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A SEXUALLY DIMORPHIC LEARNED BIRDSONG IN THE NORTHERN CARDINAL[1]

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Abstract. In most temperate zone songbirds, singing is solely a behavior of males. However, in some species, such as the Northern Cardinal (*Cardinalis cardinalis*), both sexes sing, and in both, songs are learned. The song of male and female cardinals sounds very similar to the human ear. Whether songs learned by the two sexes can be sexually dimorphic in acoustic structure has never been examined. In the present study, I carried out detailed analyses of the acoustic structure of male and female songs. Songs of the two sexes proved to be dimorphic with respect to the degree of syllable stereotypy and the amplitude of harmonics. These findings show that vocalizations that are learned by the two sexes can be sexually dimorphic.

Key words: *bioacoustics, birdsong,* Cardinalis cardinalis, *sexual dimorphism, vocal learning.*

INTRODUCTION

In many songbirds, singing is a behavior of males. However, in some species, both sexes sing learned songs during the breeding season. If both sexes produce songs, it is natural to ask whether the songs of males and females are distinct so that they can be used for acoustic sex recognition. Although many bird vocalizations have been shown to be sexually dimorphic (Gahr and Güttinger 1986, Taoka and Okumura 1990, Ballintijn et al. 1997), whether songs of oscines are sexually dimorphic has never been systematically examined. In this study, I examined the acoustic morphology of male and female Northern Cardinals (*Cardinalis cardinalis*), a species in the Temperate Zone in which females sing as well as males.

The vocalizations of birds can be generally separated into calls and songs. Songs of oscines differ from calls in one major way: learning usually plays more of a role in the development of song than of calls (reviewed by Kroodsma 1982). All the vocalizations that are demonstrated to be sexually dimorphic are either categorized as calls or it has yet to be shown that they are truly learned by both sexes. The developmental differences of calls and songs have important implications for sexual dimorphism. Unlearned vocalizations develop under genetic control independently of auditory experience (Konishi 1963). In species with sexually dimorphic calls, genetically determined vocal development is likely to give rise to stereotyped vocalizations that are predictable and universal among members of each sex within a species, in much the same way as other sexually dimorphic traits, such as plumage color, which develop relatively uniformly within each sex. In the case of learned vocalizations, however, the extent of acoustic variability introduced in the process of vocal learning argues against the presence of consistent and universal sex-specific acoustic traits that can be reliably used for sex recognition. Can learned songs of oscines be sexually dimorphic, and if so, how do they differ between the two sexes?

I have explored this issue in the Northern Cardinal, a monogamous, nonmigratory species ranging from south-eastern Canada to Guatemala (Bent 1968). Both sexes of the Northern Cardinal learn to sing during the first year of their lives (Lemon and Scott 1966, Dittus and Lemon 1969, Yamaguchi 1996), and in both sexes songs are used only during the breeding season (Laskey 1944, Bent 1968, Ritchison 1988). Male and female cardinals have individual repertoires of 8 to 12 song types, most of which are shared among all individuals in a local population. There is no song type that is unique to one sex (Halkin 1990). Initially, I did not expect to find any differences in the songs of the two sexes,

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both because of the developmental plasticity discussed above, and because the songs of the two sexes sound very similar to the human ear. However, field playback experiments show that cardinals respond differently to songs of the two sexes, suggesting that there are some differences in the songs of the two sexes and that the birds are capable of recognizing them (Yamaguchi, in press).

In the present experiment, I carried out detailed sound analyses to characterize acoustic parameters of the songs of the two sexes, and compared these between the two sexes. The results show that there are consistent and significant differences in the acoustic structure of the songs of the two sexes, despite their striking similarity to the human ear.

METHODS

SAMPLE SONG RECORDINGS

Eighteen male and 18 female songs recorded from 11 males and 9 females in southern Arizona between March and June of 1993 and 1994 were subjected to sound analyses. One to three song exemplars were collected from each individual. All songs were recorded using a Dan Gibson parabola microphone and a Sony TCD5M cassette tape deck. Great care was taken to avoid overloading while recording. There was no systematic difference in recording distance in males and females. Eight song types were represented in the pool of 36 songs analyzed. Song types were shared by almost all birds residing in one location, and were acoustically distinct from each other. Acoustic variation found in different song types could confound the analyses of sex differences. To control for this effect, a sample of songs was chosen with equal number of male and female exemplars (two to three from different individuals) of each song type.

