



The evolution of bird song: male and female response to song innovation in swamp sparrows

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Closely related species of songbirds often show large differences in song syntax, suggesting that major innovations in syntax must sometimes arise and spread. Here we examine the response of male and female swamp sparrows, *Melospiza georgiana*, to an innovation in song syntax produced by males of this species. Young male swamp sparrows that have been exposed to tutor songs with experimentally increased trill rates reproduce these songs with periodic silent gaps (Podos 1996, *Animal Behaviour*, **51**, 1061–1070). This novel temporal pattern, termed ‘broken syntax’, has been demonstrated to transmit across generations (Podos et al. 1999, *Animal Behaviour*, **58**, 93–103). We show here that adult male swamp sparrows respond more strongly in territorial playback tests to songs with broken syntax than to heterospecific songs, and equally strongly to conspecific songs with normal and broken syntax. In tests using the solicitation display assay, adult female swamp sparrows respond more to broken syntax than to heterospecific songs, although they respond significantly less to conspecific songs with broken syntax than to those with normal syntax. We conclude that sexual selection by female choice is in this case conservative, acting against the spread of innovation. The conservative effect of female preferences must sometimes be overcome, however, to allow the evolution of the major structural differences in song observed between species.

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Among the many kinds of signals animals use to communicate, the songs of songbirds stand out for their complexity and variety. Songs of closely related species often differ radically both in the structure of the elements that compose the song (‘phonology’) and in the pattern in which these elements are presented (‘syntax’). In the clade of New World sparrows that we study, for example, even sister species can have songs with very different structures (Fig. 1). How has this diversity arisen? Because song is a learned trait, most approaches to answering to this question invoke models of cultural evolution derived from population genetics models: variation arises as the result of copy error when song is transmitted across generations, and over time, song evolves as the result of drift or selection acting on this variation (Nottebohm 1972; Slater 1986, 1989; Kroodsma 1996; Lynch 1996; Payne 1996). Consistent with this view, longitudinal studies of wild bird populations have documented evolutionary changes occurring over only a few generations in

a variety of song features, including the fine structure of notes (Jenkins 1978; Grant & Grant 1996), the addition, deletion or reordering of notes (Ince et al. 1980; Payne 1996), or the blending of notes from multiple models (Slater 1989; Payne 1996).

Copy error, drift and selection may account for local dialectical differences or population ‘traditions’ in song (Thielcke 1972; Slater 1986; Martens 1996), but it is not clear whether these processes are sufficient to account for the large structural differences observed between species in a clade of birds (e.g. Fig. 1), for two reasons. First, in both field and laboratory studies, changes in song structure observed across generations tend to be minor and occur largely at the level of phonological differences, as compared to variation observed among species, which often includes major syntactical differences as well. This problem is analogous to the difficulty in explaining macroevolutionary patterns on the basis of microevolutionary processes. Second, available evidence suggests that cultural selection and biological selection on song are both strongly stabilizing. Young songbirds typically show a strong preference for learning songs that fall

