



Song is not a reliable signal of general cognitive ability in a songbird

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Learned aspects of song affect female mating preferences in a number of species of songbirds, including swamp sparrows, *Melospiza georgiana*. One explanation for why female songbirds attend to such song features is that these song attributes convey information on the general cognitive ability of singers. The fact that song attributes and cognitive ability are affected during development by the same stressors makes a connection between the two plausible. Here we test the hypothesis that song is a signal of cognitive ability by relating five measures of song quality to five measures of cognitive performance in 49 captive male swamp sparrows. The five song measures are repertoire size, mean and minimum vocal deviation (measures of vocal performance), and mean and maximum typicality (measures of song learning). Cognitive performance was measured as the speed with which five cognitive tasks were mastered: a novel foraging task, a colour association, a colour reversal, a spatial learning problem and a detour-reaching test. In general linear mixed models controlling for neophobia, none of the song measures were predictive of any of the cognitive performance measures. Thus the results do not support the hypothesis that song attributes signal general cognition in swamp sparrows.

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Humans across a wide range of cultures express a preference for more intelligent over less intelligent mates (Marlowe, 2004; Prokosch, Coss, Scheib, & Blozis, 2009; Shackleford, Schmitt, & Buss, 2005; Souza, Conroy-Beam, & Buss, 2016). This preference is often present in both sexes, but is particularly pronounced in females (Furnham, 2009; Li, Bailey, Kenrick, & Linsenmeier, 2002; Shackleford et al., 2005). Female preferences for more intelligent males have also been found in other animals, including fish (Shohet & Watt, 2009), rodents (Spritzer, Meikle, & Solomon, 2005) and birds (Keagy, Savard, & Borgia, 2009, 2011). Human females may use cues such as vocabulary size (Rosenberg & Tunney, 2008) or oral reading ability (Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004; Prokosch et al., 2009) to assess male intelligence, but how females in nonhuman animals might assess the intelligence of prospective mates is more mysterious. Presumably, many male display traits important to female choice are unlikely to contain information on male cognitive ability, such as (in birds) the length of tails (Andersson, 1982; Møller, 1988), the brightness of plumage (Hill, 1991; Whittingham & Dunn, 2016), or the colour of

bills (Simons & Verhulst, 2011). Learned displays constitute a possible exception, where a link between a display and intelligence seems much more likely (Peters, Searcy, & Nowicki, 2014). Birdsong is highly dependent on learning (Beecher & Brenowitz, 2005; Marler & Mundinger, 1971) and often affects female choice (Searcy & Andersson, 1986; Searcy & Yasukawa, 1996), and thus seems particularly likely to provide information on cognitive ability (Boogert, Giraldeau, & Lefebvre, 2008; Boogert, Anderson, Peters, Searcy, & Nowicki, 2011). Here we test the hypothesis that song signals cognitive ability in swamp sparrows, *Melospiza georgiana*, by relating several measures of cognitive performance to a recently developed measure of success in song learning (Lachlan, Anderson, Peters, Searcy, & Nowicki, 2014).

Previous studies of the relationship between song and cognition in songbirds have focused largely on what have been considered to be measures of song complexity, such as song duration, number of elements per song and number of unique elements per song in zebra finches, *Taeniopygia guttata* (Boogert et al., 2008; Templeton, Laland, & Boogert, 2014), song bout length in European starlings, *Sturnus vulgaris* (Farrell, Weaver, An, & MacDougall-Shackleton, 2012), and song repertoire size in song sparrows, *Melospiza melodia* (Boogert et al., 2011; Sewall, Soha, Peters, & Nowicki, 2013). If we equate song complexity with diversity of song types or song

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elements, some of these metrics seem more appropriate as measures of complexity (number of unique elements per song, song repertoire size) than do others (song duration), but note that in European starlings song bout length is strongly correlated with song phrase repertoire size (Eens, 1997). These complexity measures are a logical focus for cognitive studies, in that one or more of them have been associated with female mating preferences in each of the above species (zebra finches: Riebel, 2009; Vyas, Harding, Borg, & Bogdan, 2009; starlings: Eens, Pinxten, & Verheyen, 1991; song sparrows: Reid et al., 2004; Searcy, 1984). Song complexity, however, is ambiguous as a measure of learning success. On the one hand, individual song elements and song types are definitely learned from models in these songbirds (Eales, 1985; Eens, Pinxten, & Verheyen, 1992; Marler & Peters, 1987; Nordby, Campbell, & Beecher, 1999), so measures such as number of unique elements per song or song repertoire size can be interpreted as measuring the amount of material that has been learned. On the other hand, in some songbird species (including swamp sparrows) individual males do not include in their adult repertoires all the songs that they have memorized (Marler & Peters, 1981; Nelson, 2000; Nordby, Campbell, & Beecher, 2007; Peters & Nowicki, 2017; Prather, Peters, Nowicki, & Mooney, 2010), so measures of adult song complexity may not accurately reflect the amount of learning.

