Accuracy of song syntax learning and singing consistency signal early condition in zebra finches

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Birdsong is a sexually selected and culturally transmitted multidimensional signal. Sexually selected traits are generally assumed to indicate condition. In oscine songbirds, song is learned early in life. The developmental stress hypothesis proposed that poor early developmental condition can adversely affect song learning. The quality and accuracy of learned song features could thus indicate male quality to conspecifics. Surprisingly, studies testing this hypothesis to date mostly compared adult males' song repertoires without looking at song imitation. The few that did reported inconsistent effects and analyzed a limited number of song features. Here, we examined the effects of early condition (by brood size manipulation) on learned song in zebra finches, *Taeniopygia guttata*, in comparing both the number of specific elements copied from an adult song tutor and a great number of previously neglected syntax-, complexity-, and performance-related song features. The treatment did not significantly affect average number of imitated elements, the standard measure of quality of song imitation in this species. However, developmental condition had 2 significant main effects on adult song: birds from large broods (i.e., of poor early condition) in comparison to birds from small broods copied syntactical dependencies of song elements from the song motif of their tutor less accurately and had less consistent sound duration between song motifs. These findings support the developmental stress hypothesis. We discuss how this sheds light on the potential role of such long-term signals of male developmental condition in female mate choice and potential constraints underlying condition-dependent expression of song features. *Key words:* brood size manipulation, condition-dependent signal, developmental stress hypothesis, song learning, *Taeniopygia guttata*, zebra finch. *[Behav Ecol 19:1267–1281 (2008)]*

INTRODUCTION

Since Darwin's (1871) proposition that songs of songbirds evolved in response to sexual selection by female mate choice, many studies have found that individual variation in song does indeed affect the outcome of mate choice and male–male competition (Andersson 1994; Gil and Gahr 2002; Searcy and Nowicki 2005). Exaggerated mating signals should be costly to develop or maintain in order to constitute reliable indicators of male quality (Zahavi 1975; Grafen 1990) and condition (Rowe and Houle 1996; Hunt et al. 2005).

Demonstrating the cost of singing has, however, proved a challenge (Gil and Gahr 2002) as interindividual variation occurs along many dimensions (quality and quantity of song repertoire, structural song variables, and aspects of performance). Although the importance of song in mate choice is well documented (Searcy and Yasukawa 1996), experimental demonstration of condition dependence has been mostly limited to quantity of song output (Gil and Gahr 2002). Evidence for condition dependence of other song features is as yet scant or even controversial (Gil and Gahr 2002; ten Cate et al. 2002). However, song analyses are often limited to measuring repertoire size and song output only, neglecting other features of song complexity or singing performance (e.g., phonological syntax and its consistency). This is an important consideration as the different dimensions of bird song could be constrained by different and specific costs. An increase in song output like the length or rate of songs is likely to require added time or energy expenditure (Nowicki et al. 2002; but see Oberweger and Goller 2001). The production costs are much less obvious for other song features also important in female choice such as song complexity, which is often set equal to a measure of repertoire size, for example, the number of different song types or song elements an individual learns and sings (Gil and Gahr 2002; Nowicki et al. 2002; but see Vallet et al. 1998), however, complicating matters further, differences in complexity can also arise if 2 individuals differ in the usage of syntactical rules (Okanoya 2004).

Nowicki et al. (1998, 2002) proposed that learned features of song could indicate male condition or quality because the development of costly to build brain structures mediating song learning and production occurs during the period of fastest development, that is, when young birds are most vulnerable (see also Catchpole 1996; Doutrelant et al. 2000; Buchanan et al. 2003). Different song features might thus signal different aspects of male condition simultaneously or at different moments in time (multiple message hypothesis, Møller and Pomiankowski 1993; ten Cate et al. 2002). Some dimensions of the signal could respond rapidly to change in condition such as song rate (Birkhead et al. 1998; but see de Kogel and Prijs 1996),

whereas others might reflect past condition. The latter ones could be those song features learned early in life (e.g., repertoire size, but see Brenowitz et al. 1995; Kroodsma et al. 1997; Nowicki et al. 1999) or some performance-related song features (Buchanan et al. 2003; Spencer et al. 2003; Zann and Cash 2007) potentially owing to the long-term negative effects of developmental stress on individual condition (de Kogel 1997; Buchanan et al. 2003; Naguib et al. 2004). Based on such long-term signals of condition, females could gain reliable information about how well males fared during early development.

Several studies have now tested the developmental stress hypothesis and reported effects of early environmental stressors (reduced food availability, corticosterone administration or parasite infection, and natal brood size) on nestling and adult condition, song control brain nuclei, song complexity, and singing performance (Buchanan et al. 2003, 2004; Spencer et al. 2003, 2004, 2005a; MacDonald et al. 2006; Soma et al. 2006). However, these studies have not tested whether developmental stress causes differences in male song (imitation) learning although this is one of the central assumption of the nutritional stress hypothesis (Nowicki et al. 1998, 2002). Most studies testing this hypothesis compared adult males' song repertoires only without looking at song learning. To date, the only 3 studies that did (Nowicki et al. 2002; Gil et al. 2006; Zann and Cash 2007) reported inconsistent effects. Nowicki et al. (2002) showed that hand-reared male swamp sparrows, *Melospiza georgiana*, with limited food availability and controlled quality of song exposure by tape tutoring produced less accurate copies of the model songs from which they learned but did not have smaller repertoire size than the control males. In domesticated aviary-reared zebra finches, *Taeniopygia guttata*, Gil et al. (2006) experimentally altered early condition by brood size manipulations (Naguib et al. 2004) but found no effect of the treatment on the amount of song elements learned from an adult model, on repertoire size, or song rate. In nondomesticated aviary-reared zebra finches, Zann and Cash (2007) found that experimental food restriction affected singing performance but neither repertoire size nor the accuracy of song learning from the foster father. Spencer et al. (2003), who did not assess song learning, reported comparable, but not identical, effects in their study in caged domesticated zebra finches testing for the effects of early reduced food availability and corticosterone administration on song complexity and singing performance. Thus, from those 3 studies analyzing both song features and learning (Nowicki et al. 2002; Gil et al. 2006; Zann and Cash 2007), there is only 1 showing evidence for developmental condition affecting song learning (Nowicki et al. 2002) and 1 on singing performance (Zann and Cash 2007; Nowicki et al. 2002 did not assess any performance-related song features) and none on repertoire size. It is currently unclear which of a number of possible factors can explain these different outcomes as the studies used different species, populations, treatments, and designs and measured different song aspects.

Building on these earlier studies, we designed a carefully controlled song-tutoring procedure and a much more detailed song analysis to address the apparent contradicting findings regarding the effects of developmental condition on male learned song in the zebra finch. We used brood size manipulations as a means to manipulate male condition because earlier studies in this species have shown that this does indeed induce phenotypic variation affecting fitness and survival (de Kogel and Prijs 1996; de Kogel 1997; Naguib et al. 2004, 2006). To increase the strength of our design, we left out the intermediate brood sizes (with intermediate effects on condition) and worked with a paired design with small (2–3 chicks) and large broods (5–6 chicks) only. Our manipulated brood sizes were within the natural range (i.e., 1–6 chicks per brood for zebra finches, Zann 1996), thus manipulating developmental conditions within an ecologically relevant range. Our design overcomes the earlier problems of 1) potentially confounding effects of the number of siblings on song learning accuracy (Gil et al. 2006) and 2) possible effects of the treatment on the tutor's song quality (Spencer et al. 2003; Zann and Cash 2007) as follows: With the onset of the sensitive phase for song learning, high- and low-condition males were pairwise exposed to the same adult song tutor not previously exposed to the treatment. Moreover, other than earlier studies in this species, which either used the number and similarity of copied elements as sole measures of song learning (Gil et al. 2006) or only compared adult song structure (Spencer et al. 2003), we combined a song structure–based comparison with a tutor–tutee song-sharing assay. This allowed us to test for effects of early condition not only on overall adult song structure but also on the learning of element phonology and the rarely studied accuracy of syntax learning (Funabiki and Konishi 2003). We thus carried out 3 main analyses to ask whether males reared in either small or large broods differed 1) in the accuracy of song learning, 2) measures of song structure that reflected song complexity and singing performance, and 3) in singing consistency (i.e., repeatability in song structure).

METHODS

Brood size manipulation and song-tutoring procedure

Subjects were offspring of 30 breeding pairs of wild-type outbred domesticated zebra finches housed in 80 × 40 × 40 cm cages in a large bird room at Leiden University (The Netherlands). The study was first run in 2004 (14 breeding pairs) and replicated in 2005 (16 breeding pairs). We crossfostered the first brood of each pair when chicks ($n = 113$) were 3 ± 1.7 days post-hatching (2004: 3.9 ± 1.6, $n = 56$; 2005: 2.1 ± 1.4, $n = 57$) in 2 different brood sizes: either small consisting of 2–3 chicks (19 broods) or large consisting of 5–6 chicks (11 broods). To control for parental differences in rearing, we made sure that there was no correlation between initial and experimental brood sizes (Pearson 2004: $r_{14} = 0.18$, $P = 0.5$; 2005: $r_{16} = 0.42$, $P = 0.1$). To reduce disturbance to a minimum, all chicks of one brood were moved to foster parents on the same occasion. We tried to distribute full sibs across several foster broods, but this was constrained by a lack of breeding synchronization of the pairs and by our effort to have foster broods with an age composition comparable to natural broods (Welch 2-sample *t*-test: $t_{57} = 0.85$, $P = 0.4$; an age rank number was given based on hatching order, de Kogel and Prijs 1996). These efforts resulted in 3 broods with only unrelated chicks, 14 mixed (some unrelated and some related chicks), and 13 broods where the whole brood was moved to foster parents (for the different brood sizes [$BS_{2,3,5,6}$] the breakdown for full sibs [FS] versus nonsibs [NS] is for BS_2: $n = 1$ brood with 0 FS/2 NS, $n = 2$ with 2/0; BS_3: $n = 2$ with 0/3, $n = 7$ with 2/1, $n = 7$ with 3/0; BS_5: $n = 1$ with 2 + 2/1, $n = 3$ with 2 + 3/0, $n = 1$ with 4/1, $n = 2$ with 5/0; BS_6: $n = 1$ with 2/4, $n = 1$ with 3 + 3/0, and $n = 2$ with 6/0).

