

Does learning produce song conformity or novelty in white-crowned sparrows, *Zonotrichia leucophrys*?

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Song learning in birds makes it possible for males to faithfully imitate tutors and also to generate novel improvisations. Within local dialects of the Puget Sound white-crowned sparrow, most males share the terminal trill phrase in their songs. In contrast, the introductory note complex is more variable within local populations and appears to encode individual identity. We studied the song-learning process during initial territory establishment in a wild population of white-crowned sparrows. Although most adult males sing a single song type, many yearling males overproduce song types early in their first singing season before deleting all but one song type from their repertoire. We asked whether this attrition process favours retention of a song with a note complex that resembles that of a male's neighbour, as would be predicted by various hypotheses assuming a benefit to song sharing, or whether it favours retention of a distinctive note complex, which would produce individuality in song. We found that males that initially overproduced song types retained shared note complexes, and that these males were more likely to share their adult note complex with neighbours than were young males that did not overproduce. Only 51% of recruits overproduced, however, and we close by speculating that overproduction and close song sharing may be correlates of male quality and learning ability.

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Song learning in birds, a familiar example of a socially learned behaviour, can produce either conformity with a stimulus, as when a young pupil models its song(s) on those of one or more tutors, or novelty, if the young bird improvises or invents his song (Marler & Peters 1982c; Slater & Lachlan 2003). Song conformity resulting from imitative learning has been emphasized in previous research because it is the process leading to the formation of local song dialects or neighbourhoods, which may persist for many years (Podos & Warren 2007). The question of how individual males might benefit from sharing song(s) with their neighbours has attracted much research interest. Among the hypotheses often considered are that shared songs may be preferred by females, may address threat to specific receivers, may be deceptively mimetic, and serve as a badge of familiarity (Beecher et al. 1997). In contrast, song novelty may be favoured for different reasons, the most obvious being the advantage(s) to being individually recognizable (Tibbetts & Dale 2007). Individual recognition by song is universal, or nearly so, in songbirds (Lambrechts & Dhondt 1995; Stoddard

1996) and should be facilitated by unique acoustic 'signatures'. Individually distinctive song(s) may be advantageous in establishing and maintaining territories and/or could be favoured by a female mating preference for novelty. The goals of this paper are not to identify the function(s) of conformity or novelty in song, but rather to study the developmental mechanism(s) that produce conformity or novelty, and to describe the local geographical pattern in song structure that results from the learning process. Local clustering of songs has been shown in some populations of white-crowned sparrow (Cunningham et al. 1987; Bell et al. 1998; Nelson et al. 2001), but not in others (Trainer 1983; Nelson et al. 2001). However, none of these studies identified the particular song phrase(s) that varied on a local scale.

The white-crowned sparrow is well known for accurate imitation of song, which results in 'song dialects' (Marler & Tamura 1962; Kroodsmas et al. 1984). One subspecies, the Puget Sound white-crowned sparrow, *Z. l. pugetensis*, forms a linear series of about 12 song dialects along the Pacific northwest coast of North America (Baptista 1977; Nelson et al. 2004). Most adult males sing a single song type typical of the local dialect, although as described below, 'overproduction' of two or more song types is common early in the breeding season (Nelson 2000). Two parts of the song, the note complex and the trill (Fig. 1), display different patterns of geographical variation. The terminal trill of the song varies little