Another approach to assessing song learning is to measure the accuracy with which adult birds reproduce the songs they are known to have heard early in life during the period when song models are memorized. This approach is much easier to implement with laboratory-reared birds than with free-living ones, because the set of model songs can be controlled experimentally in the laboratory, whereas for free-living birds that set may be both very large and very difficult to delimit. We have shown that laboratory-reared song sparrows differ in how accurately they copy model songs recorded locally, and that adult females from the same local population prefer well-copied songs to poorly copied ones (Nowicki, Searcy, & Peters, 2002b). We have also assessed the association of cognitive measures to success in copying model songs in hand-reared song sparrows (Anderson et al., 2017). This approach produces convincing measures of song learning, but sample sizes are typically limited because of the logistical difficulty of hand-rearing wild birds.

Lachlan, Verhagen, Peters, and ten Cate (2010) and Lachlan, Anderson, Peters, Searcy, & Nowicki (2014) suggested an alternative method for measuring accuracy of song learning that can be applied to free-living songbirds, so that quality of learning can be assessed in a larger sample of males than is practicable in hand-rearing studies and without the potential concern that learning in a laboratory setting differs from learning in the field. Rather than measuring how well a subject's song matches a specific song model, the method measures how well the subject's song matches the average features defining a category of songs. The method is therefore best applied to species of songbirds in which populations produce a limited set of song categories, or 'song types', each of which is sung by multiple males. The method requires first grouping a population of songs into song types using objective clustering procedures. Once clusters are defined, the 'typicality' of any one song can be measured by its proximity to the centre of the cluster to which it belongs (Lachlan et al., 2010, 2014). The typicality of a male's songs is then a measure of how well that male has succeeded in learning and reproducing the common features of particular song types (Lachlan & Nowicki, 2012). Typicality is distinct from stereotypy: the latter measures how consistently a male produces his version of a song type (Rivera-Gutierrez, Pinxten, & Eens, 2010; Smith, Brenowitz, Beecher, & Wingfield, 1997), whereas typicality measures how similar a male's version is to the versions produced by other males. The assumption that typicality

measures success in song learning is bolstered if it can be shown that a signaller benefits from producing more typical rather than less typical songs.

The assumptions of the typicality method fit well with the biology of swamp sparrows. Swamp sparrow songs almost always consist of a single syllable repeated in a steady-rate trill. Syllables are constructed from two to five notes drawn from a limited set of note type categories (Lachlan & Nowicki, 2015; Marler & Pickert, 1984). Lachlan et al. (2014) used a dynamic time-warping algorithm to compare hundreds of songs drawn from one swamp sparrow population, and then clustered songs based on their acoustic properties (see below). The clusters they uncovered corresponded well with song types identified by human observers through visual inspection of spectrograms. When tested with songs varying in typicality, female swamp sparrows gave a stronger courtship response to songs of high typicality (close to the centroids of their clusters) than to songs of low typicality (far from their centroids) (Lachlan et al., 2014). In parallel tests, male swamp sparrows gave a stronger aggressive response to songs of high typicality than to songs of low typicality (Lachlan et al., 2014). An earlier study found that female swamp sparrows prefer songs of males with good developmental histories (Searcy, Peters, Kipper, & Nowicki, 2010), and Lachlan et al. (2014) showed that variation in song typicality could explain these preferences.

Here we test the hypothesis that song signals cognitive ability by relating speed of learning of five cognitive tasks to five measures of song quality in wild-caught swamp sparrows. Two of these song measures assess song typicality, which we have argued above is a good measure of the quality of song learning in swamp sparrows. A third measure is song repertoire size, which we use in parallel to other studies of song and cognition, as reviewed above, even though it is only equivocally tied to sexual selection in swamp sparrows (Searcy, Searcy, & Marler, 1982) or to song learning in songbirds in general. The final two song measures are mean and minimum vocal deviation, which assess how closely a song approaches the maximum achievable combination of trill rate and frequency bandwidth (Podos, 2001). Vocal deviation is not considered a measure of song learning, but rather of vocal performance, that is, of the ability to perform difficult motor skills in vocal production (Byers, Hebets, & Podos, 2010; Podos & Nowicki, 2004). Because vocal deviation is not expected to reflect song learning, it seems less likely to be associated with cognition than are the other song measures; we nevertheless include vocal deviation in this study, as there is evidence that it is another song parameter tied to sexual selection in swamp sparrows (Ballentine, Hyman, & Nowicki, 2004; DuBois, Nowicki, & Searcy, 2011).

METHODS

Study Sites and Subjects

The study was carried out during May–July in the years 2014–2016. Subjects were 49 adult male swamp sparrows from Conneaut Marsh (Pennsylvania State Gamelands 213), in Crawford County, Pennsylvania, U.S.A. The subjects were initially captured on their territories using mist nets, banded with unique combinations of coloured leg bands, and then released. Song repertoires of banded males were then recorded in the field using Marantz PMD 660 or 670 digital recorders, Shure SM-57 microphones and Sony PBR-330 parabolas. Recordings were examined visually using spectrograms made with Syrinx (Burt, Campbell, & Beecher, 2001). Ballentine (2006) found that male swamp sparrows typically cycle through their entire repertoire before repeating a song type, so that if a male is recorded continuously until he repeats a song type, the entire repertoire is obtained in over 90% of cases. We considered

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