability of song sparrows given their tendency to vary successive versions of a given song type in normal singing (Stoddard et al. 1988; Podos et al. 1992). To the contrary, we observed a tendency for young males to modify about a quarter of their songs away from those of their neighbours. In these cases, the young bird typically modified his song so it was not only less similar to the best matching neighbour's version, but less similar to the versions of all neighbours having this song type. The key variable in these cases appears to have been how many neighbours shared the song type: the young bird was more likely to modify his version of a song type away from his neighbours, the more of these neighbours that shared this song type. We tentatively offer the following hypothesis for why the young bird might modify his song so as to reduce its similarity to a neighbour's version of the song type. While song sharing, as suggested above, may be advantageous in general, it may also be advantageous to have individually distinctive song types. Individual recognition of song is a critical component of neighbour interactions in song sparrows (Stoddard et al. 1991), in songbirds in general (Stoddard 1996), and indeed in any animal that uses signals (especially long-distance signals) to indicate territory boundaries and to modulate interactions with long-term neighbours (Sherman et al. 1997; Starks 2004). And when more neighbours share a particular song type, the pressure for individuality should be even greater.

Thus, we suggest that in song sparrows, and perhaps in many other species as well, song learning consists of two opposing processes of conformity and individualization. The conformity consists of the young bird accurately copying the songs of the tutor-neighbours of his natal summer and autumn and later dropping songs that poorly match the songs of the neighbours of the next spring (his first breeding season). The individualization consists of the bird modifying some of the songs he has retained so that they no longer match the tutor or neighbour versions as well in the final crystallized repertoire as they did in the earlier plastic repertoire. Thus, a young bird winds up conforming to the songs of his neighbourhood while at the same putting his individual signature on at least some of these songs.

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