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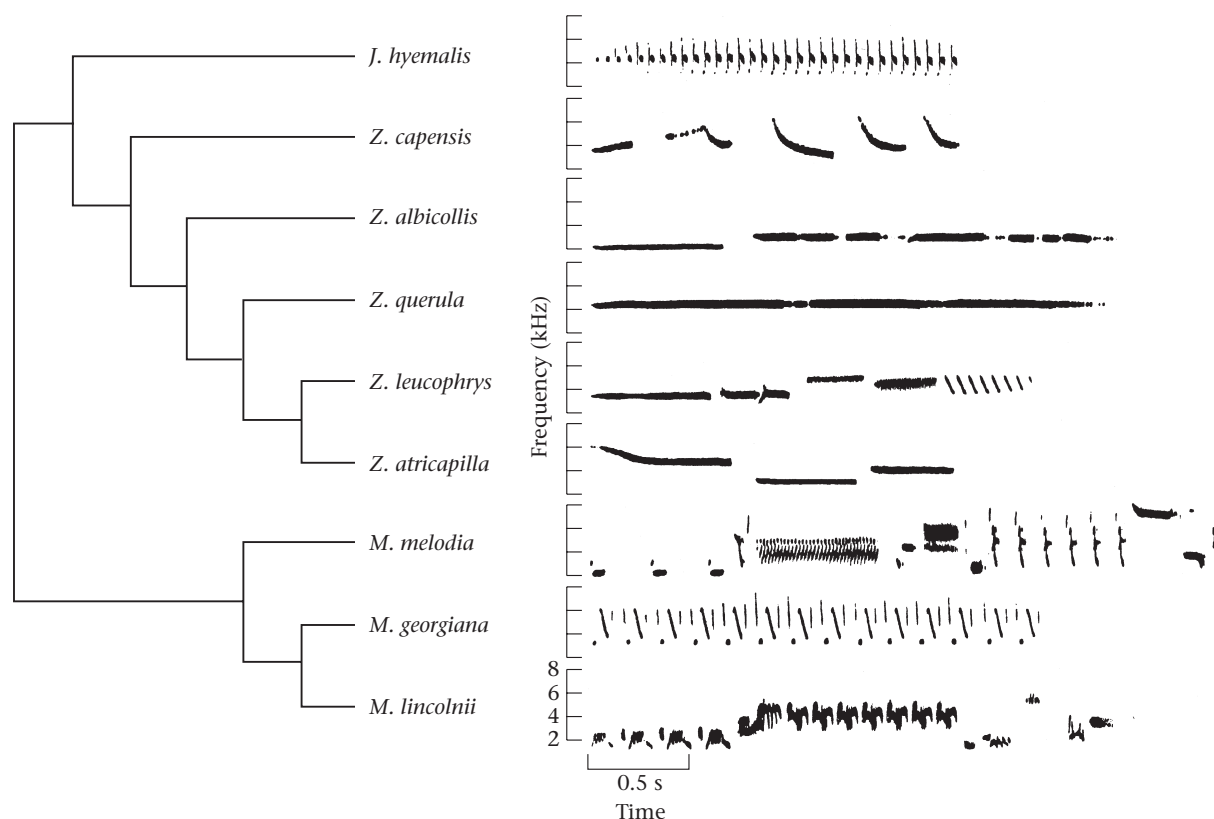


Figure 1. Examples of song diversity across three closely related genera of sparrows (*Junco*, *Zonotrichia* and *Melospiza*), arranged according to Zink & Backwell's (1996) phylogenetic hypothesis for this group. Note that closely related species differ extensively not only in the structure of phonological units, but also in large-scale syntactic features, such as the number and order of segments of trilled and untrilled elements.

within a narrow, species-typical range of variation (Marler 1970; Nottebohm 1972; Marler & Peters 1989; Nelson & Marler 1993; Catchpole & Slater 1995), so the further a song is from the species norm, the less likely it will be copied and transmitted to the next generation. Similarly, songs that depart from the species norm elicit diminished responses in both male-male and male-female interactions (King et al. 1980; Baker et al. 1987; Nelson 1988; Searcy 1990; Searcy & Yasukawa 1996) thus lowering the expected fitness of males that sing them.

Podos and colleagues (Podos 1996; Podos et al. 1999) recently suggested an alternative mechanism that could account for the evolution of structural innovation in bird song, based on their studies of song production and learning in the swamp sparrow *Melospiza georgiana*. Swamp sparrow song typically consists of a single syllable repeated in a continuous trill at a steady rate (Fig. 2a,c). A motor constraint appears to limit how fast male sparrows can repeat syllables in such trills (Podos 1997). This constraint arises from the need to coordinate vocal tract motions, such as those of the beak, during song production and reflects an upper limit on how fast such coordinated movements can be produced (Nowicki et al. 1992; Podos 1997; Hoese et al. 2000). When young male swamp sparrows are tutored with songs with trill rates increased by digital manipulation beyond the rates at which they are normally produced, they learn syllables from those

