Acoustical and Syntactical Comparisons between Songs of the White-backed Munia (Lonchura striata) and Its Domesticated Strain, the Bengalese Finch (Lonchura striata var. domestica)

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ABSTRACT—The Bengalese finch is a domesticated strain of the white-backed munia. The process of domestication began some 250 years ago in Japan and several modifications in coloration and behavior occurred. We recently found that songs of Bengalese finches are much more complex in their temporal organizations than songs of related species such as zebra finches. We hypothesized that this complexity occurred during domestication. To explore this hypothesis, we compared syntactical and acoustical parameters of songs between the wild and domesticated strains of white-backed munia. Acoustical morphologies of the song elements were strain-specific: similarities among song elements were higher within individuals of each strain, but the degrees of morphological variations were comparable between the strains. In the time domain, white-backed munias sang a highly stereotyped song: a song element was always followed by one of certain song elements in a deterministic way. Bengalese finches, on the other hand, sang complex song with one song note followed by several possible song notes. Male songs should evolve largely under two different pressures: female preference and risk of predation. The low degree of complexity found in wild white-backed munias may be the result of compensating these two factors. In Bengalese finches, because of the domestication, predation is no longer a selection pressure. Thus, it is likely that Bengalese finch songs had undergone changes that were favored by females.

INTRODUCTION

Birdsong is a learned vocalization that is dependent upon auditory environment (Konishi and Nottebohm, 1969; Marler, 1991; Marler and Peters, 1977; Nottebohm, 1968). In general, birdsong has dual functions: female attraction and territory defense (Catchpole, 1982; Searcy, 1986; Sossinka and Bohner, 1980; Walter *et al.*, 1991). In estrildine finches such as Bengalese finches (*Lonchura striata* var. *domestica*), however, the song is solely used in courtship display and functions only in sexual context but never in aggressive context. Thus, phenotype of birdsong in estrildine finches should be sensitive to the process of sexual selection (Williams *et al.*, 1993).

The Bengalese finch became increasingly popular as an experimental animal to study neural basis of song control

(Okanoya, 1997; Doupe, 1997). One remarkable feature of its song is that, contrary to other songbirds studied to date, adult finches require continuous auditory feedback for the real-time control of ongoing song (Okanoya and Yamaguchi, 1997; Woolley and Rubel, 1997). Generally, close-ended learners that learn their song only once in early life do not require auditory feedback as adult (Thorpe, 1958; Konishi, 1965). The data obtained on Bengalese finches is thus the first and only demonstration to date in birdsong studies that songs of a close-ended learner still need auditory feedback for the maintenance of adult song (Okanoya and Yamaguchi, 1997).

The Bengalese finch is a domesticated strain of a southeast Asian estrildine finch, the white-backed munia (*Lonchura striata*). Their habitat ranges from wild field and agricultural area, to human residential area. They live in a flock of around 100 (Restall, 1996). Several white-backed munias were imported in Japan from China about 250 years ago. About 140 years ago, white plumage mutations occurred in the white-backed munia, that was by then called as "Jyu-shimatsu" (ten sisters) because of their gentleness and tameness, that made this strain of the finch even more popular as a cage bird.

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Bengalese finches are tame and hardy birds often used as fostering parents to rear offsprings of other finches that lost ability to breed by its own in captivity (Goodwin, 1982). Because artificial selections favored parental traits of the Bengalese finch, several behavioral and morphological modifications must have occurred through domestication. We suspect one of such modifications occurred in the song, although song was never subject of direct artifitial selection during the process of domestication.

Birdsong is a behavior that has undergone the processes of natural selection and sexual selection. In the wild, selective pressures such as predation risk, time allocation for foraging, female preference, and energy cost, should each modify the morphological feature of birdsong (Yasukawa, 1989; Hutchinson *et al.*, 1993). However, Bengalese finch song may represent an example of modifications that occurred in a unique environment of domestication. By comparing the wild and domesticated strains of the same species, we might be able to reveal selection pressure that actually shaped morphology of species typical songs.

