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Female response to song reflects male developmental history in swamp sparrows

William A. Searcy · Susan Peters · Silke Kipper · Stephen Nowicki

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Abstract One explanation for why female songbirds attend to male song is that the quality of a male's song is associated with the quality of his developmental history. We tested this hypothesis by playing back to female swamp sparrows (*Melospiza georgiana*) songs recorded from males of either inferior or superior developmental histories, as assessed by their rates of mass gain during the first 18 days post-hatching. Females showed significantly higher levels of courtship display in response to songs of males with superior growth than to songs of males with inferior growth. Out of nine song traits measured, only song duration correlated with variation in female response; duration was also the only trait that differed significantly in univariate comparisons between the superior growth songs and the inferior growth songs. In a multivariate analysis, however, inferior growth songs were best discriminated from superior growth songs by combining three song traits: trill rate, stereotypy, and the number of notes per syllable. We suggest that early developmental stress degrades song in many small ways, and that it is the cumulative effect of the resulting deficits that explains lower female response.

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W. A. Searcy (✉)
Department of Biology, University of Miami,
Coral Gables, FL 33124, USA
e-mail: wsearcy@miami.edu

S. Peters · S. Nowicki
Department of Biology, Duke University,
Durham, NC, USA

S. Kipper
Animal Behavior Group, Institute of Biology,
Freie Universität Berlin,
Berlin, Germany

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Introduction

Mating preferences in female songbirds are influenced by a number of structural properties of male song (Searcy and Yasukawa 1996; Nowicki and Searcy 2005; Catchpole and Slater 2008). A general hypothesis to explain such preferences is that song reflects aspects of male quality, so that a female benefits either directly (through her own reproductive success) or indirectly (through the fitness of her offspring) by choosing a male with certain song features. Since some of the preferred song features are fixed once adulthood is reached (Immelmann 1969; Nordby et al. 2002), the hypothesized link between song and male quality must be forged at least in part early in development. The developmental stress hypothesis (Nowicki et al. 1998; Buchanan et al. 2003; Nowicki and Searcy 2004) suggests this link arises from the fact that individuals differ both in the magnitude of the environmental stresses they experience in early life and in their genetic resistance to these stresses, and consequently differ in phenotypic development in general and in brain development in particular, with the latter translating into variation in song among males. Whether developmental differences are caused entirely by environmental factors or are additionally dependent on genetic background, a positive association is predicted between the quality of the developmental histories of male songbirds and the preferences of females for their songs. Here, we test this prediction for swamp sparrows (*Melospiza georgiana*).

A number of studies have manipulated the post-hatch environment of male songbirds and measured subsequent effects on adult song. That brief stresses (often lasting a month or less) experienced early in the first year might affect display behavior in adulthood is not at all obvious; nevertheless, almost all such studies have found an effect on some aspect or aspects of adult song (Searcy and Nowicki 2009). In some cases, early stress has affected song complexity and duration. For example, European starlings (*Sturnus vulgaris*) stressed by an unpredictable food supply during their second and third months developed shorter songs with smaller syllable repertoire sizes than did unstressed controls (Buchanan et al. 2003; Spencer et al. 2004). Similarly, early infection with malaria caused male canaries (*Serinus canaria*) to develop smaller syllable repertoires (Spencer et al. 2005a). In one study of zebra finches (*Taeniopygia guttata*), both early nutritional limitation and treatment with corticosterone (a stress hormone) caused males to develop shorter songs with fewer syllables (Spencer et al. 2003), whereas in another study, nutritionally stressed males developed longer, slower songs (Zann and Cash 2008). In a third study, nutritional limitation of young birds did not affect song duration or complexity but did affect the accuracy with which song was learned from tutors (Brumm et al. 2009). In other experiments with zebra finches, manipulation of brood sizes affected neither song duration nor complexity (Gil et al. 2006; Holveck et al. 2008), but in one case again affected how accurately song was copied from models (Holveck et al. 2008). A previous experiment with our study species, the swamp sparrow (*M. georgiana*), found that nutritional stress had no effect on repertoire size but did cause young males to develop songs that were poorer copies of tutor songs (Nowicki et al. 2002a).