The following six acoustic parameters were measured using the SIGNAL sound analysis system (Engineering Design 1987): (1) maximum frequency, (2) minimum frequency, (3) dominant frequency, (4) frequency range, (5) syllable repetition accuracy, and (6) the relative amplitude of harmonics. Song duration varies greatly, making it an unlikely candidate for consistent sexual dimorphism (Lemon and Chatfield 1971, Yamaguchi, pers. observ.). For example, song duration can vary between 0.40 to 5.52 sec within the same male. Songs were digitized with a sample rate of 25K pts $\sec^{-1}$, high-pass filtered at 1.5 kHz and anti-aliasing filtered at 10 kHz.

FREQUENCY MEASUREMENTS

Sound spectrograms were generated with a frame length of 1,024 pts Discrete Fourier Transform (frequency resolution = 24.4 Hz), a time step size of 200 (time grid resolution varied between 6.5 msec and 24 msec), and minimum amplitude of −33 dB relative to peak. An on-screen cursor was used to measure the maximum and minimum frequencies of each song phrase. The frequency range of each song was computed from these measurements. An average dominant frequency for an individual song was calculated based on the dominant frequencies of the first 1.31 sec of each phrase from an amplitude spectrum (32K pts spectrum range).

SYLLABLE REPETITION ACCURACY

Cardinal songs typically consist of a few phrases, each phrase containing notes or syllables that are repeated multiple times. A note was defined as a continuous tracing on a spectrogram, separated from other tracings by more than 8 msec, and a syllable was defined as a group of notes that is repeated in a phrase. In cardinal songs, syllables and notes are typically repeated within a phrase in a stereotyped manner. To test whether the degree of syllable/note stereotypy within a song differs between the sexes, I computed pair-wise cross correlation coefficients of syllables (or notes) based on digital spectrograms. Cross correlation is an objective way to evaluate the structural similarity of a pair of spectrograms; higher coefficients indicate greater similarity between the two sounds (Clark et al. 1987). Phrases consisting of repeated notes or syllables were disassembled and stored as individual notes. One to four consecutive pairs of syllables or notes from each phrase (e.g., Fig. 1A) were used for cross correlation. The same number of syllable/note pairs were sampled to calculate cross correlation coefficients for each pair of male and female songs. Spectrograms of each note were generated with a frame length of 256 pts and a time step size of 200. Average cross correlation coefficients were first calculated for each phrase, then the average coefficient across phrases within each song were computed for further statistical analysis. I labeled the average cross correlation coefficient of the entire song the "Syllable Repetition Accuracy" (SRA) of that song. For all sample songs of each song type, equal numbers of note pairs from similar positions within each song were used for SRA calculation to control for sampling error.

HARMONIC AMPLITUDE DIFFERENCE

There are harmonic overtones in cardinal songs, but in most of them, the fundamental frequency is the loudest and the amplitudes of harmonics are considerably suppressed. To determine whether the degree of harmonic suppression varied between the sexes, I quantified the amplitude difference between the fundamental frequency and the second harmonic and compared the figures for the two sexes. Power spectra were calculated based on three different time frames within each song (e.g., Fig. 1A, shaded areas marked with xf), with a spectrum window of 512 pts (time resolution of 20.5 msec, frequency resolution of 48.8 Hz). Time frames with fundamental frequencies lower than 5 kHz were randomly chosen for power spectra calculation, so that all the second harmonics to be analyzed fell within the 10 kHz spectrum analysis range, which covers the hearing range of most passerines (Fay 1988). Within all songs of a given song type, approximately homologous segments of syllables or notes were chosen to produce a spectrum in order to minimize sampling error. The amplitudes at the fundamental frequency and at the second harmonic were measured using an on-screen cursor, and the difference between the two was calculated (Fig. 1B). Amplitude differences from three spectra were averaged for a song, and I labeled this average the "Harmonic Amplitude Difference" (HAD) of that song. Thus, a larger HAD indicates a suppressed harmonic component and a pure tonal quality. A smaller HAD indicates a louder second harmonic component resulting in a nasal sound quality.

STATISTICAL ANALYSIS

The question addressed in the analyses is whether the acoustic parameters measured differed reliably between the two sexes. Because song types are acoustically diverse, the measured parameters could differ among song types as well as between the sexes. In an effort to tease apart the influences of song type and sex on the measured variables, I used a two-way analysis of variance (ANOVA; sex and song type were factors). I first tested whether the variation in parameters is explained by sex and song types. If the results indicated that sex significantly influenced the measured parameters, then a post hoc two-way Bonferroni test was carried out to test for the difference between the two sexes. If, in addition to sex, song type significantly influenced the parameter, then I considered whether the interaction between sex and song type was significant. In other words, the interaction effect was examined to determine whether the patterns of sex difference observed are universal across all song types. Residuals were examined and it was confirmed that the data did not deviate from the statistical assumptions. The significance level of 0.05 was used for all statistical tests.

