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Birdsong learning as a social process

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This paper describes a 30-year investigation into the role of social and ecological factors affecting song learning in song sparrows, *Melospiza melodia*. It addresses the question of why song sparrows learn the songs they do, given that they are exposed to many more songs than they will keep for their final repertoire of 7–11 song types. A young song sparrow moves from his natal area at about 1 month of age, eventually settling in an area where he learns the songs of the resident males and attempts to establish his own territory. Birds that share many songs with their neighbours in their first breeding season (the spring following their hatch summer) survive for more years on territory than birds that do not. Many features of the song-learning process lead to a high level of sharing with first-year neighbours, including preferentially learning the songs of their tutor-neighbours who survive the winter, and learning songs that are shared by several tutors. Social interaction appears to be critical in song learning, but indirect effects (eavesdropping on adults countersinging) seem to be at least as important as direct interaction between the young bird and his tutor-neighbours. Although our evidence suggests that the song-learning strategy of young song sparrows is beneficial to them, a preliminary analysis suggests it may not benefit their tutors.

Song is a common form of communication in a wide variety of animal groups (Searcy & Andersson, 1986). Song in the oscine passerines (songbirds) is of special interest because it is learned. Vocal learning has evolved in only three groups of birds (songbirds, parrots and hummingbirds) and a small number of mammals (Jarvis, 2004), including of course humans. The songbirds are particularly interesting because of the amazing variety of song-learning patterns that have been discovered within this group of 4000+ species (Beecher & Brenowitz, 2005; Kroodsma, 1988, 1996). Because song is learned in songbirds, songbirds can be used to address a series of questions about vocal learning. Of the many songs heard by a young bird, which does he learn, which does he reject, and why? Whom should the bird learn from? Do song learners benefit from their learning strategy? Do song tutors benefit from being copied? In this paper I describe a research programme that addresses these and related questions, and which thereby provides an unusual opportunity to examine the function of vocal learning.

In most songbirds, song functions in intrasexual competition and mate attraction. While this paper focuses on cases where only males sing, singing by both sexes appears to be the ancestral condition in songbirds, and is common in tropical and nonmigratory species generally (see recent reviews by Logue & Hall, 2014; Odom, Hall, Riebel, Omland, & Langmore, 2014). In most territorial temperate-zone passerines, only males sing, and the major intrasexual context is 'posting' the territory with long-distance song and communicating with neighbours to negotiate territorial boundaries (review in Catchpole & Slater, 2008).

The study of song learning in the laboratory was pioneered by Peter Marler (e.g. 1970), who realized that the ultimate in experimental control of acoustic and timing variables could be achieved by isolating the song learner and delivering tutor song via tape recorder (later, computers). From this experimental paradigm came many important generalizations about song learning, including the concept of the sensitive period for song memorization, and the species-specific stimulus filtering mechanism for species song (often referred to as the 'innate template'). In what has become established as the prototypical, textbook example, Marler (1970) showed that a white-crowned sparrow, *Zonotrichia leucophrys*, male will develop normal song only if he hears conspecific song during an early sensitive period (roughly the second month of life). Moreover, the bird will reject heterospecific song heard during this period, as well as conspecific song heard after the sensitive period. The tape tutor paradigm that Marler developed has been

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particularly valuable in identifying the sensory mechanisms that guide and constrain song learning (e.g. Soha & Marler, 2000, 2001).

Although they are sometimes overlooked in discussions of avian song learning, striking differences between the song-learning programmes of different passerine species have been revealed in comparative studies (Beecher & Brenowitz, 2005; Kroodsma, 1978, 1983; Marler & Peters, 1988a; Nelson, 1999; Slater, 2003). Key differences include how long the sensitive period stays open (in some cases throughout life), how many songs the bird keeps for his final repertoire (ranging from one to over a hundred), whether the bird imitates tutor songs or improvises or invents new songs, whether the bird requires early exposure to conspecific song, and how constrained the bird is to copy only songs that fit species-specific parameters (Beecher & Brenowitz, 2005).

Despite years of intensive study, however, there is a major lacuna in the study of birdsong: we know virtually nothing about the *function* of song learning. Presumably, song learning evolved in the oscine passerine lineage because of advantages it conferred on the song learner. Yet exactly what are these advantages? They have not been identified for a single species to date.

The likely explanation for this gap in our knowledge is the difficulty of studying song learning under natural conditions. Hints that it is necessary to consider song learning in its natural context came first from experiments showing that birds learn more readily from live tutors than from tape-recorded song (Baptista & Petrinovich, 1984; Chaiken, Bohner, & Marler, 1993; Clayton & Pröve, 1989; Cunningham & Baker, 1983; Kroodsma & Pickert, 1984a, 1984b; Kroodsma & Verner, 1978; Nicolai, 1959; Payne, 1981; Price, 1979; Rice & Thompson, 1968; Thielke, 1970; Waser & Marler, 1977). Moreover, some of the rules of song learning derived from tape tutor studies bend, if not break, when the song tutors are actual birds. For example, whereas tape tutor studies had indicated that the sensitive period for white-crowned sparrows closes at approximately 50 days of age, and that heterospecific songs are uniformly rejected (Marler, 1970), Baptista and Petrinovich (1984, 1986) showed that if a young white-crowned sparrow was exposed to a tape tutor through 50 days of age and thereafter exposed to a live tutor, the young bird would learn the song of the live tutor, and in some cases would do so even if the tutor was a heterospecific.