If results are inconsistent on which song traits are affected by early stresses, it might nevertheless be true that early stress consistently changes song in directions that make it less preferred by females. Some evidence supports this point. Thus, for European starlings, in which developmental stress caused songs to become shorter and less complex, there is good correlational evidence from field and laboratory studies that female starlings prefer longer, more complex songs (Eens et al. 1991; Mountjoy and Lemon 1996). In some zebra finch studies, stress again caused song to become shorter and less complex, and in laboratory studies, female response to songs with these characteristics has been lower (Clayton and Pröve 1989). In other cases, however, developmental stress has altered song traits whose effects on female preferences are not known, for example, quality of learning in zebra finches and swamp sparrows.

Spencer et al. (2005b) performed a more direct test of whether developmental stress alters song in ways that decrease its attractiveness to females. These authors stressed male zebra finches early in development, either nutritionally or with corticosterone, and tested females for response to the songs of the stressed males using an operant procedure. Females showed significantly lower response to songs of previously stressed males than to songs of controls. A post hoc analysis showed differences in the test songs in duration and complexity that might account for the female response patterns.

Here, we examine the relationship between female preferences for song and male developmental history in swamp sparrows. Little is known about the song preferences of female swamp sparrows, except that they respond preferentially to local songs over foreign ones (Anderson 2009) and to songs combining rapid trill rate with broad frequency bandwidth (Ballentine et al. 2004), and that they show some evidence of a preference for more complex repertoires (Searcy et al. 1982). In this study, we manipulate early nutrition in male swamp sparrows in order to generate males with a range of developmental histories. We then use observed growth rates to choose the males with the best and worst developmental histories; these males differ in both the developmental environment that they experienced and in their reaction to that environment, which may be due to their genetic background. We then test the prediction that female swamp sparrows will prefer the songs of good quality males to those of poor quality males. Finally, we use a post hoc analysis to explore the song traits that females might be using to discriminate the two sets of songs.

Methods

Rearing of male swamp sparrows

Test songs were recorded from male swamp sparrows that were hand-reared with manipulated nutrition, following the methods of Nowicki et al. (2002a). We collected 44 swamp sparrow young at 2–6 days post-hatching from Conneaut Marsh, Crawford County, PA, USA, between 13 June and 17 June 2004. All young were assigned immediately to equal-sized control and experimental treatment groups, with young from the same brood split between treatments so as to separate effects of treatment from effects of genotype. All subjects were initially housed in a single, large sound isolation room (Acoustic Systems RE-142, 1.9×1.8×2.0 m) and reared under identical conditions except for their feeding regimes. After fledging at around 10 days post-hatch, fledglings from the same treatment group were housed together in large cages (46×30×33 cm), about six birds per cage, within the sound isolation room. At 18 days of age, the subjects were moved from the large cages and each housed individually in one half of a standard cage (Prevue double breeder, 46×23×25 cm full cage) with a divider in the middle. The day after the last day of training, when the birds were about 14 weeks old, they were housed singly in an undivided standard cage and moved out of the sound isolation room into a large animal housing room where they were kept until recording began.

Birds were hand fed from the time they were collected until independence at 24 days of age. We fed the birds using a standard hand-rearing diet (see Marler and Peters 1988 for details) delivered in 1 ml syringes. We kept track to the nearest 0.1 ml of the amount of food delivered to each bird at each feeding. As nestlings, the birds in the control group were fed until sated, and the birds in the experimental group were fed approximately 70% of that amount; as fledglings, the experimental group was fed approximately 60% of the control group. Birds were provided food exclusively through hand feeding until 18 days of age when we additionally provided a variety of foods in their cages (peas, corn, tofu, ground hardboiled eggs mixed with vitamins, mealworms, and soaked and dry seed) so that they could learn to feed themselves.

We weighed the birds daily from collection to day 30. Following the method of Ricklefs (1967), we calculated growth rate as *K*, the rate parameter from a logistic equation fitted to the mass data up to day 18, using as an asymptote the peak mass attained for each individual during that period.