The treatment affected juvenile condition in the expected direction, and in line with earlier studies (de Kogel 1997; Naguib et al. 2004), male and female birds reared in large broods when compared with male and female birds reared in small broods showed reduced size during development and at adulthood (day 35: mean tarsus length $\pm$ 1 standard error (SE) for small broods $= 15.5 \pm 0.07$ mm, $n = 48$; large broods $= 15.1 \pm 0.07$ mm, $n = 57$, $F_{1,27} = 10.92$, $P = 0.0015$;

day 180: small broods = 15.5 ± 0.05 mm, $n = 47$; large broods = 15.1 ± 0.07 mm, $n = 53$, $F_{1,27} = 20.60$, $P < 0.0001$; no sex effects or interactions with sex). We also found that adult birds from large broods had a higher standard metabolic rate than those from small broods, which means higher energy requirements (Verhulst et al. 2006).

Chicks stayed with their foster parents until 33.5 ± 3.3 days post-hatching, that is, until nutritional independence (2004: 34 ± 3, $n = 53$; 2005: 33 ± 3, $n = 52$). The experimental birds were then separated from their foster parents for song tutoring. Twenty-six males and 26 females from the foster broods were assigned to 13 tutoring groups (6 in 2004, 7 in 2005). Each group consisted of 2 genetically unrelated males and females from different foster groups (1 chick per brood size and sex) and as song tutor an unrelated adult male and his mate. The song-tutoring procedure lasted until 68.9 ± 2.7 days post-hatching (2004: 70.2 ± 2.8, $n = 12$ males; 2005: 67.8 ± 2.2, $n = 14$ males) and was therefore well within the sensitive period for song acquisition between days 35 to 65 (Slater et al. 1988). Afterward, tutees were housed in single-sex groups of 4–5 birds randomly with regard to their rearing background and tutoring group. Throughout, birds were on a 13.30:10.30 h light:dark schedule (lights on at 7:00 Central European Time [CET]) at 20–22 °C and 35–50% humidity. They had ad libitum access to a commercial tropical seed mixture (Tijssen, Hazerswoude, Holland), drinking water, and cuttlebone. They were supplemented 3 times weekly with 3–4 g of egg food (Witte Molen B.V., Meeuwen, Holland) per bird, twice weekly with branches of millet, and once weekly with germinated tropical seeds.

This study was conducted in line with the Association for the Study of Animal Behaviour guidelines on animal experimentation and the Dutch laws on animal experimentation and approved by Leiden University committee for animal experimentation (Dierexperimentencommissie Universiteit Leiden, DEC 04090).

Song recording

Recordings were made after birds had crystallized their stable adult song, which takes place around 100 days post-hatching (Slater et al. 1988). We recorded nondirected songs of the 26 male tutees at 141 ± 13 days post-hatching (small broods 2004: 141 ± 9, $n = 6$; large broods 2004: 140 ± 7, $n = 6$; small broods 2005: 137 ± 11, $n = 7$; large broods 2005: 144 ± 20, $n = 7$) and of their 13 song tutors and 17 foster fathers (3 foster fathers were also used as tutors but not for chicks they had raised) when they were more than 180 days old. We recorded the foster fathers' songs to include them in our song similarity analysis because the song heard early in life can guide song tutor choice in zebra finches (Clayton 1987; Slater and Mann 1990; Mann and Slater 1994).

For recordings, birds were placed singly in a cage (70 × 30 × 45 cm) on a wooden shelf (100 × 55 cm) at 120-cm height in 1 of 2 identical sound attenuation chambers (100 × 200 × 220 cm). Songs were recorded at 75 cm distance from the cage with a Sennheiser MKH40 microphone (Wedemark, Germany) and MZN16 P48 power supply using Ishmael software (version 1.0.2, http://cetus.pmel.noaa.gov/cgi-bin/MobySoft.pl; automatic energy detection settings for 2000–10000 Hz, detection threshold 1, detection limits 0.2–100 s, buffer 3 s). The conditions in the chambers were similar to those of the bird colony room. We moved males in and out of the chamber in the afternoon (means ± 1 standard deviation (SD) CET; in: 16:36 ± 01:52; out: 15:27 ± 01:47). Most of them (41 of 53) started singing on the next day or on the day after, usually after light went on at 7:00. The remaining males that did not do so were returned to their home cage for a resting

period of at least 1 day before another trial (mean number of trials ± 1 SD: 3.8 ± 2.9, $n = 12$). Recording sessions lasted 1.6 ± 0.8 days ($n = 87$). We obtained 101 ± 123 files per bird (range = 3–533, $n = 53$; average duration of recorded files = 6 s).

Song analysis

Song motif selection
The song of zebra finches consists of a series of introductory elements followed by several repetitions (range 1–23) of 1 individually distinctive motif consisting of a sequence of individually distinctive elements (Sossinka and Böhner 1980) that are delivered in a relatively fixed but not wholly stereotyped sequential order (Sturdy et al. 1999). For our analysis, we randomly chose 5 renditions of each male's motif.

Within the directory with all recorded sound files of each bird, a custom-written software randomly selected 5 files (Niklas J. Tralles; the software can be obtained on request from the authors). Within each selected file (often containing more than 1 song), we selected the song with the highest number of motifs or the first song appearing in the file when several songs had the same number of motifs. Then within the selected song, we randomly selected 1 motif with a dice or with the custom-written software when the song had more than 6 motifs (the software randomly selected 5 files among dummy numbered files corresponding to the number of motifs within the selected song). Truncated songs or motifs were not included for selection. For 4 birds (1 tutee from a large brood and 3 foster fathers), we had only 3 or 4 recorded files. For these, we randomly selected 2 motifs from the same sound file but from 2 different songs when the file had more than 1 song. If motifs were sampled from the same song (1 instance for 2 foster fathers), we made sure not to select the same motif twice. As all songs begin with introductory elements that are highly similar between individuals and because the number of introductory elements is highly variable between renditions of motifs, these elements can easily exaggerate or water down the number of shared elements between 2 motifs. The variable number of introductory elements mostly occurs before the first motif within a song, thus comparing this motif with the subsequent rendition in a song allows one to identify the core motif. This is what we used for analysis for which we digitally deleted those excess introductory elements only appearing in some, especially the first motifs of songs, but keeping those introductory elements that occurred at the beginning of each rendition of the motif within songs (Praat software v. 4.2.07 for Windows, freely available from http://www.praat.org).

Element labeling
We carried out all subsequent bioacoustic analyses with Luscinia sound analysis software (version 1.0, freely available from http://luscinia.sourceforge.net). Next to standard functions, this sound analysis software also offers an automated feature to compare the order of element sequences between song motifs.

For each selected motif, we let Luscinia apply a high-pass cutoff filter at 50 Hz to remove low-frequency background noise and then calculate a fast Fourier transform of the product of the waveform and the moderate-resolution Gaussian windowing function. This rendered spectrographs with a resolution of 10 kHz with a temporal resolution of 1 ms. The computational determination of fundamental frequency of song elements is sometimes difficult in zebra finches because the harmonics (multiple frequencies of the fundamental frequency that are used in its automatic calculation) can be suppressed in the elements (Williams et al. 1989). We therefore used both the automatic pitch detection and manual fine tuning feature in

Table 1

Labels and definitions of the 12 song structure parameters measuring song complexity or singing performance

	Parameter	Definition
Song complexity	Element number	Total number of elements per motif
	Element categories	Total number of different element categories in a motif
Singing performance	Motif duration	Total duration of motif (ms), including silent gaps between elements
	Sound duration	Duration of motif over which sound is present (ms), excluding silent gaps between elements
	Element rate	Number of elements delivered per second, calculated in dividing element number by motif duration
	Peak frequency average	Mean of frequency values (Hz) with the highest amplitudes per element
	Peak frequency maximum	Maximal value of frequency (Hz) with the highest amplitude per element
	Peak frequency minimum	Minimal value of frequency (Hz) with the highest amplitude per element
	Fundamental frequency average	Mean of fundamental frequency values (Hz) per element (approximate perceptual pitch)
	Fundamental frequency maximum	Maximal value of fundamental frequency (Hz) per element
	Fundamental frequency minimum	Minimal value of fundamental frequency (Hz) per element
	Harmonicity	Mean of the noisiness over the element duration; it measures the proportion of energy in the spectrum that falls within 50% of the phase cycle as would be expected if the signal was perfectly harmonic (a high value corresponds to a low noisiness)

Luscinia (Appendix A1). Zebra finch songs contain a number of noisy structures that are difficult to visually inspect in detail even on spectrograms made from high quality recordings with high signal to noise ratios. Luscinia offers an "echo reduction" feature which allows reducing the appearance of reverberations on the spectrograph. We generally measured elements with the same settings of echo reduction (bypassed) and dynamic range (70 dB), but especially with noisy elements, we could greatly improve the spectrographic quality (i.e., the signal to noise ratio) in slightly varying these settings (Appendix A2).