Although differences between song learning from tape tutors and song learning from live tutors have been the subject of considerable debate (Baptista & Gaunt, 1997; Nelson, 1997, 1998), there is consensus on one major point, which is that a live adult singer is a more potent stimulus during song development than are songs presented through loudspeakers alone (e.g. Casey & Baker, 1993). But at the same time, it is unclear if this difference can be extrapolated to real-world contexts in any simple way. As Marler and Peters (1988b) noted, both the ‘tape tutor’ and ‘live tutor’ experimental set-ups are ‘unnatural’. The tape tutor design can be extrapolated to the real world if in nature a young bird learns his songs by listening to an adult bird singing solo and out of sight. In contrast, the laboratory live tutor design assumes that the young bird normally learns from a song tutor who is up close and interactive. Neither may be true. This simple observation leads to the conclusion that the function of song learning must be studied under natural conditions, in the field. Laboratory experiments, with their greater experimental control, still have a place in this search; particularly ‘seminatural’ ones that are carried out in a way that captures key features of the natural social environment. And needless to say, these seminatural laboratory studies require prior field studies that identify likely candidates for these ‘key features of the natural environment’.

In this paper I describe a case study of our 30-year research programme attempting to identify the key social factors in song learning in the song sparrow, *Melospiza melodia*. Other research efforts that have pursued this same goal include Kroodsma (1974) on Bewick's wrens, *Thryomanes bewickii*, Jenkins (1978) on saddlebacks, *Philesturnus carunculatus*, Payne (1983) on indigo buntings, *Passerina cyanea*, Bell, Trail, and Baptista (1998) on white-crowned sparrows, Liu and Kroodsma (2006) on chipping sparrows, *Spizella passerina*, and Nelson and Poesel (2009) on white-crowned sparrows. Generally these studies have shown that after natal dispersal, young birds learn the songs of their future territorial neighbours. But because young birds learn only a subset of the songs they hear (sometimes only a single song), the crucial question becomes: why do they learn (retain) the particular songs they do as opposed to others to which they were exposed?

BACKGROUND AND METHODS

The song sparrow is a common species found throughout North America. Song sparrows have the most genetically distinct populations of any bird in North America. We are studying a subspecies (*M. m. morphna*) found in the Pacific Northwest. The total number of subspecies of song sparrow is much debated, but the most recent study puts the number at 25 (Patten & Pruett, 2009). This context must be kept in mind, since, as will be discussed later, there may be significant biological differences between the song-learning programmes of some of these different subspecies.

Our study population is a sedentary (nonmigratory) population of song sparrows in an undeveloped 534-acre park in Seattle, Washington, U.S.A. Although the park has some of the characteristics of an island, being bounded on the north by Puget Sound, its other boundaries are with residential areas, generally hospitable to song sparrows, if less so than the park. Song sparrows in this population are year-round resident on their territories, although they are fully territorial only in and around the breeding season, which is roughly March through July. Birds sometimes make small lateral moves if an adjacent territory opens up, but otherwise are strictly sedentary.

Song sparrows in this population typically have 7–11 distinct song types. Most often they will share some but not all of their songs with one neighbour, a somewhat different set of songs with a second neighbour, and so on. An example is shown in Fig. 1. This pattern of song sharing has been observed in other Washington populations (Cassidy, 1993; Hill, Campbell, Nordby, Burt, & Beecher, 1999; Reeves & Beecher, n.d.) and in a California population (Wilson, Towner, & Vehrencamp, 2000), but it is not found in the eastern subspecies, *M. m. melodia* (Hughes, Anderson, Searcy, Bottensek, & Nowicki, 2007). We consider this interesting population difference later.

Song sparrows are age-limited song learners: they do not modify their song repertoires after their first year of life (Nordby, Campbell, & Beecher, 2002). A laboratory study using tape-recorded song as tutor song showed that eastern song sparrows learn most of their songs during a sensitive period spanning roughly the second and third months of life (Marler & Peters, 1987). However, tape tutor studies can underestimate the sensitive period, and moreover eastern subspecies of song sparrows may have a very different song-learning programme from western subspecies (see Discussion). On the basis of field studies of our western song sparrow population, we have established that song learning continues into the bird's first spring, and is completed by the time he is 9–10 months old. Some of this late learning may occur in late summer or autumn of the natal year, but our laboratory and field studies have indicated that the primary effect occurs later, early in the following spring (January, February and early March for our birds). Although some of our laboratory studies have indicated that birds in our population are capable of

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