The birds were exposed to recordings of swamp sparrow song for 12 weeks, starting on 25 June 2004, when their average age was 13±0.3 days (mean±SE), and ending on 15 September 2004, when their average age was 95± 0.3 days. The tutoring period thus spanned the period in which most song is learned in this species (Marler and Peters 1988). We used 14 songs for training, each of a different song type and each recorded from a different individual in the study population. Songs were presented in 3-min bouts of a single song type at a rate of one song per 10 s, with 1 min of silence between bouts. Each of the 14 training songs was presented twice per day, once in the A.M. and once in the P.M., using a Marantz PMD 221 recorder and Acoustic Research Powered Partners Speakers. Song types were presented in a random order, which changed every week.

Survival of young was lower than in previous experiments using these methods (Searcy et al. 2004; Nowicki et al. unpublished) but nonetheless higher than estimated for free-living juveniles in related species (Arcese et al. 1992; Jewell and Arcese 2008). Survival was identical in the two treatment groups: ten of 22 birds (45%) survived to the age of 1 year in both cases. Among the surviving birds, seven of the control and five of the experimental individuals were male.

Test songs

When male subjects were about 290 days of age, they were moved to individual sound isolation chambers (Industrial Acoustics AC-1, 58×41×36 cm) for song recording. Once males were singing crystallized songs, they were recorded extensively using a Sony TCM 5000EV recorder and a Shure SM57 microphone. As test stimuli, we chose ten song types from the control (well-fed) group and ten from the experimental (nutritionally stressed) group. Within each treatment group, we chose songs from males representing the extremes in developmental histories, as measured by their growth rates (*K*) during their first 18 days of life. The ten song types for the poor growth treatment were taken from the four experimental males with the lowest *K* values, while the ten song types for the superior growth treatment were taken from the five control males with the highest *K* values (Fig. 1), with the number of males used being determined by the number needed to accumulate ten song types. Each song was played to only one subject.

We measured nine characteristics of the playback songs using Signal v. 4.0 (Engineering Design). Songs were digitized at a sample rate of 25 kHz. We measured (1) duration from the waveform display (on-screen cursor resolution=2.2 ms) and (2) maximum frequency and (3) minimum frequency from digital spectrograms (256 pt

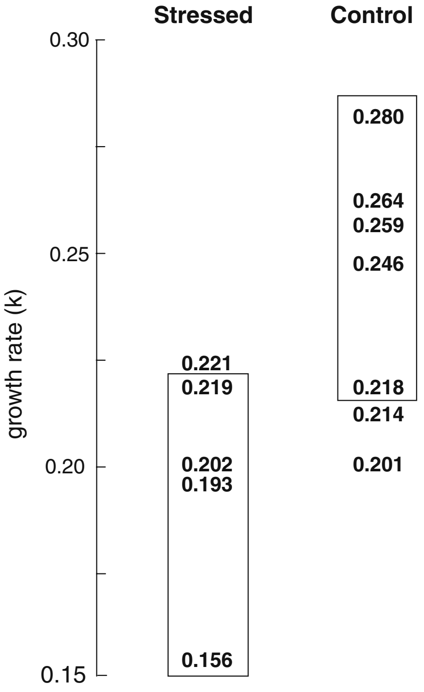

Fig. 1 Growth rates (*K*) of male swamp sparrows raised with unlimited food ("control") and with restricted food ("stressed"). Each *number* represents the value of *K* for one individual male. *Boxes* show the males that were the sources of the playback songs used to test female response

transform, frequency resolution=97.7 Hz, time resolution=10.2 ms measured at −36 dB relative to the peak amplitude frequency of the song). We calculated (4) frequency bandwidth as the difference between maximum and minimum frequency. We measured (5) trill rate of each exemplar from the waveform display (on-screen cursor resolution=1.1 ms). We then calculated (6) vocal performance as the deviation from the upper-bound regression line (performance limit regression line) calculated for our study population (Ballentine et al. 2004). We visually compared spectrograms of the playback songs to spectrograms of tutor models to determine which songs had been copied from which model; song types used as models were sufficiently distinct to make assignment of copies to particular models fairly unambiguous. We then selected the middle syllable from each playback song and compared it to the middle syllable of the identified tutor song to get a quantitative score of (7) the accuracy of the copy (using the Signal software pairwise spectrogram cross-correlation algorithm, 128 pt transform, frequency resolution=195.3 Hz, time resolution=5.1 ms, T-inc=1.0 ms). We measured (8) stereotypy by calculating pairwise cross correlations between all pairs of syllables in a song and averaging those values. Finally, we determined the (9) number of notes per syllable for each song as a measure of complexity.