MATERIAL AND METHODS

Subjects

Birds were obtained from local pet suppliers and kept in an aviary at Chiba University, Chiba, Japan. White-backed munias were caught in the wild and imported through Hong Kong. We obtained white-backed munias from two different pet suppliers. Bengalese finches were bred by Japanese breeders. White-backed munias and Bengalese finches were separately maintained in large cages. Other species of birds, such as zebra finch and strawberry finch, were also kept in the same aviary. Eight adult male Bengalese finches and 5 adult male white-backed munias were used in the present analyses. Lights in the aviary were on a 13 hr : 11 hr light/dark cycle. The birds were provided with finch seeds and fresh water every day. Figure 1

Fig. 1. A picture showing a Bengalese finch (right) and a white-backed munia. These birds are sexually monomorphic in the appearance. The Bengalese finch has white feathers with dark brown patches. The white backed munia is in dark gray plumage except for a part of rump that is white.

shows the picture of a Bengalese finch (right) and a white-backed munia.

Song recording

Each male was singly kept in a small plastic cage and the cage was brought into a sound proof room (90 × 180 × 135 cm). After the bird settled, a plastic partition that was made from the same material of the cage was inserted to divide the cage into halves. A female bird of the same strain of the subject was introduced to the vacant half of the cage. Upon introducing her, the male usually began singing vigorously. This "directed" song (Sossinka and Bohner, 1980; Walters *et al.*, 1991) was recorded by an electret condenser microphone (Sony ECM-MS907) and amplified (Sony MX-50) and then fed into a digital audio tape-recorder (Sony DAT A-8). Recording was continued until a total of two minute sequence of song bouts were obtained for each bird.

Morphological analyses

For this analysis, songs from 4 individuals from each strain were used. From the recording of song episodes, a song unit that contained all song elements identified in the entire recording was spliced on an IBM-compatible personal computer (PC) by RTS sound analysis software (Engineering Design). The song unit was further spliced into elements. Five types of elements were taken from the beginning of the song unit and each was separately saved as a file. Altogether, 20 elements were spliced out from 4 individuals from each of the two strains.

Forty song elements taken from both strains of birds were analyzed by CORMAT program of the SIGNAL sound analyses system (Engineering Design) for the spectrographic similarity. CORMAT slides sound spectrograms on time domain to find the highest spectro-temporal correlation. Resulting similarity index was submit to a multi-dimensional scaling (MDS) program (SYSTAT, Inc.) to see whether the strains were different at the level of song element morphology.

The 40 elements were scaled at 2 dimensions. Dimensional coordinates were taken for Bengalese finches and for white-backed munias separately. The two dimensions were then submit to a multivariate analysis of variance to test whether the strains were different in morphological characteristics of song elements. The test was run two tailed at a $p < 0.05$ significance level.

Parametric analyses of element morphology

The same data set as above analysis was also used in this analysis. The recordings were overviewed on Kay 5500 Digital Signal Processor. Following acoustical parameters were taken from each type of notes: 1) frequency of maximum amplitude (FMA), 2) Bandwidths measured at the 5 dB down point from FMA (BW), and 3) total length of the element (TL). Ten exemplars of each note type were selected and a mean, standard deviation, and coefficient of variation (CV) were calculated.

Syntactical analyses

Song recorded from 8 Bengalese finches (4 of which were also used in previous analyses) and 5 white-backed munias (4 of which used in previous analyses) were used in this analysis. Recorded songs were analyzed on a PC running an Avisoft SAS Lab (Specht, 1997) sound analyses system. The 2 min recordings were all sonagramed and printed. Each of the song elements was categorized into several distinct types through visual inspection and an alphabet designating each category was assigned. Thus, song output of each individual was expressed as a string of alphabets. For each song, number of unique element types was counted.