The motifs were segmented into elements according to decisions made by 4 people experienced with the analysis of zebra finch song (M.-J.H., A.C.VdC., K.R., and CtC.). Elements are not always separated by silent intervals (e.g., Sossinka and Böhner 1980; Williams and Staples 1992), and birds can learn small units within complex elements (Williams 1990) and break song production between units within a complex element (Cynx 1990). Therefore, we also based our segmentation decisions on other cues than silent intervals like rapid changes in fundamental frequency, frequency modulation, harmonic structure, amplitude, or noisiness (Williams and Staples 1992). We analyzed all selected motifs of the 2 separate years in one go. Observers were blind with regard to brood size treatment and male status (i.e., tutee, tutor, or foster father), except in some difficult cases where we had a second round of comparisons, and observers specifically compared tutees' with their tutor's motifs to help in the decision.

Measures of song structure parameters and singing consistency
From the standard measurements of Luscinia sound analysis software, we retrieved several parameters per motif pertaining to song complexity and singing performance (12 parameters listed in Table 1). For each of the frequency parameters (Figure 1) and for the parameter "harmonicity," we obtained a value per element and then used the mean of all elements within the motif so that we had one value per parameter and per motif.

We also measured number of different element categories as an aspect of song complexity (Table 1). Earlier studies have used different classifications of element categories based

on mostly visual categorizations (Price 1979; Scharff and Nottebohm 1991; Williams and Staples 1992; Zann 1993; Sturdy et al. 1999) so we decided to use Luscinia software to arrive at a feature-based classification. To this end, we first calculated a distance measure between each pair of elements within the complete data set (i.e., including all tutees', tutors', and foster fathers' motifs; 265 motifs for 3736 elements) using a refined dynamic time warping algorithm (see algorithm details at http://luscinia.sourceforge.net). We could adjust the influence of a parameter on the final distance measure. We based our choice of parameter weightings on the experience gained from a previous study (Lachlan RF, Verhagen L, Peters S, ten Cate C, unpublished data) and from several pilot trials to match our cluster analysis–based element categorization (with an UPGMA algorithm, i.e., Unweighted Pair Group Method with Arithmetic mean) and previously described categories (Price 1979; Scharff and Nottebohm 1991; Williams and Staples 1992; Zann 1993; Sturdy et al. 1999; Leadbeater
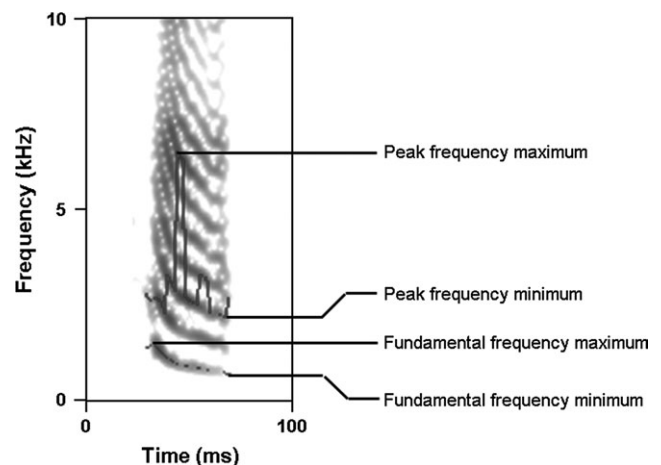

Figure 1
Spectrograms of a song element showing the automated measures of frequency parameters by the Luscinia software (for definitions, see Table 1).
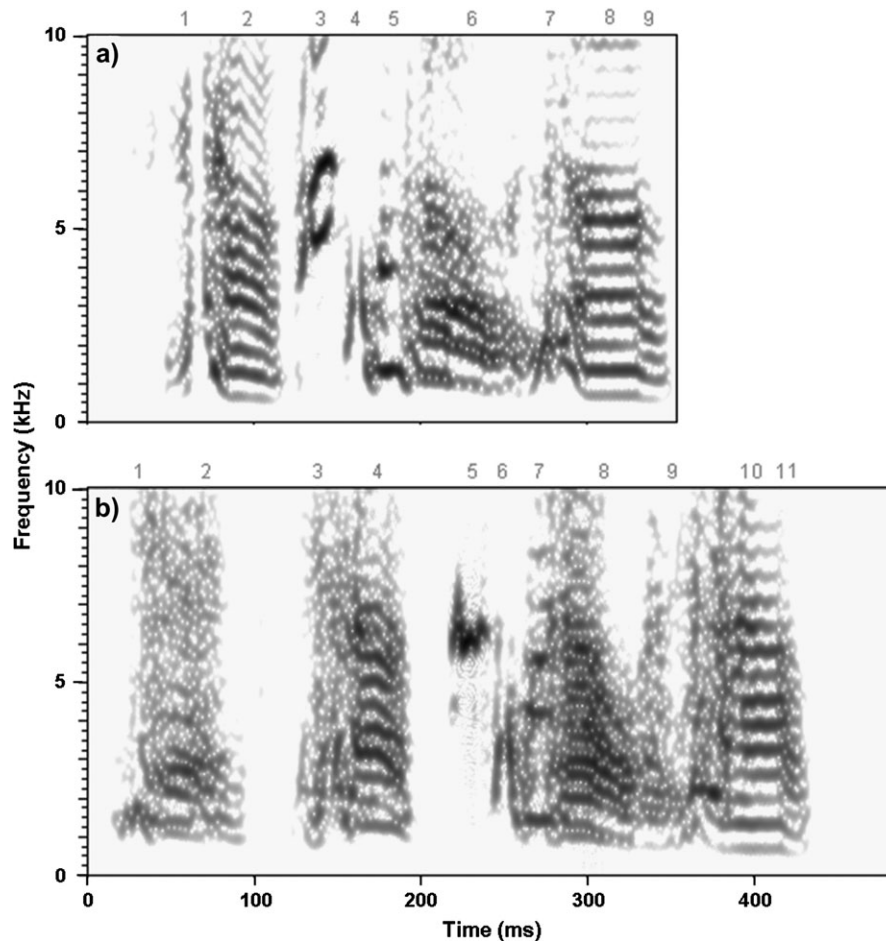
Figure 2
Spectrograms showing the song motifs of a tutor (a) and one of its tutees (b) to illustrate their numbers of shared elements and shared transitions. Elements 1, 2, 5, 6, 7, 8, and 9 in the tutor's motif are, respectively, shared with elements 3, 4, 7, 8, 9, 10, and 11 in the tutee's motif. These 2 motifs thus share 7 elements and 5 element transitions. Although human observers and the Luscinia software generally agreed on the categorization of motifs (see Methods), element 4 in the tutor's song motif and element 6 in the tutee's song motif provide one of the few examples of where the 2 disagreed. In such cases, for consistency, the software's decisions were used for the analyses.

et al. 2005). The resulting settings we applied as standard throughout this study are described in Appendix A3, and further details on the clustering of the elements in categories are available in Appendix C.

We estimated singing consistency in calculating the repeatability of each of the song structure parameters across the 5 motifs per bird following Lessells and Boag (1987) using a 1-way analysis of variance (ANOVA) with parameter as the dependent variable and bird identity as between-subjects factor. The standard error (SE) of the repeatability estimate R was calculated as the square root of the sampling variance of the intraclass correlation (Becker 1984). We compared the repeatability estimates calculated separately for birds from small and large broods with a test of homogeneity (Sokal and Rohlf 1995).

Measures of song sharing
If there are only a limited number of different elements and element combinations, some males will share some elements by chance. To be confident that a particular male has learned from another individual, the amount of sharing should be higher than expected by chance. For our analysis of what was learned when and from whom, we therefore did not only compare the amount of sharing between tutors and tutees and

foster fathers and tutees but also between random males from the colony (the foster father and song tutor pairs).