songs as well as they do from normal songs, but are unable to reproduce them at the increased trill rate (Podos 1996). Instead, in reproducing these songs males either (1) reduce the trill rate, (2) simplify syllables by omitting notes, or (3) modify the syntax by introducing periodic gaps in the trill (e.g. Fig. 2b). Songs incorporating this last innovation, termed 'broken syntax' (Podos 1996), differ from normal songs on a level that approximates more closely the magnitude of structural differences observed between species than do the sorts of changes observed previously in longitudinal studies of song learning. Podos (1996) suggested that the origin of the broken syntax innovation is due to the same mechanism responsible for gait changes in running quadrupeds: a continuous increase in an output parameter (such as running speed or trill rate) leads to a discontinuity in the function of the underlying motor system (such as a gait change or the production of a different syntax) when that parameter passes some threshold beyond which the system will function more competently or with greater efficiency in a different mode of operation (Alexander 1980, 1984). There is natural variation in trill rates and we also expect variation in the morphology and performance capabilities of individuals in a population. Thus, broken syntax might arise in nature when an individual attempts to copy a faster trill than it is capable of reproducing.

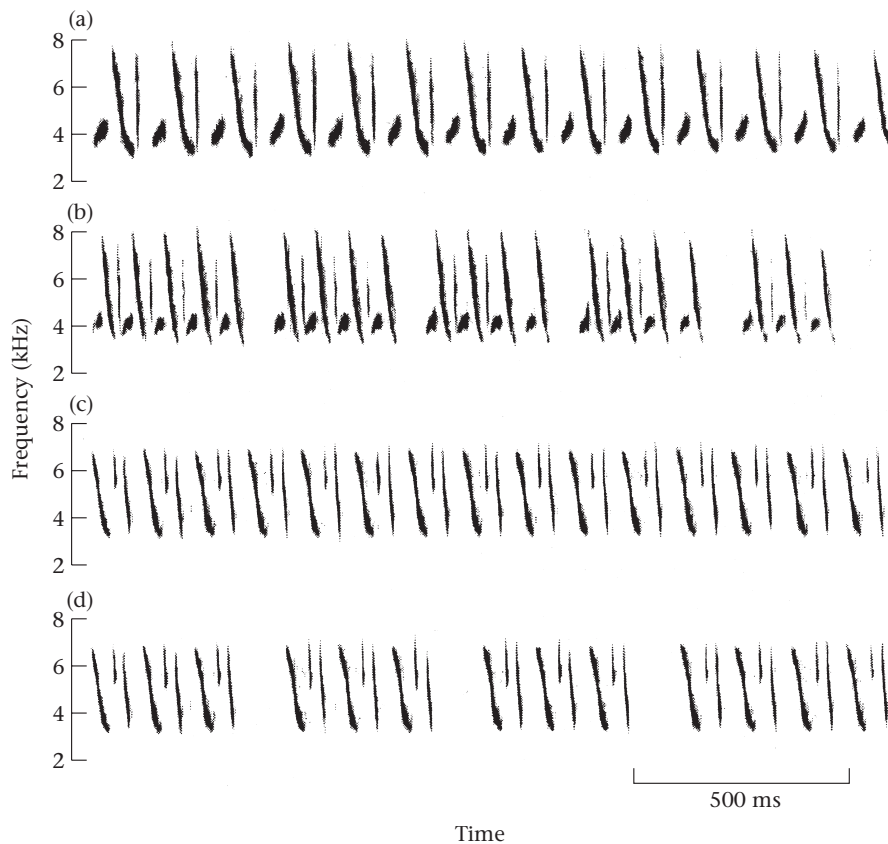


Figure 2. (a, c) Spectrograms of two natural swamp sparrow songs. The smallest units are termed 'notes'; groups of notes form 'syllables'. Different syllables are found in different song types (compare a versus c), but all normal songs are steady-rate, continuous trills. (b) Spectrogram of a song with broken syntax, produced by a hand-reared male swamp sparrow tutored with a rapid trill version of the song illustrated in a. (d) Spectrogram of a broken syntax song synthesized by digitally altering the natural swamp sparrow song shown in c.