Solicitation display assay

We tested female swamp sparrows for response to the test stimuli using the solicitation display assay (Searcy 1992; Nowicki et al. 2001). The test subjects were ten adult female swamp sparrows captured during June 2006 in the same study population from which the hand-reared males were taken and in which the tutor songs were recorded. After capture, females were held in cages housed within individual sound attenuation chambers (AC-1, Industrial Acoustics). Subjects were held in captivity for approximately 2 weeks and then released at the site of capture. Seven days before testing, each female was given a subcutaneous implant of 17-β-estradiol in silastic tubing of 1.96 mm outside diameter, containing 7–9 mm of hormone, and sealed at both ends with silastic medical grade adhesive. This dose is the same as used in previous experiments with female swamp sparrows (Nowicki et al. 2001) and is based on the dose found by Moore (1983) to produce physiological levels of circulating estradiol in white-crowned sparrows (*Zonotrichia leucophrys*), with an appropriate adjustment for the smaller size of swamp sparrows (Searcy 1992). Implants were removed at the end of the experiment.

We tested one female at a time, with the door to her chamber open and the others closed. Songs were played from a laptop computer running Signal software through a Nagra DSM speaker placed approximately 2 m from the chamber. Each female was tested with one song from the poor growth treatment and one from the superior growth treatment, with a different pair of stimuli used for each subject. Songs were presented in bouts of one song repeated 18 times at a rate of one song per 10 s. Each female was tested on 2 days with the same two stimuli. On the first day, order of the two stimuli was randomized for the first subject, reversed for the second, randomized for the third, and so forth to counterbalance order of presentation of the two treatments. On the second day of testing, order was reversed for all subjects. Within a day, presentation of the two stimuli to each subject was spaced by at least 3 h. Responses were videotaped and observed from another room. Number of copulation solicitation displays given by the female was the sole response measure (Nowicki et al. 2001).

Statistical analyses

Growth rate estimates (*K*) were normally distributed (Shapiro–Wilk statistic=0.96, *P*=0.84) and were compared between treatments using an unpaired *t* test. Differences in displays given by individual females to songs of the two treatments were normally distributed (Shapiro–Wilk statistics=0.92, *P*=0.37) and were compared using a paired *t* test. Some of the song measurements were normally distributed but others were not; for consistency, we compared experimental and control songs for all measurements using nonparametric Mann–Whitney *U* tests. We also used a backwards stepwise discriminant function analysis to test whether multiple song traits could be used to discriminate the experimental from the control songs; this is a parametric test but is usually considered to be robust to violations of the normality assumption (Klecka 1975). To relate female response to song traits, we needed to control for between-female variation in responsiveness. We did this by expressing each female's response to a particular song as the deviation from her mean response, and relating this measure to each song trait using Spearman rank correlations. All tests are two-tailed.

Results

Mean growth rate (±SE) was 0.198±0.012 for the five experimental males and 0.240±0.011 for the seven control males (Fig. 1). This difference in growth rates was significant according to an unpaired *t* test ($t_{5,7}$=−2.54, *P*=0.030). The two groups differed significantly in mass on all days but one between 7 and 21 days of age (*P*<0.05 by *t* tests for each day); from 22 days onwards, we found no significant differences.

Female swamp sparrows gave a mean of 6.9 (±2.2) displays for songs from the superior growth treatment compared to a mean of 3.9 (±1.7) displays for the songs from the poor growth treatment. Nine of ten female subjects displayed more for the particular song of a superior growth male they were played than for the song from an inferior growth male (Fig. 2). The difference in female response between treatments was significant according to a paired *t* test (t_{10}=2.85, P=0.019).