To measure the amount of song sharing between tutors and tutees, we compared each of the 5 motifs of each tutee with each of the 5 motifs of its tutor, resulting in 25 motif pairs per tutor–tutee pair. For song motif comparisons, we used the same dynamic time warping algorithm, distance measures, and parameter weightings as above (details in Appendix A1). The dynamic time warping algorithm in Luscinia software has been shown (Lachlan RF, Verhagen L, Peters S, ten Cate C, unpublished data) to produce sharing scores between zebra finch songs which agree very closely with those generated by visual inspection of spectrograms by trained observers (as closely as other computational algorithms). To assess the number of shared elements, a distance measure was calculated between all possible element pairs of the 2 compared motifs (using the exact same procedure as described above for the cluster analysis). Based on pilot work and on visual inspection of element resemblance, we digitally set a threshold of distance measure at 0.12 below which elements were remarkably visually identical to each other (Figure 2). Element pairs with a distance measure below this set threshold were therefore classified as shared elements. In case, 1 element was involved in 2 different pairs which both got a distance

Table 2

Paired comparisons of the song-sharing scores for the proportions of shared elements and shared transitions between tutor–tutee, foster father–tutee, and foster father–tutor pairs, including also the scores measuring the level of improvisation shown by tutees when compared with the song of their tutor (i.e., Tutor/Tutee) and of their foster father (i.e., Foster father/Tutee)

	Shared elements				Shared transitions	
Paired comparisons	t_{25}	P	Adjusted α[a]	Effect size[b]	Absolute difference[c]	Effect size[b]
Tutee/Foster father versus Tutor/Foster father[d]	0.7	0.5	0.005	0.17	0	0.11
Foster father/Tutee versus Tutee/Foster father	1.3	0.2	0.006	0.16	5	0.03
Foster father/Tutee versus Tutor/Foster father[d]	1.8	0.1	0.006	0.38	5	0.07
Tutee/Tutor versus Tutor/Tutee	2	0.1	0.007	0.24	6	0.04
Tutee/Tutor versus Tutor/Foster father[d]	3.1	0.005	0.008	0.80	53*	1.59
Tutee/Tutor versus Tutee/Foster father	4.8	<0.001	0.01	0.90	48*	1.48
Tutor/Tutee versus Tutor/Foster father[d]	4.9	<0.001	0.013	1.12	47*	1.60
Tutee/Tutor versus Foster father/Tutee	5.7	<0.001	0.017	1.15	53*	1.50
Tutor/Tutee versus Tutee/Foster father	5.7	<0.001	0.025	1.20	42*	1.48
Tutor/Tutee versus Foster father/Tutee	7.6	<0.001	0.05	1.51	47*	1.51

*$P < 0.05$

[a] The P values of each paired-sample t-test is compared with the adjusted level of significance following sequential Bonferroni (e.g., in first row, the 2 song-sharing scores do not differ because the P value = 0.5 is higher than the adjusted α-level = 0.005). The paired comparisons between scores in the first 4 rows are not significant, whereas all the remaining ones are.

[b] Calculated as Cohen's d: $0 < d < 2$. The effect size is generally considered to be large when $d \geq 0.8$ (Cohen 1988).

[c] For the post hoc tests following Friedman test, 32 is the critical difference above which the difference between 2 scores is significant.

[d] Song-sharing scores measuring the random overlap between song motifs in our study population.

measure below the set threshold, only the element pair with the lowest distance measure was classified as shared element. Each element of the tutor's motif could be classified as shared element only once within a given motif–motif comparison.

To learn a song correctly, a tutee has to not only copy the different elements of the model but also arrange them in the right order. To assess these 2 dimensions of learning, we calculated 2 song-sharing scores for each of the 25 motif pairs per tutor–tutee pair. The first score measured the accuracy in element learning as the proportion of tutor's elements in the song motif of the tutee, which we labeled "shared elements Tutee/Tutor." The second score measured as an aspect of accuracy in syntax learning the proportion of tutor's element transitions in the song motif of the tutee, which we labeled "shared transitions Tutee/Tutor." We define an element transition as 2 adjacent elements within a song. Therefore, with a shared transition, there is always also sharing of the 2 elements involved. To assess differences between tutees in how accurately they arrange learned elements in the right order, the measure shared transitions Tutee/Tutor must therefore correct for the total number of shared elements. Therefore, we divided the number of shared transitions (see algorithm in Appendix B) by the total number of shared elements minus 1, which is equivalent to the total number of possible shared transitions between elements shared between the 2 motifs. The proportion of shared elements was also included as explanatory variable in the statistical analyses of the proportion of shared transitions in response to treatment.

To estimate improvised elements and element transitions in tutees' motifs, we calculated the proportions of tutee's elements and element transitions in the song motif of the tutor, which were respectively labeled "shared elements Tutor/Tutee" and "shared transitions Tutor/Tutee." For these scores, each element of the tutee's motif could be classified as shared element only once.

The same scores were also calculated to measure the amount of song sharing between foster fathers and tutees ("shared elements Tutee/Foster father," "shared transitions Tutee/Foster father," "shared elements Foster father/Tutee" and "shared transitions Foster father/Tutee") and the random overlap be-

tween song motifs in our study population (i.e., the amount of song sharing between the foster father and the tutor of each tutee). These last song-sharing scores were labeled "shared elements Tutor/Foster father" and "shared transitions Tutor/ Foster father" and measured the proportions of foster father's elements and element transitions in the song motif of the tutor.

For each of the resulting 10 different song-sharing scores, we used the means of the 25 repeated-measures per individual pair comparison in all analyses.

Statistics

To test the prediction that tutees learned their song only from their tutor, we tested differences in the proportions of shared elements and shared transitions between tutor–tutee, foster father–tutee, and foster father–tutor comparisons. For the proportions of shared elements, we used 1-way repeated measures ANOVA followed by paired-sample t-tests. To correct for multiple comparisons, we applied sequential Bonferroni corrections. This procedure incurs a substantial reduction in the statistical power with a high probability of making a Type II error (false negative) for some of the tests (Nakagawa 2004). We, therefore, also reported the effect sizes as Cohen's d computed using pooled SD (Cohen 1988; Rosnow and Rosenthal 1996). For the proportions of shared transitions, which could not achieve a normal distribution even after transformation (Table 2), we ranked the data and performed a Friedman test followed by post hoc tests (Siegel and Castellan 1988).

We tested treatment effects on the 12 song structure parameters (Table 1) with repeated-measures linear mixed models and on the proportions of shared elements and shared transitions between tutors and tutees with generalized linear mixed models. In all models, we included the year of treatment as a fixed factor to test whether the effects of the treatment differed between the 2 years in which it was conducted. We first assessed the statistical significance of crossed random factors (birth nest and foster brood) in fitting a similar model without the random effect. We calculated its departure from the main model using maximum likelihood theory (except for the proportions of shared elements where we had to use
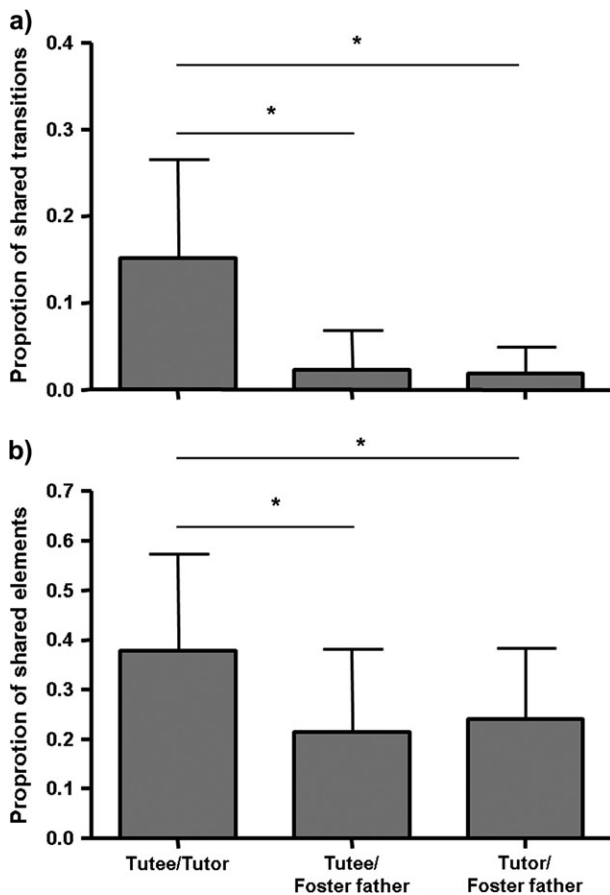
Figure 3
Comparison of the amount of song sharing between tutors and tutees, foster fathers and tutees, and foster fathers and tutors. Shown are (a) shared transitions Tutee/Tutor, shared transitions Tutee/Foster father," and shared transitions Tutor/Foster father and (b) shared elements Tutee/Tutor, shared elements Tutee/Foster father, and shared elements Tutor/Foster father for birds of both treatment groups. Shown are grand means $\pm$ 1 SD (for each data point, $n = 26$). *$P < 0.05$.

a quasibinomial distribution and thus penalized quasilikelihood theory). We retained the random factor "birth nest" in only 1 model (footnotes of Table 6). For all other models, the models without the random effects did not differ from the main model (all $P > 0.05$). We then sequentially deleted from models nonsignificant higher order interactions between factors and then nonsignificant factors until reaching the minimal adequate model (details in footnotes of Tables 3, 4, and 6).

We ran all model analyses in R software (2.4.1 for Windows, http://www.r-project.org) and all other statistical analyses in SPSS software (12.0.1 for Windows, SPSS, Chicago, IL). We checked all measurements for normality before analysis with 1-sample Kolmogorov–Smirnov tests and transformed them when necessary (details in footnotes of Tables 2, 3, 4, 5, and 6). All statistical analyses were 2-tailed with $\alpha = 0.05$, and all means (of untransformed variables) are given $\pm$ 1 SD except when stated otherwise.

RESULTS

In line with earlier reports on zebra finch song learning, the male tutees learned their song from the male song tutor they were housed with just after independence rather than from their foster father during rearing (proportions of shared elements: $F_{2.5,70.3} = 19.8$, $P < 0.0001$, with Huyn Feldt correction;

proportions of shared transitions: Friedman test $Fr_4 = 54.1$, $P < 0.0001$; significant post hoc tests for the following paired comparisons of song-sharing scores in Table 2: Tutee/Tutor vs. Tutee/Foster father, Tutee/Tutor vs. Foster father/Tutee, Tutor/Tutee vs. Tutee/Foster father, and Tutor/Tutee vs. Foster father/Tutee; Figure 3a,b). The proportions of shared elements and shared transitions between tutees and their tutors also differed from the observed random patterns of overlap in our study population (significant post hoc tests for the following paired comparisons in Table 2: Tutee/Tutor vs. Tutor/Foster father and Tutor/Tutee vs. Tutor/Foster father), whereas the proportions of shared elements and shared transitions between tutees and their foster fathers did not (nonsignificant post hoc tests for the following paired comparisons in Table 2: Tutee/Foster father vs. Tutor/Foster father and Foster father/Tutee vs. Tutor/Foster father; Figure 3a,b).