Although the introduction of broken syntax into swamp sparrow song suggests a mechanism by which large-scale innovations in song might arise, such an innovation will only be maintained in a population if two conditions are met. First, the broken syntax innovation must be able to be transmitted to subsequent generations and, second, songs with broken syntax must function adequately as communication signals. In other words, the innovation cannot be selected against by either cultural or biological selection. Podos et al. (1999) demonstrated that the first of these conditions could be met. Hand-reared swamp sparrows tape-tutored with broken syntax songs learned from them as readily as from normal songs and with equal accuracy. Most importantly, broken syntax was itself learned in some cases; that is, some males tutored with broken syntax songs reproduced those songs with the broken syntax of the model.

In this paper we address the second of these conditions, asking how well songs having the broken syntax innovation function as communication signals. Because song is a dual-function signal (Catchpole & Slater 1995), it is important to measure the effect of an innovation such as broken syntax on both male-male and male-female communication. Here we test adult male swamp sparrows for response to broken syntax using territorial playback, and

we test adult female swamp sparrows for response to broken syntax using the solicitation display assay. In both cases, we test subjects (1) for discrimination between songs with broken syntax and heterospecific songs, to assess whether broken syntax songs function at all, and (2) for discrimination between songs with broken syntax and normal swamp sparrow songs, to assess whether song with broken syntax function better or worse than songs with normal syntax.

In our experiments, we use broken syntax songs produced by digitally altering natural songs, rather than broken syntax songs produced by male swamp sparrows tutored with rapid trills. The reason for this choice is that songs produced by hand-reared, tape-tutored males may differ from normal songs in aspects other than the one syntax feature of interest. The broken syntax songs produced by hand-reared males tutored with rapid trills also have rapid trills in the trill segments between gaps (e.g. Fig. 2b; see Podos 1996; Podos et al. 1999), whereas the broken syntax songs that we use in our tests have normal, slower trill rates (e.g. Fig. 2d). To see whether this difference in trill rate might affect response, we also tested female subjects for discrimination between songs with normal trill rates and song whose trill rates we artificially increased beyond the species norm.

METHODS

Playbacks to Males

We used territorial playback to test 24 territorial adult male swamp sparrows for discrimination between normal syntax and broken syntax songs and, in separate trials, for discrimination between broken syntax and heterospecific songs. Tests were done in the vicinity of Conneaut Lake, Pennsylvania, U.S.A. We played songs from a speaker placed on a male swamp sparrow's territory (Sony TCM 5000EV recorder, Nagra DSM speaker), at a rate of six songs/min, for 6 min. We used mean distance to the speaker during playback and a 3-min postplayback period as the sole response measure. Distances were estimated as in previous studies (Searcy et al. 1997). In both sets of tests (normal versus broken, and broken versus heterospecific), we presented each of the 12 pairs of contrasting tapes to two different males. The order of presentation (e.g. normal first, or vice versa) was randomized, with at least 2 days between tests. Wilcoxon matched-pairs signed-ranks tests were done on the mean response of the two subjects per tape; thus the sample size is the number of stimulus pairs ($N=12$).

Playbacks to Females

We tested 20 female swamp sparrows using the solicitation display assay (King & West 1977; Searcy 1992), comparing response to normal versus broken syntax songs and, in separate trials, to broken syntax versus heterospecific songs. Females were captured from the field 7–10 days before they were tested. All females were captured as breeding adults, although their relative stage in the breeding cycle when captured varied from incubation to feeding young fledglings. To help control for concomitant differences in hormonal state, all females were given a subcutaneous implant of 17- β -oestradiol in silastic tubing of 1.96 mm outside diameter and containing 7–9 mm of hormone 7 days before testing began (see Searcy 1992 for further background). Each female was housed singly in a sound attenuation chamber. We played songs through a loudspeaker (Marantz PMD 221 recorder, Nagra DSM speaker) positioned just outside the chamber, at a rate of six songs/min, for 3 min, and videotaped responses through the open chamber door. While testing one female, we kept the doors of the other chambers closed to minimize habituation. Number of solicitation displays performed during 3 min of playback was the sole response measure, as in previous studies (Searcy et al. 1997).