The string was analyzed and transition probabilities from one note type to others were calculated. Result was a matrix of transition probabilities. Based on this matrix, a transition diagram visually showing the pattern of song syntax was drawn. When a song is completely linear, that is, when a pattern of element-to-element transitions is

unitary definable, the transition matrix should contain only N non-zero cells out of $N \times N$ cells. If, on the other hand, the song is very variable and contains all possible patterns of transitions, the matrix should contain many non-zero elements. Thus, when the number of song elements N is divided by the number of non-zero transitions in the matrix, that index should indicate how linear the song is. This linearity index (Scharff and Nottebohm, 1991) was calculated for all songs.

Overall amplitude of the song

Songs recorded from 8 Bengalese finches and 5 white-backed munias (all of these songs were used in previous syntactical analyses) were used in this analysis. A 5 sec portion of continuous singing was spliced from the recording and a root-mean-square (RMS) value was calculated on that portion. Values were expressed as dB (re.

arbitrary voltage but fixed for all measurements) and compared between the two species using t-statistics. Alpha smaller than 0.05 with two tailed probability was required for the significance.

RESULTS

Morphological differences between the songs of the two strains

Phonological structures of song elements (morphology) were apparently different between the two strains of birds. Fig. 2 shows representative sound spectrograms taken on a Bengalese finch and a white-backed munia. In general,
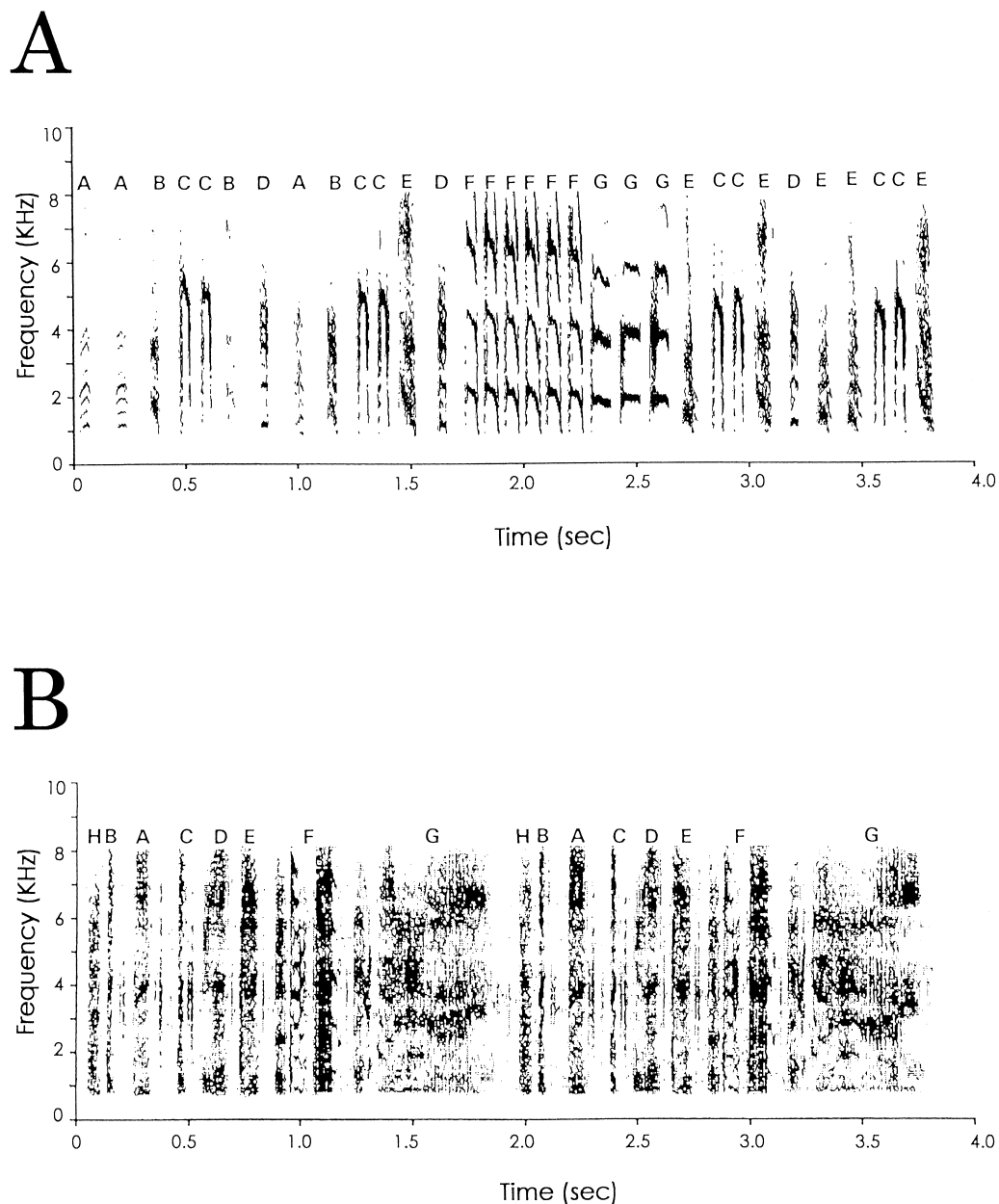