Duration was the only song trait that differed significantly between the superior growth songs and the inferior growth songs in univariate analyses (Table 1), and the robustness of even this difference is questionable given the multiple comparisons involved. The difference in duration is in the direction that might be expected: superior growth songs are longer than inferior growth songs. Duration was also the only song trait that correlated significantly with female response (Table 2), with females responding more to a song the greater its duration. Thus, it is possible that duration is solely responsible for the difference in female response to the two song treatments. It is noteworthy, however, that the inferior growth songs differ from the superior growth songs in many ways, which, though not statistically significant individually, may have a cumulative importance. Consistent with this view, a backwards stepwise discriminant analysis retains three song measures in the function discriminating superior growth from inferior growth songs: trill rate, stereotypy, and notes/syllable. The resulting discriminant function is significant (Wilks' lambda=0.451, $F_{3,16}$=6.49, P=0.0044).

Table 1 Songs from the superior growth treatment and the inferior growth treatment compared for nine song traits

Song trait	Superior growth	Inferior growth	*U*	*P*
Duration	1.81±0.08	1.60±0.07	21	0.028
Maximum frequency	7284±231	6993±129	41.5	0.52
Minimum frequency	2943±71	3039±94	38.5	0.38
Bandwidth	4340±270	3954±119	37.5	0.34
Trill rate	8.03±1.75	5.87±0.76	37	0.33
Vocal deviation	14.3±3.9	20.3±1.5	37	0.33
Cross-correlation	0.571±0.05	0.596±0.05	45	0.71
Stereotypy	0.90±0.01	0.89±0.02	44	0.65
Notes per syllable	3.4±0.34	3.0±0.26	34	0.19

Values are means±SE. *U* is the test statistic from the Mann–Whitney *U* test. Sample sizes are ten for each treatment

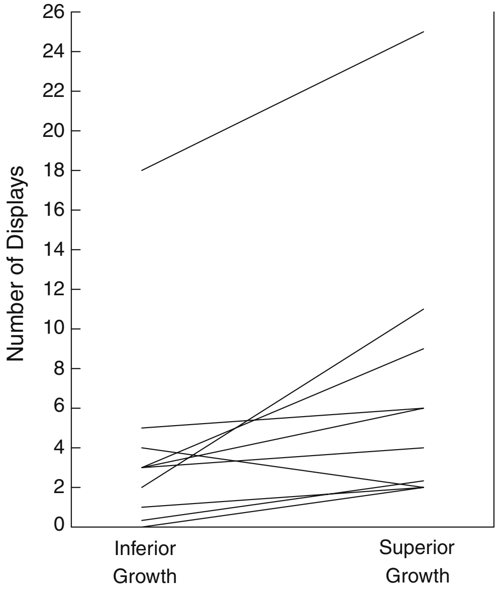

Fig. 2 Response of female swamp sparrows to songs of males with inferior early growth rates compared to response to songs of males with superior early growth rates. Each *line* represents the paired responses of one female

Discussion

Manipulation of early nutrition affected the growth rates of male swamp sparrows in the expected way, as previously shown in this (Nowicki et al. 2002a) and related species (Searcy et al. 2004). We chose playback songs from the two nutritional-treatment groups to represent the extremes in developmental history: one group of songs from those males from the good-nutrition treatment with the highest growth rates and the second from those males from the poor nutrition treatment with the lowest growth rates. Female swamp sparrows then showed significantly greater response in terms of courtship display to the songs of males with good growth histories than to songs of males with poor growth histories. Our results thus support a link between

Table 2 Spearman rank correlations between measures of playback songs and female response

Song trait	Correlation	*P* value
Duration	0.637	0.006
Maximum frequency	0.184	0.42
Minimum frequency	−0.294	0.20
Bandwidth	0.287	0.21
Trill rate	0.395	0.085
Vocal deviation	−0.354	0.12
Copy accuracy	0.056	0.81
Stereotypy	0.201	0.38
Notes/syllable	−0.087	0.71

the attractiveness of songs to females and the growth history of the males that sing those songs. In other words, females act as if they use song as an index to the quality of a male's early development.