RESULTS

FREQUENCY MEASURES

As already indicated, there are no song-type differences between the sexes; both sexes share the same song types. None of the frequency parameters measured (maximum, minimum, dominant frequency, and frequency range) differed between the songs of the two sexes (Table 1, Fig. 2). Thus, songs of the two sexes do not differ with respect to frequency.

SYLLABLE REPETITION ACCURACY (SRA)

Syllable stereotypy varied significantly between the songs of the two sexes (Table 1), but not among different song types ($F_{7,20} = 2.4$, $P = 0.06$). Males repeated their syllables with significantly greater stereotypy than females. There was no significant interaction effect of sex and song type ($F_{7,20} = 0.4$, $P > 0.5$) so that male songs were more stereotyped than female songs for all the song types examined. Therefore, I concluded males consistently repeat syllables in a more stereotyped manner than females do regardless of song types (Fig. 3A).

HARMONIC AMPLITUDE DIFFERENCE (HAD)

Spectral structure differed considerably between the songs of the two sexes. HAD was significantly higher in male songs than in female songs, indicating that female songs contain significantly louder second harmonics than male songs (Table 1). Although HAD differed among different song types ($F_{7,20} = 19.7$, $P < 0.001$), male songs expressed less of second harmonics than female songs did within each song type, and this trend was consistent across different

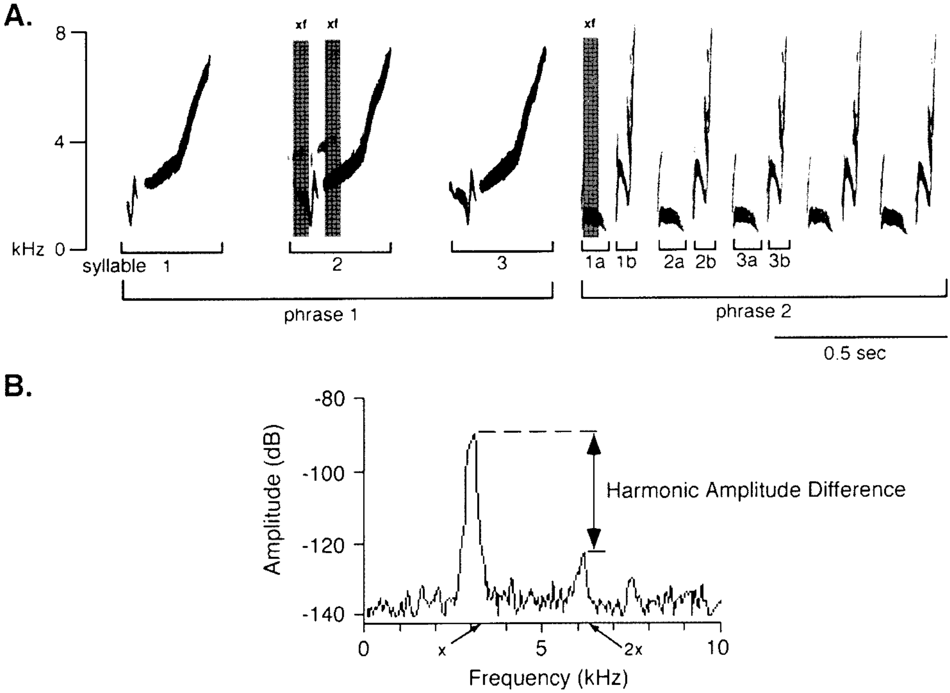

FIGURE 1. Method used to measure acoustic parameters of male and female songs. (A) A spectrogram illustrating structure of a song consisting of two phrases, each containing repeated notes/syllables. Notes contained in phrase 1 are not considered to be two-noted syllables because they are separated by less than 8 msec (see Methods). For Syllable Repetition Accuracy (SRA) measures, cross correlation coefficients between syllable 1 and 2, 2 and 3 for phrase 1, and coefficients between syllable 1a and 2a, 2a and 3a, 1b and 2b, 2b and 3b for phrase 2 were calculated, and the average coefficient for each phrase was computed. Then, these values were averaged for each song. Shaded segments marked with xf indicate sections of sounds used to generate amplitude spectra to estimate Harmonic Amplitude Difference (HAD) of a song in B. (B) Mean HAD were calculated based on three spectra generated from time frames such as those indicated by shaded area with xf in (A). The amplitude difference of the first peak (the fundamental frequency, marked with X) and the second peak (the second harmonic overtone, marked with 2X) was measured. Note that portions of songs sampled for spectra generation had a fundamental frequency below 5 kHz. For each pair of male and female songs used in the analysis, homologous syllable pairs were chosen for SRA calculation, and similar loci were chosen for spectra calculation.

song types (interaction effect of sex and song type; $F_{7,20} = 0.8$, $P > 0.5$). Therefore, I conclude female songs contain harmonics that are consistently louder relative to the fundamental than male songs do regardless of song type (Fig. 3B).