Fig. 2. Representative sonagrams of the songs taken from a Bengalese finch (**A**) and a white-backed munia (**B**). Transition diagrams for these songs are shown in Fig. 4 (**A**) and 5 (**A**). Each note type was identified by a separate alphabet. A note was defined as a continuous trace of a sonagram that was separated by clearly visible silent intervals.

Bengalese finch notes were more discrete than white-backed munia notes. This observation was confirmed by the spectrographic correlation analyses. The 2-dimensional solution of the 40 song elements taken from the 4 Bengalese finches and 4 white-backed munias is shown in Fig. 3. Data points from Bengalese finches are generally more positive (average 0.3935) than the data from white-backed munias (average –0.1945) at the dimension 1. The two strains are about the same on the dimension 2, though (–0.0645 and 0.065).

Multivariate analysis of variance run on the coordinate values detected a significant difference between the two strains ($F = 3.824$, df = 2, 37, $p = 0.031$). Post-hock univariate ANOVA detected significant differences between the strain on the dimension 1 ($F = 7.027$, df = 1, 38, $p = 0.012$) but not on the dimension 2 ($F = 0.368$, df = 1, $p = 0.547$).

Parametric analyses

To find acoustical correlates with the dimension 1 that significantly divided the two strains, we correlated acoustical parameters measured on the song elements used in the morphological analysis. Among the 3 parameters, only FMA significantly correlated with the dimension 1 ($r = –0.57$, $p < 0.01$). However, FMA was not different between the two strains by univariate t-statistics ($p = 0.29$). Average FMA was 3874Hz
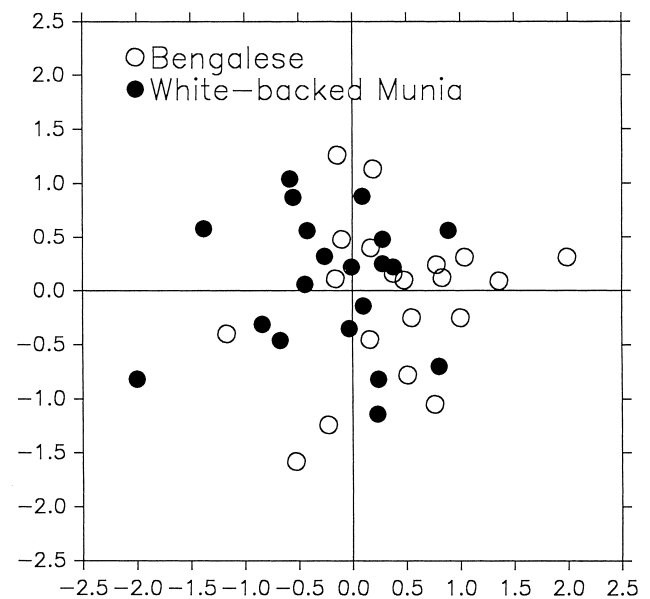
Fig. 3. Multidimensional scaling of morphological similarity among 40 song elements taken from Bengalese finches and white-backed munias. Dimension 1 significantly separated song notes of the two strains ($p = 0.01$). More Bengalese finch song elements were distributed in the right side of the figure while more white-backed munia elements were found in the left side.
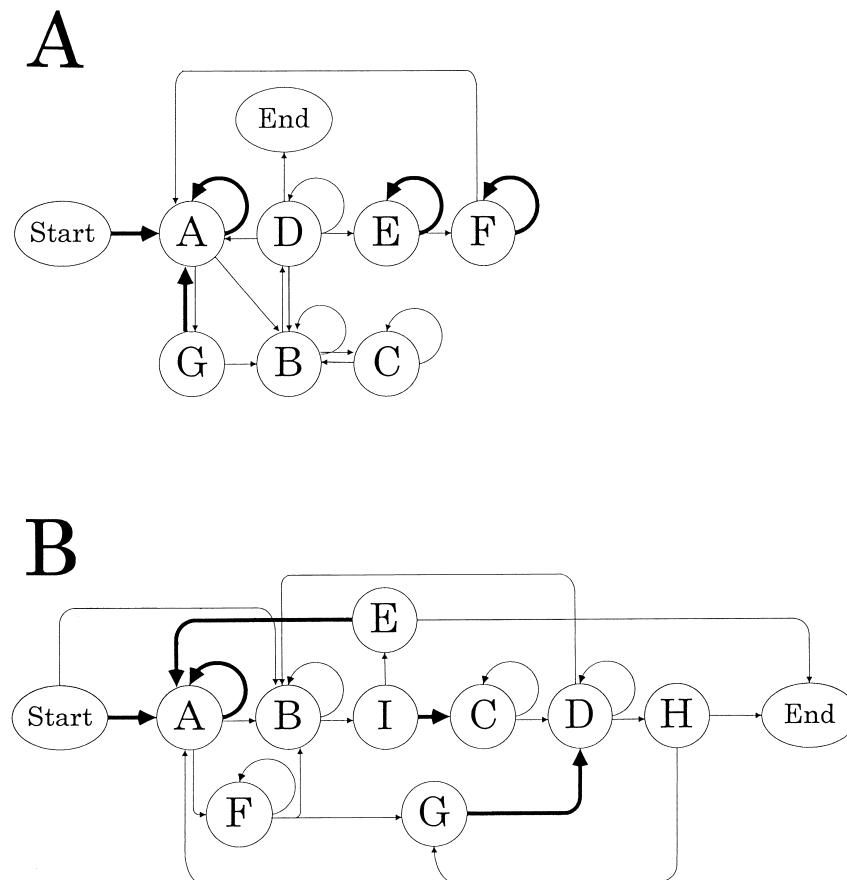
Fig. 4. Two examples of transition diagrams of Bengalese finch song. Bengalese finches have somewhat complex patterns of note-to-note transition. Diagram A was drawn from the song shown in Fig. 2 (**A**) as sonagram.

for the Bengalese finches and 4455 Hz for the white-backed munias. Average BW was 660 Hz for the Bengalese finches and 814 Hz for the white-backed munias (p = 0.28). Average TL was 113 ms for the Bengalese finches and 121 ms for the white-backed munias (p = 0.50). None of these acoustical parameters of the two strains of birds were significantly different.