When it came to the relationship between the brood size in which tutees were reared and the sharing scores between tutees' and their tutors' song motifs, tutees from small broods learned more often elements that followed each other in the song motif of their tutor than tutees from large broods (shared transitions Tutee/Tutor: $F_{1,24} = 7.3$, $P = 0.01$; Table 3, Figure 4a) and added fewer new elements between the elements they learned from the song motif of their tutor (shared transitions Tutor/Tutee: $F_{1,24} = 6.8$, $P = 0.02$; Table 3). This was not because tutees from small broods either learned a higher proportion of elements from the song motif of their tutor than tutees from large broods (shared elements Tutee/Tutor: $F_{1,24} = 1.9$, $P = 0.2$; Table 4, Figure 4b; see the absolute element numbers per motif and the absolute number of learned elements in pairwise comparisons in Figure 5a,b) or because they added a lower proportion of new elements to their song motif in comparison to the song motif of their tutor (shared elements Tutor/Tutee: $F_{1,24} = 1.0$, $P = 0.3$; Table 4). Although the proportion of shared transitions between tutees and their tutors increased with the proportion of elements they shared (effect of shared elements Tutee/Tutor on shared transitions Tutee/Tutor: $F_{1,23} = 8.6$, $P = 0.01$; effect of shared elements Tutor/Tutee on shared transitions Tutor/Tutee: $F_{1,23} = 7.7$, $P = 0.01$; Table 3), this relationship did not differ between treatments (nonsignificant interactions between brood size and shared elements Tutee/Tutor or shared elements Tutor/Tutee; see Table 3). The significant effect of brood size on the proportions of shared transitions was thus independent of the expected and observed overall positive relationship between proportions of shared elements and shared transitions (Table 3).

Although tutees did not learn from their foster father's song motif, the higher the proportion of shared elements between their respective foster fathers and tutors was, the higher the proportion of shared elements between tutees and their tutors (effect of shared elements Tutor/Foster father on shared elements Tutor/Tutee: $F_{1,24} = 5.0$, $P = 0.03$; Table 4). This effect was independent of treatment (nonsignificant interaction between brood size and shared elements Tutor/Foster father; see Table 4) and was absent on the other sharing scores between tutees' and their tutors' song motifs. The proportions of shared elements or shared transitions between foster fathers and tutors did not affect the proportion of shared transitions between tutees and their tutors (no effects of shared transitions Tutor/Foster father on shared transitions Tutor/Tutee) and did not facilitate learning of elements and element transitions from the tutor's song motif (no effects of shared elements Tutor/Foster father and shared transitions Tutor/Foster father on shared elements Tutee/Tutor and shared transitions Tutee/Tutor, respectively; Tables 3 and 4).

For both treatments, the song structure parameters (Table 1) were significantly repeatable between the 5 analyzed motifs

Table 3

Results of the generalized linear model analyses testing for the effect of brood size, the proportions of shared elements between tutors and tutees, and the scores measuring random overlap between song motifs on the proportions of shared transitions between tutors and tutees

	Effect size ± 1 SE	F	d.f.	P
Shared transitions Tutee/Tutor				
Final model				
Brood size	0.07 ± 0.04	7.3	1,24	**0.01**
Shared elements Tutee/Tutor	0.26 ± 0.09	8.6	1,23	**0.01**
Rejected terms				
Shared transitions Tutor/Foster father	−0.03 ± 0.12	0.05	1,22	0.8
Brood size × Shared elements Tutee/Tutor	−0.04 ± 0.19	0.04	1,20	0.8
Brood size × Shared transitions Tutor/Foster father	0.001 ± 0.33	0.0001	1,19	0.99
Shared elements Tutee/Tutor × Shared transitions Tutor/Foster father	−2.17 ± 1.27	2.9	1,18	0.1
Brood size × Shared elements Tutee/Tutor × Shared transitions Tutor/Foster father	−4.35 ± 3.09	2.0	1,14	0.2
Shared transitions Tutor/Tutee				
Final model				
Brood size	0.06 ± 0.04	6.8	1,24	**0.02**
Shared elements Tutor/Tutee	0.26 ± 0.09	7.7	1,23	**0.01**
Rejected terms				
Shared transitions Tutor/Foster father	−0.06 ± 0.12	0.3	1,22	0.6
Brood size × Shared elements Tutor/Tutee	−0.08 ± 0.20	0.1	1,20	0.7
Brood size × Shared transitions Tutor/Foster father	0.16 ± 0.32	0.2	1,19	0.6
Shared elements Tutor/Tutee × Shared transitions Tutor/Foster father	−1.57 ± 1.19	1.7	1,18	0.2
Brood size × Shared elements Tutor/Tutee × Shared transitions Tutor/Foster father	−2.83 ± 3.09	0.8	1,14	0.4

Full model: brood size × proportion of shared elements × score measuring random overlap between song motifs × year of treatment, with a Gaussian distribution. The proportions of shared transitions were arcsine transformed (both $Z_{25} < 0.6$, $P > 0.8$). 'Brood size' and 'year of treatment' were binary variables (SMALL or LARGE and 2004 or 2005, respectively). We used arcsin transformation of shared elements Tutee/Tutor, shared elements Tutor/Tutee and shared transitions Tutor/Foster father in analyses. The statistics for year of treatment and its interactions are not shown because these factors never had a significant effect. d.f. = degrees of freedom.

per tutee (all $R > 0.22$, $F_{12,52} > 2.35$, $P < 0.05$; Table 5). Next to between-individual variation in song, there were nonetheless differences between the treatments. Tutees from small broods were more consistent in the parameter "sound duration" which indicates the duration over which sound is present within a given motif ($Ts_1 = 2.1$, $P = 0.03$; still significant after sequential Bonferroni because adjusted alpha = 0.05; Figure 6) and showed a tendency to sing more consistent "motif duration" between motif renditions ($Ts_1 = 1.9$, $P = 0.051$; adjusted alpha = 0.025) than tutees from large broods (Table 5). Motif duration and sound duration were highly correlated with each other (Pearson $r_{128} = 0.97$, $P < 0.0001$) as well as with "element number" (both $r_{128} > 0.76$, $P < 0.0001$).

Although tutees from small and large broods differed in singing consistency (Table 5), they did not differ significantly in any of the song structure parameters measuring song complexity and singing performance, and we found this absence of effects in the 2 years in which the brood size manipulation was conducted (Table 6).

DISCUSSION

The variation of the early nutritional and social environment arising from the brood size manipulations induced condition dependence of song in males. This was manifested in accuracy of syntax learning and consistency of motif sound duration. Interestingly, the average number of different element categories that is an aspect of repertoire size and complexity, parameters of foremost interest in sexual selection studies on male birdsong, was not affected, thereby replicating the effects of other experimental stressors on element repertoire size in zebra finches (this study, Spencer et al. 2003; Gil et al. 2006; Zann and Cash 2007) or song repertoire size in swamp sparrows (Nowicki et al. 2002). However, these species have rather small

repertoires, and early condition might affect adult repertoire size differently in species with large repertoires (Doutrelant et al. 2000; Nowicki et al. 2000; Spencer et al. 2004) for which, however, tests on song learning still need to be forthcoming.

Interestingly, our data show that the 2 treatment groups did also not differ in quantitative differences in element learning (see also Gil et al. 2006; Zann and Cash 2007). Our finding of a treatment effect on an aspect of syntax learning is qualitatively new and might provide an interesting explanation for at least some of the variation found in syntax learning in earlier song learning studies.

Zebra finches often copy groups of elements (ten Cate and Slater 1991; Williams and Staples 1992) suggesting concerted learning of elements' phonology and sequential positions. In adult crystallized song, syntactical rules seem to be based on sequences of elements (Lachlan RF, Verhagen L, Peters S, ten Cate C, unpublished data). However, element sequences can be rearranged differently among birds tutored by the same adult singer (Williams 2004). Clearly, the issue of how tightly element transition and element learning are linked deserves further study. The observation that more element learning meant more transition learning provides support that the 2 are linked, but controlling for this in our analysis, we still found an additional effect of the brood size on the proportion of shared transitions. Thus, although birds from small and large broods did not differ in the accuracy of element learning, they differed in the way they rearranged learned element sequences, which suggests syntax learning differences.