We tested each female twice with a pair of normal versus broken syntax stimuli and twice with a pair of broken syntax versus heterospecific stimuli. Testing of contrasting stimulus pairs occurred on the same day, with at least 3 h between tests. The order of stimuli in a pair was randomized on the first day of testing and reversed on the second; no order effects were detected. We used 10 stimulus sets randomly selected from the 12 sets of stimulus songs used in the male tests, presenting each pair of stimulus tapes to two females. Wilcoxon matched-

pairs signed-ranks tests were performed on the mean response of the two subjects per tape; again, the sample size is the number of stimulus pairs ($N=10$).

The broken syntax songs produced by hand-reared males tutored with rapid trills also have rapid trill rates in the trill segments between gaps (e.g. Fig. 2b; see Podos 1996; Podos et al. 1999), whereas the broken syntax songs that we used in the above tests had normal, slower trill rates (e.g. Fig. 2d). Thus, if females prefer faster trill rates than are normally produced, they might respond as strongly, or even more strongly, to the broken syntax/rapid trill rate temporal pattern that hand-reared males produce as they do to normal syntax/normal trill rate patterns. To investigate this possibility, we presented 20 different female swamp sparrows with natural versus rapid trill rate songs, using the solicitation display assay and analysing the data on a per-tape basis as above ($N=10$).

Experimental Stimuli

We digitized songs recorded in the wild and modified them using SIGNAL software (Beeman 1996). Normal stimuli songs were recorded directly from these digitized files. To construct broken syntax songs, silent periods were introduced between multisyllable segments so as to mimic closely the broken syntax produced by males in earlier learning experiments (Podos 1996; Podos et al. 1999) in the number, position and duration of gaps (e.g. Fig. 2d). We constructed 12 broken syntax songs, each from a different natural song. We used 12 song sparrow, *Melospiza melodia*, songs as heterospecific stimuli; these songs were digitized from field recordings using identical procedures as for the swamp sparrow songs.

We made the 10 rapid song stimuli by digitally shortening the silent spaces within syllables and between successive syllables in 10 different natural swamp sparrow songs, following procedures used previously (Podos 1996; Podos et al. 1999). Trill rates were increased in these songs by 32–52%.

All songs used to make test stimuli were recorded from the same region where we obtained test subjects. Song sparrows typically nest in and around the marshes where swamp sparrows breed in this population, so we expect that all subjects had prior experience listening to a diverse array of swamp sparrow and song sparrow songs before being tested. Because the recordings we used were made 5 years before the tests we report here were done, however, we deem it very unlikely that any test subject was familiar with any of the individual birds from whom we recorded stimulus songs.

RESULTS

Males averaged significantly closer to the speaker (i.e. response was stronger) for playback of broken syntax songs than for heterospecific songs (Fig. 3a). Males did not discriminate between normal and broken syntax songs (Fig. 3b); in fact, males responded slightly more strongly to broken syntax songs, although this difference was not significant.