Coefficients of variation (CVs) based on 10 exemplars of each note were obtained on the five song elements in an individual song. An average of these CVs was compared on the 4 individuals of each strains by independent t-tests. No significant differences were found in any of these tests (FMA, p = 0.27; BW, p = 0.21; TL, p = 0.93). Thus, acoustical stereotypy of the song elements was not different between the Bengalese finch and the white-backed munia.

Syntactical variations

Song syntax was much more complex in Bengalese finches than in white-backed munias. Figures 4 and 5 show two representative transition diagrams from two individuals of each of the species. Bengalese finch songs have more repeating notes and more loops and embedded structures (Fig. 4) while white-backed munia songs are generally linear (Fig. 5). Average song linearity calculated on the 8 Bengalese finch

songs was 0.33 while that on the 5 white-backed munias was 0.61. Difference was significant by an independent t-test (p = 0.00) (Fig. 6). Average numbers of song element types were 9.25 for the 8 Bengalese finches and 8.40 for the 5 white-backed munias. Difference was not significant by an independent t-test (p = 0.64) (Fig. 6).

Overall amplitude of the song

An average amplitude was 25 dB for the 8 Bengalese finch songs and 11 dB for the 5 white-backed munias (reference level is arbitrary). The difference between the two strains was significant by t-test (p = 0.00). Since measurements were taken with the identical setting for these two strains, the difference obtained here should reflect good approximation of the difference in sound pressure level in the songs of these two strains. Bengalese finches were singing, on average, 14 dB louder than the white-backed munias (Fig. 6).
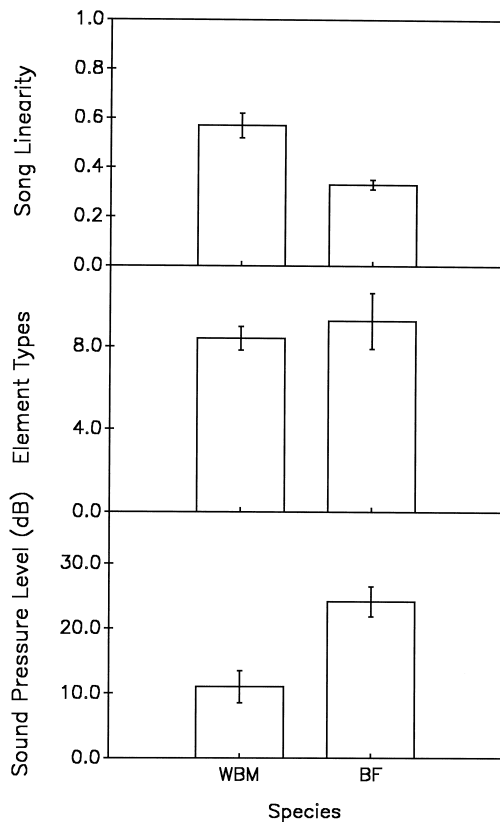
DISCUSSION