If events associated with the development of song can have a continuing impact on singing performance in adults, notably on the ordering of elements or song types (reviewed in Williams 2004), the interesting question arises which inaccuracies derive from constraints operating during the memorization or during the motor phase of song learning (Slater 1989). In zebra finches, these 2 phases overlap (Slater et al. 1988) making it
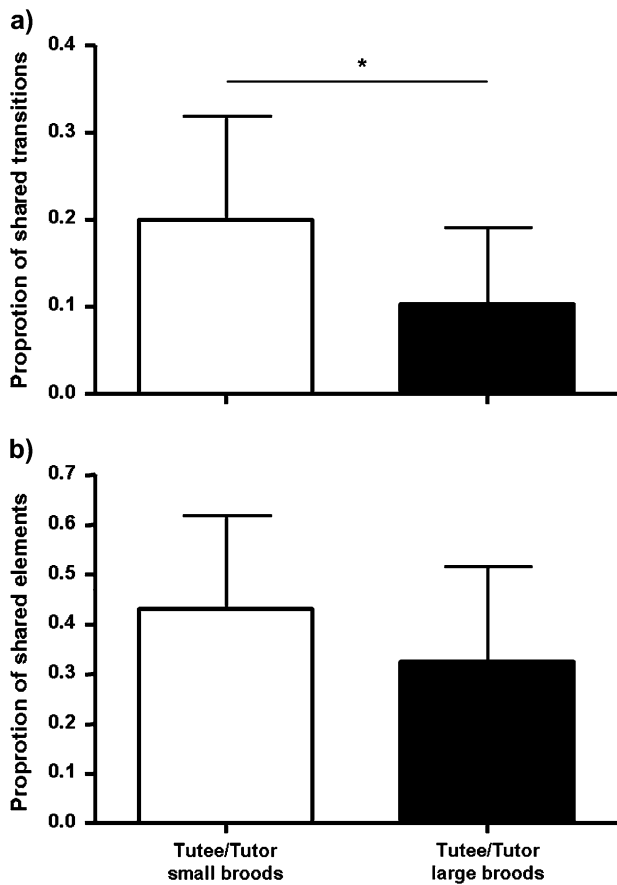
Figure 4
Effects of brood size manipulation on learning from tutor. Shown are (a) shared transitions Tutee/Tutor (i.e., proportion of tutor's element transitions in the song motif of the tutee) and (b) shared elements Tutee/Tutor (i.e., the proportion of tutor's elements in the song motif of the tutee) for birds from small and large broods. Shown are grand means $\pm$ 1 SD (for each mean, $n = 13$). *$P < 0.05$.

straints for the production and maintenance of the male song signal (reviewed in Gil and Gahr 2002). Developmental stress can affect the size of song control brain nuclei (Nowicki et al. 2002; Buchanan et al. 2004; Spencer et al. 2005a; MacDonald et al. 2006), but the relationship between this effect and the effect we report on syntax learning remains to be established. Our brood size treatment followed the procedures from Naguib et al. (2004), which did not find an effect of this treatment on the size of any of the measured song nuclei (i.e., HVC, RA, and LMAN, Gil et al. 2006). However, the treatment might have affected features of the song system other than nucleus size, such as cell size or density, synaptic density or neurophysiological properties, and neuronal projections that connect the nuclei, as already suggested by Nowicki et al. (1998, 2002). Early condition can also affect song development indirectly because differences in male condition might have affected their social status and thereby affected where, when, and how males were exposed to different singers. In the lab situation, there might have been different dominance relationships among the experimental birds (which unfortunately we did not monitor) during the brood size treatment, in tutoring groups and/or when caged in single-sex groups. It might have affected song imitation by the subordinate birds (Tchernichovski and Nottebohm 1998; Tchernichovski et al. 1999) and/or their singing consistency, but it is easy to imagine that postnutritional flocking behavior and social aggregation patterns in the wild will also affect quality and quantity of exposure to adult song. Moreover, the establishment and maintenance of dominance hierarchy are known to have important physiological effects—provoking notably large increases of corticosterone (Wingfield 1994) in both the dominant and subordinate birds (Creel 2001)—that might be a part of the proximate mechanisms underlying the treatment effects on syntax learning and singing consistency.

If the syntax of the model song available to the tutees in the pairwise design was more difficult to learn or to produce for the birds from large broods, the question arises whether the element structure and the organization of the elements within the song may influence the choice of model to be copied (Marler and Peters 1977, 1988). We cannot refute that the birds from large broods if they had had the choice might have selected an "easier" song to learn from (calibration hypothesis, Podos et al. 2004) and that song tutor selection would have been guided by the overlap between the tutor and foster

difficult to delineate the exact nature of these constraints. Neural, physiological, physical, and social constraints have been suggested as, probably nonmutually exclusive, con-

Table 4

Results of the generalized linear model analyses testing for the effect of brood size and the scores measuring random overlap between song motifs on the proportions of shared elements between tutors and tutees

	Effect size $\pm$ 1 SE	F	d.f.	P
Shared elements Tutee/Tutor				
Final model				
Brood size	0.46 $\pm$ 0.33	1.9	1,24	0.2
Rejected terms				
Shared elements Tutor/Foster father	0.28 $\pm$ 1.06	0.1	1,23	0.8
Brood size $\times$ Shared elements Tutor/Foster father	3.64 $\pm$ 2.41	2.3	1,21	0.1
Shared elements Tutor/Tutee				
Final model				
Shared elements Tutor/Foster father	2.44 $\pm$ 1.12	5.0	1,24	**0.03**
Rejected terms				
Brood size	0.25 $\pm$ 0.30	1.0	1,24	0.3
Brood size $\times$ Shared elements Tutor/Foster father	2.70 $\pm$ 2.22	1.5	1,21	0.2

Full model: brood size $\times$ score measuring random overlap between song motifs $\times$ year of treatment, with a quasibinomial distribution. Brood size and year of treatment were binary variables (SMALL or LARGE and 2004 or 2005, respectively). The parameter shared elements Tutor/Foster father was arcsin transformed. The statistics for year of treatment and its interactions are not shown because these factors never had a significant effect. d.f. = degrees of freedom.
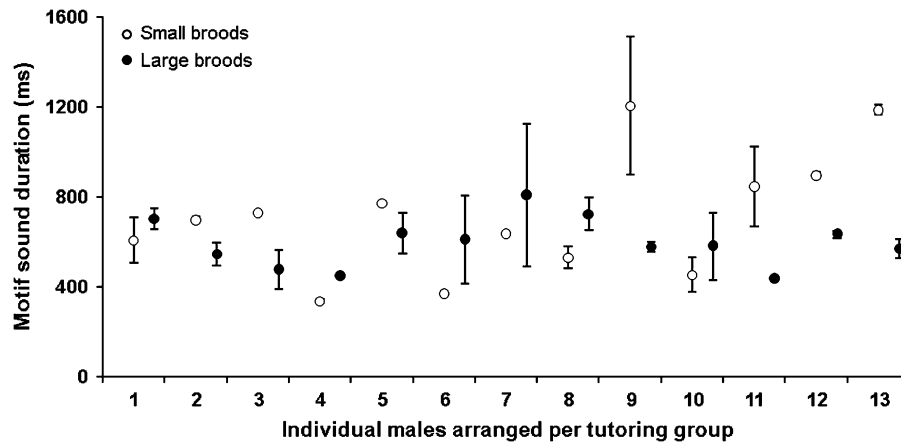
Figure 5

Effect of brood size manipulation on within-individual variation in motif sound duration. Shown are means 6 1 SD (for each data point, n ¼ 5 motifs). The x axes gives a unique ID number to tutors and tutees from a particular tutoring group.

father songs (this study, Clayton 1987; Slater and Mann 1990; Mann and Slater 1994).

The aspects of song (syntax learning and singing consistency) that were affected by our treatment have as yet been little studied in the context of male–male competition and female mate choice, but there is evidence from some species that syntactical patterns rather than an increase in repertoire size affect signal value (e.g., Rehsteiner et al. 1998; Riebel and Slater 1998; Collins 1999; Leitão and Riebel 2003; Okanoya 2004). As yet, singing consistency is not routinely measured, but there is some evidence in several songbird species that consistent vocal performance indicates male quality (Lambrechts and Dhondt 1986; Christie et al. 2004; Byers 2007).

Interestingly, although the variation in singing consistency could be detected by conspecifics without knowledge of the model song, the assessment of variation in the accuracy in syntax learning (i.e., learned order of elements shared with the model song) might need knowledge of the model song. This raises the questions of experience dependence of receivers' perception. At this stage, we can only speculate as how this

might affect male–male competition in the zebra finch, a colonial breeder where the role of song is poorly understood in male–male interactions (Zann 1996). However, the role of song in female mate choice is well demonstrated in this species (for references, see Zann 1996; Holveck and Riebel 2007). Evidence is accumulating that early song exposure influences adult acoustic perception in female songbirds (Riebel 2003a, 2003b) and at least one study suggests that early exposure to song might also affect female preference functions for an aspect of phonological syntax. Isolate female canaries, *Serinus canaria*, showed a different preference function for trill rates than experienced females (Draganoiu et al. 2002). Zebra finches are capable of discriminating conspecific songs that differ only in element order (Braaten et al. 2006), even in the position of a single odd element in a series of repeated elements (Verzijden et al. 2007). Experimentally delayed learners show less stereotyped song (Jones et al. 1996), and there is an age-dependent increase in song stereotypy in zebra finches (Pytte et al. 2007), which suggests that variability in male song could signal age.