Our conclusions on what specific song traits females use to assess developmental history are based on correlations and should be regarded as provisional until experimental studies are done manipulating individual song traits and then testing female response. One interpretation of these results is that song duration is the one song trait that best reveals male developmental history and consequently the one trait that females attend to most closely. This interpretation is superficially compatible with results on European starlings (Buchanan et al. 2003) and zebra finches (Spencer et al. 2003), in which song duration was affected by developmental stress. In starlings, however, song duration is inextricably associated with song complexity because songs are lengthened by adding new and different syllables (Eens 1997). The same is true to a lesser degree in zebra finches (Zann 1993; Zann and Cash 2008). Because early nutritional stress affects the size of some of the brain nuclei that store and control song (Nowicki et al. 2002a; Buchanan et al. 2004; Spencer et al. 2005a; MacDonald et al 2006), and the sizes of these nuclei are correlated with song complexity (Garamszegi and Eens 2004), it seems logical that developmental stress would affect song duration when duration is tied to complexity. Swamp sparrows, however, lengthen their songs by adding more repetitions of a single syllable type, so there is no inherent tie between duration and complexity. Song duration independent of complexity is usually thought of as a measure of song output reflecting present condition (in the sense of energy balance) rather than early developmental history (Searcy and Nowicki 2005), so it is puzzling to find this trait affected by developmental history in swamp sparrows. We suggest that duration in this and similar cases may be a performance trait as well as a condition signal, trading off against other performance measures such as trill rate and bandwidth, and reflecting muscular coordination and neural control (Podos and Nowicki 2004).

Another interpretation of our results—one that we favor—is that early developmental stress together with genetic quality affect song development in many small ways, with lower female response to developmentally inferior males being due to the cumulative effect of a collection of such traits. In our results, eight of nine traits have means that would be considered “worse” for the inferior growth songs than for the superior growth songs (remembering that higher vocal deviation means lower performance), even though only the difference in duration is statistically significant in univariate analyses (Table 1). The one exception to this trend is the cross-correlation measure of learning accuracy, a trait that showed a significant difference in the expected direction in a previous nutritional stress experiment with swamp sparrows (Nowicki et al. 2002a). Discriminant function analysis suggests that songs of the two groups could best be distinguished by three of the traits that do not differ significantly in univariate analyses: trill rate, stereotypy, and notes/syllable. The first two of these can be considered performance measures and the last a measure of complexity.

We see two reasons for favoring the interpretation that early developmental history is tied to multiple characteristics of song and that these in turn collectively affect female response. First, it seems unlikely that either stress-induced perturbation of the learning and development of birdsong or genetic effects would be confined to only a single facet of such a complex, multidimensional signal. Prior work has proven that several song characteristics might be affected within one species (e.g., Spencer et al. 2003; Zann and Cash 2008; Holveck et al. 2008; Brumm et al. 2009). Second, one would expect selection to act on females to attend to any signal feature or combination of features that might reliably reveal something about a male's developmental history.

For females to integrate information from many and sometimes subtle song cues requires that they have the perceptual and cognitive abilities to make such comparisons. In particular, for females to assess male quality via song, females must have some reference for what a “good” song is, to serve as a standard against which comparisons can be made. For features such as song complexity, stereotypy, trill rate, or song length, it is conceivable that a simple, genetically encoded rule-of-thumb may serve the purpose: more complex is better, more stereotyped is better, faster is better, longer is better, and so on. The features suggested to be important by this study could all be explained this way. The problem is more complicated for other song features known to influence female choice. Most notably, how well song models are copied has been shown to be affected by developmental stress in swamp sparrows (Nowicki et al. 2002a), song sparrows (Nowicki et al., unpublished data), and zebra finches (Holveck et al. 2008), and copy quality has been shown to influence female preferences in song sparrows (Nowicki et al. 2002b). For this and other features, the female needs to learn some reference if she is to sort among songs of males with better or worse developmental histories. Both the ability and the opportunity to learn such reference songs may place real constraints on which song features a female integrates into her assessment of male song quality.

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