Song complexity and female preference

We compared acoustical and syntactical characteristics in songs between a wild strain, the white-backed munia, and its domesticated strain, the Bengalese finch. By doing so, we
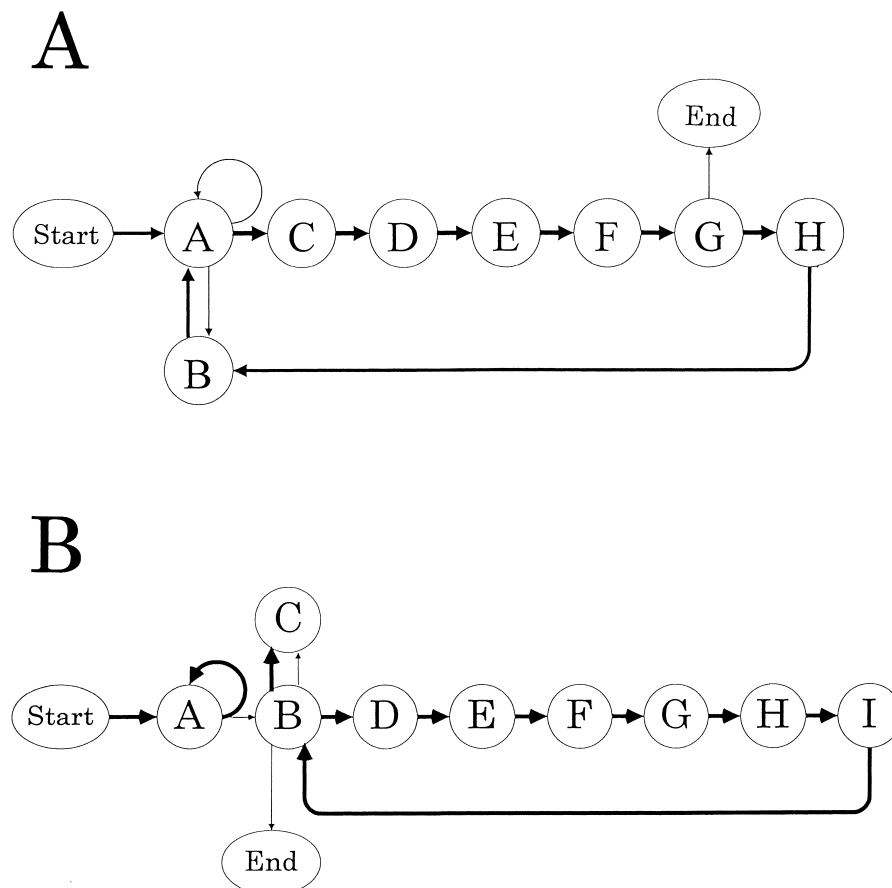
Fig. 5. Two examples of transition diagrams of white-backed munia song. Note patterns of transition are much simpler in white-backed munias compared to Bengalese finches. Diagram A was drawn from the song shown in Fig. 2 (**B**) as sonagram.

Fig. 6. Song linearity, number of element types, and overall sound pressure levels are compared between the two strains. Song linearity was significantly higher in white-backed munias (WBM), and sound pressure level was significantly higher in Bengalese finches (BF).

the variations in note type as "complexity." In our present research, song complexity in Bengalese finches appeared as dynamics in time series rather than variations in note types. In this regard, it would be of interest to test whether female birds respond to time-domain complexity.

Song complexity and auditory feedback

Adult Bengalese finches require real-time auditory feedback to produce normal song syntax (Okanoya and Yamaguchi, 1997; Woolley and Rubel, 1997). Syntactical differences between the songs of the Bengalese finch and white-backed munia suggest their dependence on auditory feedback for the maintenance of learned song might be different. Since white-backed munias sing highly stereotyped, linear song like that of zebra finches, they might not depend upon auditory feedback. If so, the dependence of auditory feedback in the Bengalese finch is an emergent property that resulted from the evolution of time-domain complexity.

Most of the studies reported to date used songbird species that sing highly stereotyped, linear song (i.e., Konishi, 1965). If more species that sing complex song in temporal domain were studied, we might found that species are different on their dependence on auditory feedback for real-time production of songs.

Neoteny and development

Song is a learned behavior in oscine songbirds. While learning song, a juvenile bird goes through several stages of song morphology (Nottebohm, 1968; Clayton, 1987). In the very beginning, song is mere trains of soft noise (subsong). Then comes a stage at which more note types than actually used as adult are stringed in a random sequence of utterance (plastic song). Finally, both note phonology and note sequence are fixed at adult stage (crystallized song). The song of adult Bengalese finches retains one of the characteristics of juvenile plastic song: element-to-element transitions are not firmly fixed and retains some flexibility. In this sense, the song of Bengalese finch remains in a juvenile "plastic" form. In other words, the Bengalese finch song might be considered as a "neoteny" of the white-backed munia song. To advance this argument, however, we do need more data on song development from both Bengalese finches and white-backed munias.