Table 5

Average values of song structure parameters for tutees from small and large broods and their singing consistency measured by repeatability estimates *R*

	Tutees from small broods			Tutees from large broods			*R* difference[a]	
	±1 SD	$F_{12,52}$	$R \pm 1$ SE	±1 SD	$F_{12,52}$	$R \pm 1$ SE	Ts_1	P
Element number	14.3 ± 5.4	32.2***	0.86 ± 0.06	12.4 ± 2.9	6.9***	0.54 ± 0.13	1.6	0.1
Element categories[b]	4.3 ± 0.7	—	—	4.2 ± 0.9	—	—	—	—
Motif duration	888 ± 352	33.1***	0.87 ± 0.05	767 ± 157	5.2***	0.45 ± 0.14	1.9	**0.051**
Sound duration	714 ± 274	33.2***	0.87 ± 0.05	596 ± 109	4.0***	0.38 ± 0.14	2.1	**0.03**
Element rate	16.6 ± 3.7	54.4***	0.92 ± 0.04	16.7 ± 4.5	23.6***	0.82 ± 0.07	0.9	0.3
PF average	3171 ± 355	22.5***	0.81 ± 0.07	3195 ± 276	7.0***	0.54 ± 0.13	1.2	0.2
PF maximum	4759 ± 509	11.0***	0.67 ± 0.11	4741 ± 287	2.4*	0.22 ± 0.13	1.3	0.2
PF minimum	1959 ± 271	14.9***	0.74 ± 0.09	1947 ± 390	22.5***	0.81 ± 0.07	−0.4	0.7
FF average	1606 ± 389	66.7***	0.93 ± 0.03	1597 ± 565	121.3***	0.96 ± 0.02	−0.7	0.5
FF maximum	1921 ± 475	65.2***	0.93 ± 0.03	1889 ± 636	93.6***	0.95 ± 0.02	−0.4	0.7
FF minimum	1313 ± 336	72.2***	0.93 ± 0.03	1331 ± 472	133.1***	0.96 ± 0.02	−0.7	0.5
Harmonicity	−2.1 ± 0.3	13.9***	0.72 ± 0.10	−2.1 ± 0.3	18.7***	0.78 ± 0.08	−0.3	0.7

PF, peak frequency; FF, fundamental frequency. *$P < 0.05$, ***$P < 0.001$. For each of the parameters, shown are grand means for the 13 tutees from small broods and 13 tutees from large broods, which average the means of 5 motifs per bird.

[a] The difference in repeatability R between treatment groups is tested with homogeneity tests Ts.

[b] Element categories did not achieve a normal distribution even after log-transformation. "Element rate" for tutees from small broods and harmonicity for tutees from large broods were log-transformed to achieve normal distributions (both $Z_{64} < 1.35$, $P > 0.06$). We used the absolute values of harmonicity prior to log-transformation because values were all negative. All other parameters were normally distributed (all $Z_{64} < 1.3$, $P > 0.8$).
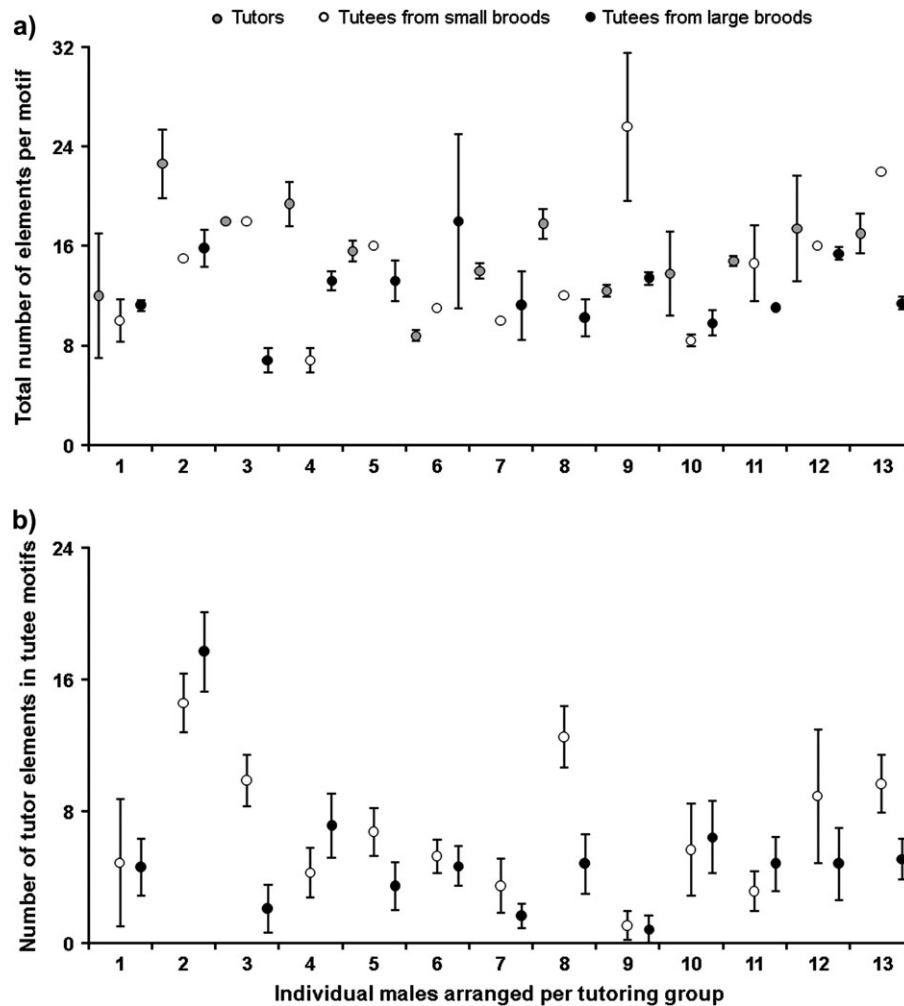
Figure 6
Total number of elements per motif and of learned elements. Shown are (a) the total number of elements (element number) in tutors' and tutees' song motifs (each data point represents the average value obtained from n ¼ 5 motifs) and (b) the number of tutors' elements in the song motifs of their tutees (average of n ¼ 25 motif–motif comparisons per tutor–tutee pair). Shown are means 6 1 SD. The x axis give a unique ID number to tutors and tutees from a particular tutoring group.

If there are some general nonlearned rules constraining element sequencing (Soha and Marler 2001; Rose et al. 2004; Gentner et al. 2006) knowledge of a specific male's model song does not have to be a prerequisite to judging its quality. In line with this, Spencer et al. (2005b) showed that adult female zebra finches randomly chosen from their breeding colony but inexperienced with the actual test songs showed an overall preference for song of unstressed versus stressed males. Likewise, for the songs of the males, we analyzed here, females unanimously discriminated between the songs of males from small and large broods (Holveck MJ and Riebel K, in preparation). However, other than Spencer et al. (2005b), we tested females of known developmental background which turned out to be highly relevant to the observed variation in the direction of female preferences. These were dependent on their own rearing background: all females showed song preferences that were assortative with respect to rearing background. This suggests that the developmental stress hypothesis might need expanding regarding the development of female song preferences (see also Ritchie et al. 2008, forthcoming).

The fact that females can discriminate the songs of males from large versus small broods does not unveil whether they based their choices on the parameters our analyses identified to differ or on some additional parameters we did not measure. However, at least for the second main treatment effect we found, namely, the consistency of motif sound duration, there is corroborative evidence for its potential role in female mate choice from an earlier study. In zebra finches, an aspect of singing consistency, namely, motif stereotypy (defined as singing the same set of invariant elements in an invariant order between individually distinctive song motifs), and the proportion of sound within motif positively predicted both female preferences and male morphology (between 22% and 51% depending on morphological traits, Holveck and Riebel 2007). Moreover, the proportion of sound versus silence within a song is also highly correlated with the production of inspiratory high notes (Leadbeater et al. 2005) which are not produced by all males in a given population and have been implicated to demand higher levels of motor control than standard expiratory elements (Goller and Daley 2001). In our and in previous studies (de Kogel 1997; Naguib et al. 2004; Holveck MJ and Riebel K, in preparation), male and female birds reared in large broods when compared with birds reared in small broods showed reduced size during development and at adulthood. Moreover, the birds in our study differed in their standard metabolic rate, those from larger broods had higher rates, meaning higher energy requirements (Verhulst et al.

Table 6

Results of the linear mixed model analyses testing for the effect of brood size on song structure parameters

	Effect size $\pm$ 1 SE	χ_1^2	P
Element number	0.12 ± 0.12	0.91	0.3
Element categories	0.02 ± 0.08	0.09	0.8
Motif duration	0.10 ± 0.12	0.62	0.4
Sound duration	0.13 ± 0.11	1.33	0.2
Element rate	0.01 ± 0.09	0.02	0.9
PF average	-23 ± 120	0.04	0.8
PF maximum[a]	39 ± 171	0.05	0.8
PF minimum	12 ± 126	0.01	0.9
FF average	9 ± 183	0.002	0.96
FF maximum	32 ± 211	0.02	0.9
FF minimum	-18 ± 154	0.01	0.9
Harmonicity	0.01 ± 0.12	0.003	0.96

PF: peak frequency; FF: fundamental frequency. Full model: brood size $\times$ year of treatment + bird identity, with a Poisson distribution for element number and "element categories" and a Gaussian distribution for the remaining song structure parameters. Motif duration, sound duration, and "element rate" were log-transformed to achieve Gaussian distribution (all $Z_{129} < 0.85$, $P > 0.45$). All other parameters were normally distributed (all $Z_{129} < 1.35$, $P > 0.059$). We used the absolute values of harmonicity because values were all negative. Brood size and year of treatment were binary variables (SMALL or LARGE and 2004 or 2005, respectively). "Bird identity" was entered as random effect and always kept in the models to account for the 5 motifs per individual. The degrees of freedom reflect the comparison of the models with and without the tested parameter following sequential deletion of brood size $\times$ year of treatment, year of treatment, and brood size. The statistics for 'year of treatment' and its interaction with brood sizes are not shown because these factors never had a significant effect.

[a] We retained birth nest as a random factor in the model on "peak frequency maximum" because the model without birth nest differed from the main model: brood size $\times$ year of treatment + bird identity + birth nest + foster brood ($\chi_1^2 = 4$, $P = 0.047$).