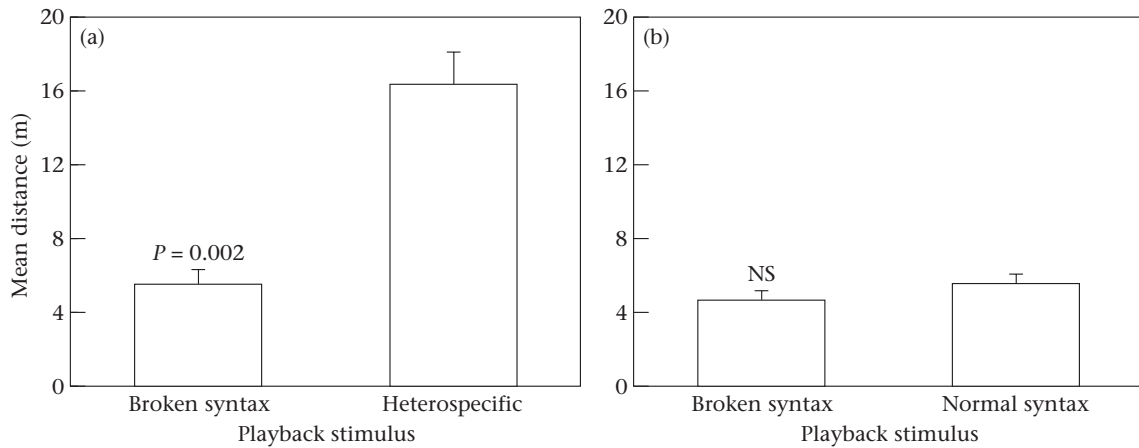


Figure 3. Results from territorial playback to male swamp sparrows. (a) Mean ($\pm$ SE) distance to speaker in response to broken syntax and heterospecific songs (Wilcoxon matched-pairs signed-ranks test: $T=0$, $N=12$). (b) Mean ($\pm$ SE) distance to speaker in response to normal and broken syntax (Wilcoxon matched-pairs signed-ranks test: $T=8$, $N=12$). Two-tailed probabilities are shown.

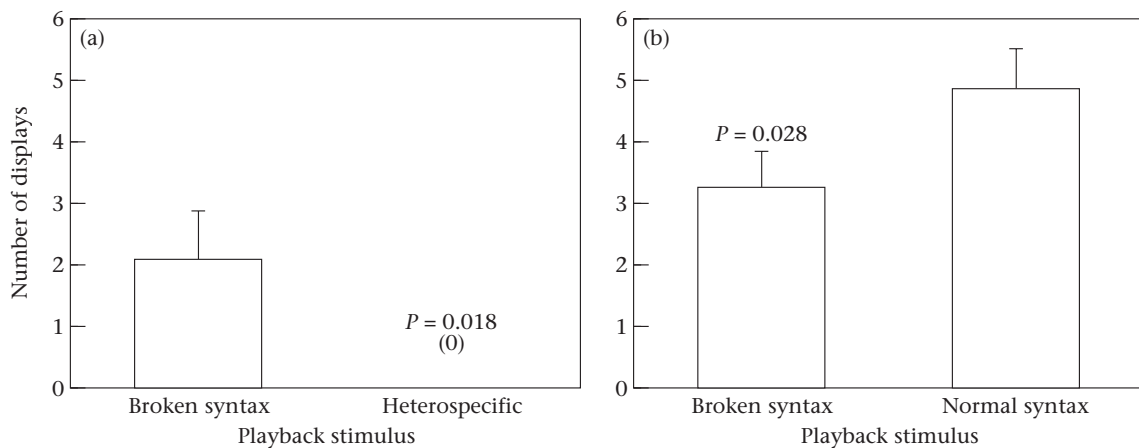


Figure 4. Results from playbacks to female swamp sparrows. (a) Mean ($\pm$ SE) number of solicitation displays in response to broken syntax and heterospecific songs (Wilcoxon matched-pairs signed-ranks test: $T=0$, $N=10$). (b) Mean ($\pm$ SE) number of solicitation displays in response to broken and normal syntax (Wilcoxon matched-pairs signed-ranks test: $T=4$, $N=10$). Two-tailed probabilities are shown.

Females also responded well to broken syntax songs, and gave significantly more copulation solicitation displays in response to broken syntax songs than to heterospecific songs (Fig. 4a). However, females responded significantly less to broken syntax songs than to normal conspecific songs (Fig. 4b). Most individuals responded both to broken syntax and to normal songs, but did so more to the latter than to the former; thus, this response difference was not the result of certain individuals in our tests having strong preference for one or the other stimulus type. Female response to fast trills ($\bar{X} \pm \text{SE} = 9.4 \pm 2.5$ displays/female) was nearly identical to response for normal trills (9.2 ± 2.5 displays/female; Wilcoxon matched-pairs signed-ranks test: $T=26.5$, $N=10$, NS, two-tailed test). Female swamp sparrows thus do not prefer trill rates that exceed the species norm, suggesting that female response to naturally occurring broken syntax songs would not be greater if the trilled segments were also more rapid than normal.