The cost of singing complex songs

Singing is costly in two terms: the cost of being preyed upon while singing, and the cost of singing itself. Male birds are at a risk of predation when engaging in singing (Ryan *et al.*, 1982; Yasukawa, 1989). Longer, complex songs should be riskier than shorter, simpler songs. Singing is often performed as advertisement. Males often sing in a place where it is much easier for predators to spot them. Because of this cost, in some species songs could change into much simpler form through the process of evolution (Gray and Hagelin, 1996).

Singing long, complex songs also have physiological cost. The volume of one of the song control nuclei, HVC, is known

expected to find traits that are favored in domesticated environment. The most remarkable difference between the two strains is that the domesticated strain sang songs with more complex note-to-note transitions than the wild strain.

Female Bengalese finches showed more copulation displays to the playback of a 6-element song over a 4-element song (Clayton and Prove, 1989). Female Bengalese finches perch-hopped more often when stimulated with a song with more elements rather than a song with a few elements (Nakamura *et al.*, 1985). These results suggest that female choice might favor upon more variety on song element types.

However, we did not find significant differences in the number of song elements between the strains. In the study by Clayton and Prove (1989), the degree of complexity in the temporal domain of the stimulus songs was not reported. That was so as the study by Nakamura *et al.* (1985). Since these authors were using tape-recorded songs, temporal-domain dynamics were probably not introduced. Thus, how song complexity in the temporal domain might cause different effects on female birds are still unknown in Bengalese finches.

Although there are several studies concerning to the "song complexity" and female choice (i.e., Catchpole, 1980; Catchpole et al., 1984; Ryan, 1988; Clayton and Prove, 1989; Eens *et al.*, 1991; Kroodsma, 1976), most of these studies implied

to correlate with the number of song repertoire in several species (Nottebohm, 1981; Brenowitz and Arnold, 1986). In adult male canaries the volume of HVC increases when they learn new song syllables while it decreases during non-singing, non-breeding seasons (Nottebohm, 1981). More brain space (HVC) may be necessary to store more song elements (Nottebohm *et al.*, 1981). Alternatively, another song control nucleus, LMAN, is known to become smaller as song crystallizes (Bottjer *et al.*, 1985). Thus, juvenile song with loosely organized patterns of note transition might require more LMAN volume. In this regard, more brain space is also required to sing a song with complex patterns of transitions as in the Bengalese finches. Our results suggest that number of song elements is not significantly different between the two strains, but the degree of song complexity as measured by song linearity is much higher in the Bengalese finches. We thus suspect that LMAN volume may be larger in the Bengalese finches while HVC volume may be comparable between the two strains.

The motor act of singing itself might be quite cheap, although preparing neural structures for singing might be costly. Horn *et al.* (1995) calculated energy consumption of crowing in chickens. Their results suggest that crowing requires only a small amount of energy relative to foraging. At present, the cost of singing itself has not been measured in songbirds, but it is certainly worth investigating. Other factors that might account for the complexity of Bengalese finch song may be the reduced cost for foraging in domesticated species. Foraging is much more costly than singing in wild dwellers in terms of time and energy (Brackenbury, 1977; Woolley and Owen, 1978). This also has not been measured in white-backed munias, but it should certainly be larger than that of domesticated Bengalese finches.

Conclusion

Male songs should evolve largely under two different pressures: female preference and risk of predation. The low degree of complexity found in wild white-backed munias may be the result of compensating these two factors. In Bengalese finches, however, since it had been domesticated over 250 years, predation is no longer a selection pressure. Thus, it is likely that Bengalese finch songs had undergone changes that were favored by females. In conclusion, behavioral comparison between the song of a wild strain and its domesticated form should prove fruitful in examining factors governing evolution of certain traits in birdsong.

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