2006) further confirming phenotypic differences in quality between birds originating from the different brood sizes. However, between-individual differences in the metabolic cost of song production are rarely studied and focus in general on quantitative not qualitative aspects (e.g., song output and amplitude, Gil and Gahr 2002). Whether and how consistent singing is limited by energetic constraints needs further study.

In conclusion, we here provide evidence that a manipulation of early condition within an ecologically relevant range revealed condition dependence of an aspect of song learning and a performance-related song feature not routinely analyzed. Both the learning of element transitions and consistency of motif sound duration are thus long-term signals of condition. Cultural transmission of song thus does not have to hinder its potential indicator quality (for a theoretical model, see also Ritchie et al. 2008). Our analyses that covered more song features than routinely measured revealed that both a culturally transmitted aspect of song and singing consistency provide information on male condition. Our finding that accuracy of syntax learning was affected supports the nutritional stress hypothesis (Nowicki et al. 1998, 2002), the observation that a performance-related song feature was also affected underlines that the multiple dimensions of song might simultaneously provide information on past and current condition and that some of this information is not dependent on previous knowledge of the song. A full understanding of how song may act as a reliable indicator of male quality requires more investigations into the multiple constraints and mechanisms controlling song development, production, and maintenance. But for now, our experiment shows that developmental conditions can

cause condition dependence of mating signals also in those taxa with cultural transmission of signal and preference.

APPENDIX A: STANDARD SETTINGS USED IN LUSCINIA SOFTWARE (http://luscinia.sourceforge.net)

1. Parameter settings for maximizing the estimated fundamental frequency of elements

We digitally varied "fundamental frequency bias" between 0.5 and 2.0 to obtain the best estimation of the fundamental frequency of each specific element. Fundamental frequency bias simply changes the way in which different hypotheses about the fundamental frequency are weighted: a high value will tend to decrease the measured fundamental frequency.

2. Parameter settings for maximizing the signal to noise ratio of noisy elements

The estimation of the fundamental frequency was sometimes difficult to render accurately especially for noisy elements despite the fundamental frequency bias feature implemented in Luscinia (see Appendix A1). We could achieve a better estimation of the fundamental frequency of these elements while reducing reverberation on the spectrograph in varying the echo reduction and dynamic range within a range of 0–50% (trackback set at 50 ms) and 50–90 dB, respectively.

3. Parameter weightings for calculation of distance measures between each pair of elements of 2 song motifs

We digitally set the weighting of element duration and fundamental frequency at 1; peak frequency and harmonicity at 0.2. We weighted each parameter value time point by its corresponding amplitude, in effect lowering the importance of soft sounds and noisy parts of an element.

APPENDIX B: ALGORITHM USED TO CALCULATE THE NUMBER OF SHARED TRANSITIONS BETWEEN THE SHARED ELEMENTS OF 2 MOTIFS

$$T_{ab} = \sum_{i=1}^{m-1} \left(\frac{2 \cdot \sum_{j=1}^{n-1} p_{ij}^T}{\sum_{j=1}^{n} p_{ij}^S + \sum_{j=1}^{n} p_{(i+1)j}^S} \right),$$

where T_{ab} = shared transitions between the shared elements of motifs a and b;
a has m elements; b has n elements;
p_{ij}^T = transition sharing between transition i in a and j in b;
$p_{ij}^T = 1$ if transition is shared; $p_{ij}^T = 0$ if not;
p_{ij}^S = element sharing between element i in a and j in b.

The algorithm corrects for the probability that transitions could be shared by accident, simply because the elements themselves were shared multiple times in the 2 motifs. In other words, if the elements in a transition are shared multiple times within the motif, the overall transition score is lower.

APPENDIX C: DETAILS REGARDING THE METHODS OF THE UPGMA TREE CLUSTERING AND OBTAINED ELEMENT CATEGORIES (LUSCINIA SOFTWARE http://luscinia.sourceforge.net)

Elements were clustered on basis of the distance measures using an UPGMA algorithm. We used the smallest set of clusters showing element categories that had previously been

Table C1

Description of the 8 most common element categories and corresponding names used by other authors

Element category	Phonology	Equivalent
Downsweep	Frequency downsweep	Slide note (Sturdy et al. 1999)
Tone	Extended harmonic structure and unmodulated frequency over element duration	Tone element (Zann 1993); Flat note (Sturdy et al. 1999)
Noisy	Extremity tight or not clearly visible harmonic structures	Noise element (Zann 1993)
Stack	Tight harmonic structure	Stack element (Zann 1993)
Trill	Vertical rapid frequency modulation	Click note (Williams and Staples 1992)
High	High fundamental frequency	High note (Sturdy et al. 1999)
Short noisy	Extremely tight or not clearly visible harmonic structures of less than 33 ms	Not previously described
High upsweep	High fundamental frequency upsweep	Not previously described

described as zebra finch element categories. Therefore, the cut off we applied grouped the elements in 12 categories including 6 well-described ones (Table C1, Figure C1). Four categories represented each only 34 elements or less (i.e., less than 1% of the total number of elements) and received the label of "other." We labeled the remaining 2 element categories based on their spectral and temporal features (see Table C1, Figure C1). Although our clustering analysis gave consistent results with previously described element categories, we want to stress that the UPGMA tree presented here makes no inferences about the level of clustering used by the birds.
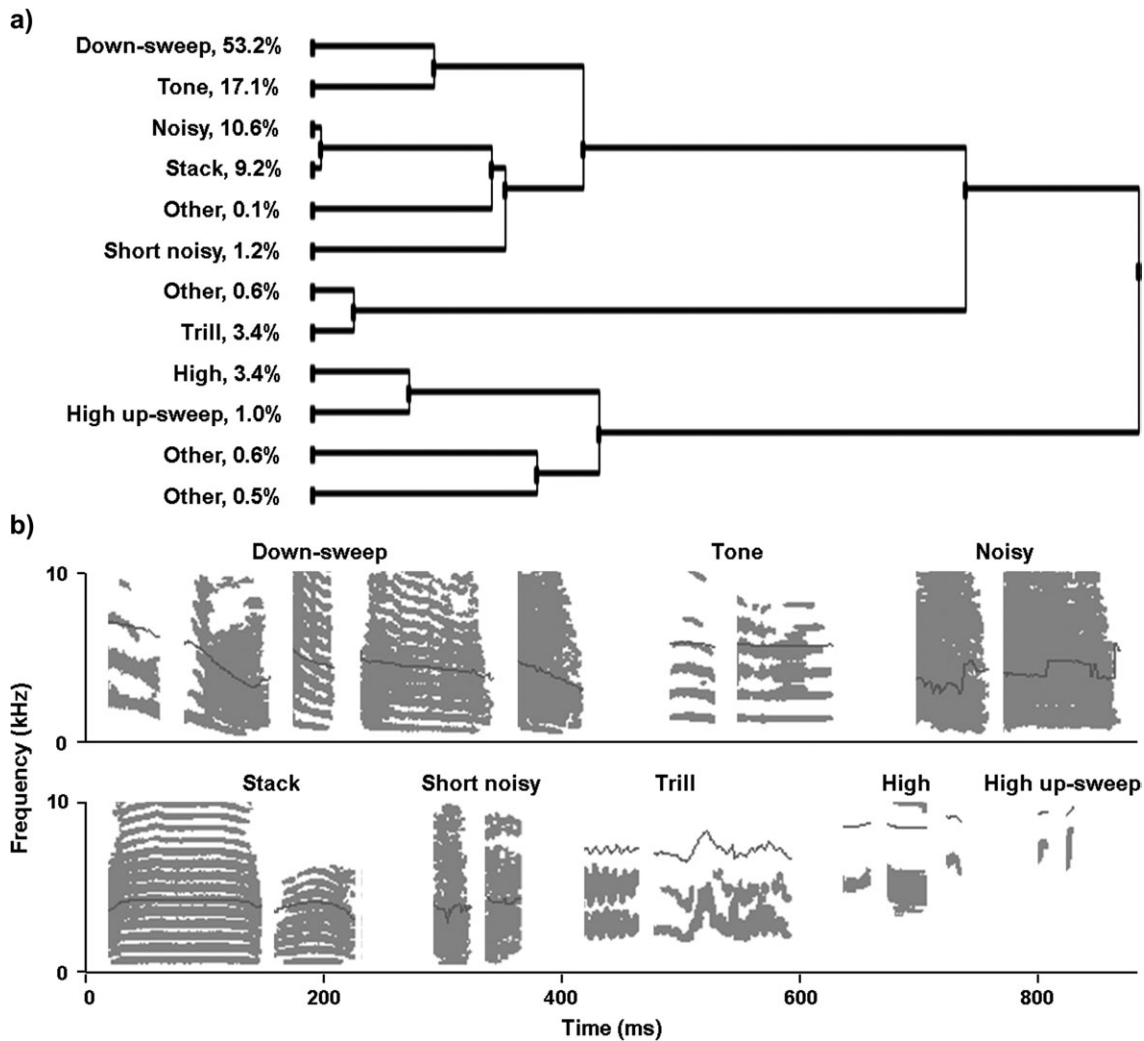

Figure C1
(a) The UPGMA tree clustering the 3736 elements from the 265 motifs of the 53 tutees, tutors, and foster fathers and (b) examples of elements for each of the 8 most represented categories (for a description of the phonology of each element category, see Table C1). Percentages of each element category are based on the 1730 elements of tutees'song motifs.

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