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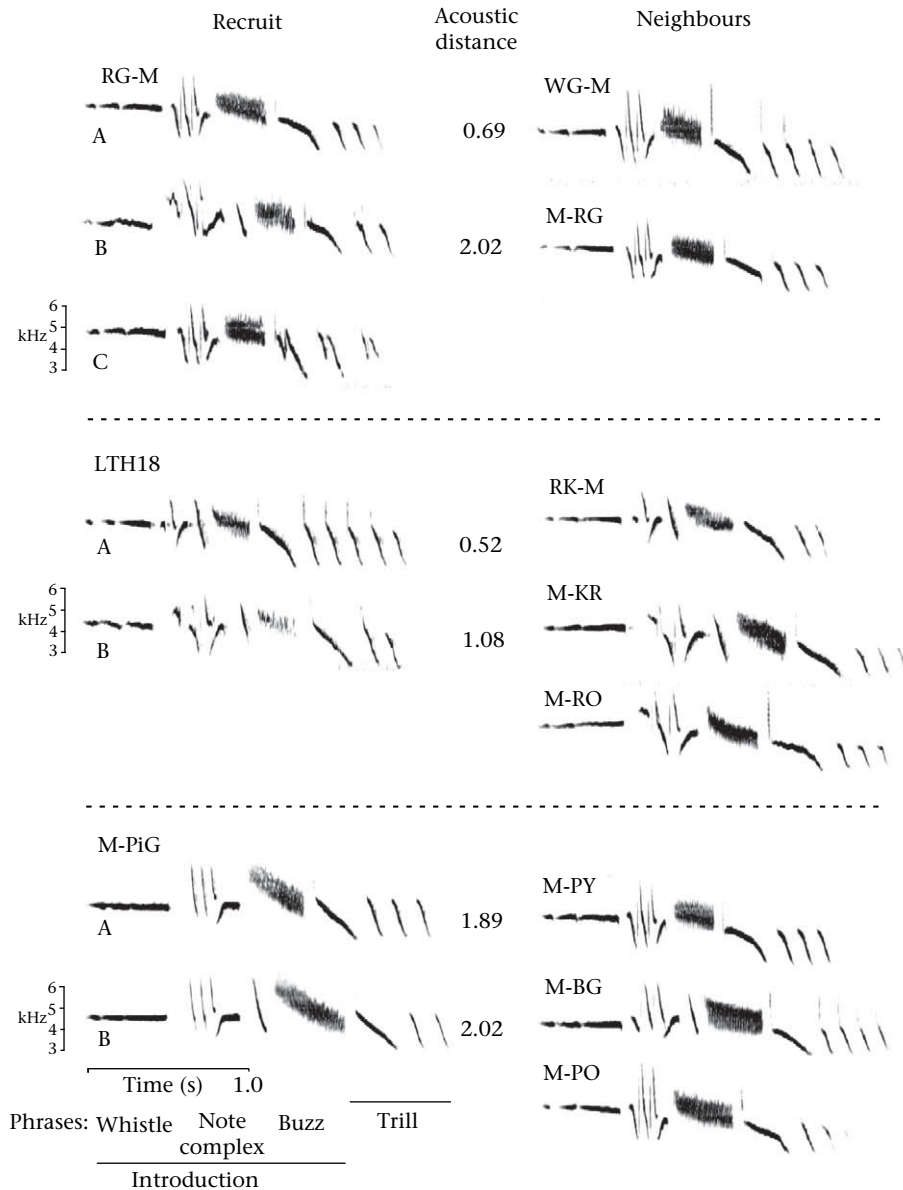


Figure 1. Examples of overproduced white-crowned sparrow song repertoires in three recruits (left column) and songs of their neighbours (right column). Song phrases are identified at lower left. Each recruit retained his song type A as his adult song type, which closely resembled at least one of his neighbours, and deleted the other type(s). Acoustic distances between the recruits' note complexes and the most similar neighbour's note complex are shown between the spectrograms. In most repertoires, the song types within a repertoire differed only in the note complex (RG-M's types A and B), but RG-M's types A and C were identical except for the trill, which is dialect 1 in type A and dialect 7 in type C. Recruit Lth18's two song types differed in all phrases, and we assume each was learned in its entirety from a different source. Recruit M-PIG's two note complexes were very similar, and differed only in the last frequency-downswept note. Both of these note complex types were sung by other males in the local population.

among most males at a given sampling location, and because of this, researchers use the trill to define the dialects. In a series of song playback experiments, male *Z. l. pugetensis* gave weaker responses to experimentally created songs containing foreign trills and local introductions than they did to control local songs or to songs with foreign introductions and local trills (Nelson & Soha 2004a, b). In contrast, the note complexes in the song's introduction are usually more diverse than trills within local populations (Nelson et al. 2004). Across the subspecies' range, 27 note complex 'types' have been described, and 10 of these are common (sung by > 5% of males) in our intensively studied population. Another experiment, using a neighbour-stranger discrimination paradigm, showed that males rely on the note complex in the song's introduction to recognize individuals (Nelson & Poesel 2007). Together

these observations and experiments suggest that the variable note complex in the introduction identifies individuals while the trill encodes information about the geographical source of a song, or its dialect.

Song learning in some sparrows consists of a two-stage process: young males first imitate, invent or improvise a number of song types and practise singing them. During the practise song stage, or plastic song, males then selectively retain one or more songs for their final adult repertoire, and discard the remainder (Marler & Peters 1981; Nelson & Marler 1994). As Beecher et al. (1997) have emphasized, the learning process is a selective one: males first choose one or more tutors to imitate for the initial overproduced repertoire, and then select a subset of those songs for the final repertoire.

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