DISCUSSION

Two general conditions must be met for a novel signal trait to become established in a population: there must be some mechanism for transmitting the trait across generations, and signals including the trait must function at least as well as those without it. Previous work has shown that young swamp sparrows are capable of learning from and reproducing broken syntax songs (Podos et al. 1999), satisfying the first requirement. This result was surprising because most studies have shown song learning to be generally conservative, in the sense that birds typically do not learn, or at least do not learn as well, from models that deviate from species-typical norms (Catchpole & Slater 1995). Podos et al. (1999) speculated that the readiness of young swamp sparrows to learn broken syntax may be explained by the coupling of sensory and motor mechanisms in song learning and production (for review, see Nottebohm et al. 1990; Marler & Doupe 2000). Given this coupling, the fact that the motor

system of male swamp sparrows can be induced to produce broken syntax under some conditions suggests that the perceptual system might also be sensitive to this feature, even if it rarely or never occurs in normal songs.

Our present results show that broken syntax songs also function in adult interactions, at least to some extent. In the context of male–male signalling, songs with the novel trait appear to be as effective as normal songs (Fig. 3). The response of males to territorial playback is not a direct measure of function, because song primarily functions in male–male interactions to repel intruders, not to trigger an aggressive response in territory owners as is typically measured in playbacks (Searcy & Nowicki 2000). None the less, males did not discriminate between broken and normal syntax in our tests (and even showed a tendency to respond more strongly to broken syntax), suggesting that this novel feature would not compromise signal function in male–male communication.

The solicitation display assay we used to test female response is a better indicator of male–female function than playback is of male–male function: the measured response is clearly related to a male's ability to stimulate females to court and copulate (Searcy & Yasukawa 1996) and studies on other species of songbirds indicate that solicitation results correspond well to mating preferences (e.g. West et al. 1981; Catchpole et al. 1986). We found that female swamp sparrows also responded to broken syntax songs, and did so significantly more than to heterospecific songs (to which they did not respond at all; Fig. 4a). Females responded significantly less to broken syntax, however, when contrasted with their response to normal syntax songs (Fig. 4b). Although we cannot directly compare our male and female results, our data suggest that females are more discriminating than males in their response to the novel trait. This difference in male and female response is not surprising, as previous studies have shown male birds to be generally less discriminating than females in their response to song (Searcy & Brenowitz 1988; Ratcliffe & Otter 1996).

The fact that females responded less to broken syntax songs than to normal songs suggests that sexual selection through female choice is stabilizing and would limit the spread of this feature if it were to arise in a population. Given that broken syntax can be culturally transmitted and appears to function equally well as a signal to males, it appears in this case that female choice specifically acts as the 'gatekeeper' selecting against innovation in song structure. That female choice is conservative may seem surprising, given the well-accepted idea that females' preferences are often responsible for the elaboration of display (West-Eberhard 1983; Schuler & Price 1993; Andersson 1994) and the demonstration in some cases of female preferences for innovations in plumage characteristics (Burley & Symanski 1998; Jones & Hunter 1998). We suggest, however, that such preferences for extremes are most likely to occur for traits where the ability to produce extremes reflects male quality. In the present case, the production of broken syntax songs may indicate just the opposite: that males producing them have lower performance capabilities (reflecting, for example, variation in jaw or beak morphology, or in neuromuscu-

lar control) and are thus unable to copy faster trill rates that occur normally in the population.

The data we present here do not support our original suggestion that broken syntax in swamp sparrow song can serve as a paradigm for how syntactical innovations arise in song, because female preferences appear to select against this trait. An important qualification to this conclusion, however, is female song preferences themselves may be influenced by learning, as is male song production (e.g. Riebel 2000). Suppose that an innovation such as broken syntax appeared in one or a few males in one generation, and that the singing of these males influenced not only song development of some males in the next generation, but also the development of song preferences in some females as well. These females might not discriminate against the innovation, and perhaps might even prefer it, in which case the innovation would be more likely to be maintained and spread in the population. More work is needed on the development of female song preferences and on the dynamics of how these preferences are exerted in natural populations, as well as on the mechanisms that underlie the generation of novel song structures, for us to develop a more complete picture of how song evolves.

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