The observed variation in harmonic content among different song types could be ascribed to differences in the frequency content of song types. To examine if harmonic structure is influenced by the fundamental frequency (Fig. 1B frequency point indicated by X) as well as by sex, I carried out an analysis of covariance (ANCOVA) with sex as a factor and fundamental frequency as a covariate. For this analysis, one spectrum from each song was selected as a sample ($n = 36$). The distribution of the data set required a quadratic regression model. The result showed that, for both sexes, the fundamental frequency contributed significantly to the variation in HADs ($R^2 = 0.67$, linear term: $F_{1,32} = 35.3$, $P < 0.001$, quadratic term : $F_{1,32} = 6.8$, $P < 0.02$, Fig. 4). In this analysis, HAD also differed significantly between the songs of the two sexes ($F_{1,32} = 20.7$, $P < 0.001$), but there was no sex difference in fundamental frequency (unpaired t-test, $t_{34} = -0.01$, $P > 0.5$). Therefore, I conclude that the harmonic amplitude difference increases with the fundamental frequency asymptotically, and the HAD is always larger in male songs than in female songs.

TABLE 1. The results of an ANOVA examining sex differences in measured acoustic parameters. Two-way ANOVA *F*-statistic (df = 1, 20) and *P*-value of acoustic parameters for factor "sex." Asterisks indicate parameters that differed between the two sexes.

Parameters	*F*	*P*-value
Frequency measurements		
Maximum frequency	1.3	0.27
Minimum frequency	1.1	0.30
Dominant frequency	4.0	0.06
Frequency range	0.5	0.48
Syllable Repetition Accuracy	10.3	<0.01*
Harmonic Amplitude Difference	26.6	<0.001*

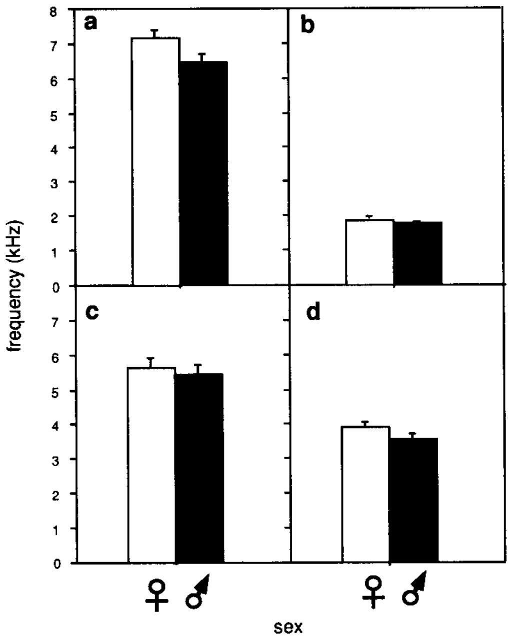

FIGURE 2. Cell plots showing mean ± SE of four frequency measures of male and female cardinal songs. a. maximum, b. minimum, c. frequency range, d. dominant frequency. None of the frequency measures differed between the two sexes.

DISCUSSION

The results show that, despite their similarity to the human ear, the songs of cardinals are consistently sexually dimorphic in syllable stereotypy and tonal quality. Male and female playback songs used in my previous field study also were sexually dimorphic with respect to these two parameters (Yamaguchi, in press). Thus, these differences between the songs of the two sexes may be used by cardinals to distinguish the sex of the singer.

How do the differences between the sexes develop? One possibility is that the sex-specific traits of songs are acquired by young birds through imitating only adult songs of their own sex. However, the possibility of a sex-specific song tradition can be ruled out on the basis of results from a separate study of song development in cardinals (Yamaguchi 1996). I found that when juvenile cardinals are given a choice of songs produced by males and females, they learn songs from both sexes equally well. Moreover, songs developed by males and females were either masculinized or feminized with respect to syllable stereotypy regardless of the sex of the model songs that were imitated. Thus, the sex dimorphism of cardinal songs is best viewed as an expression of some inherent morphological and/or physiological differences between the two sexes, not as the result of sex-specific song learning. What kind of physiological and/or morphological differences might give rise to the observed acoustic dimorphism?

One of the sexually dimorphic traits revealed by quantitative analysis, the difference in degree of syllable stereotypy, also was evident in post-hoc spectrographic observations. The frequency modulation of spectrographic traces tends to be

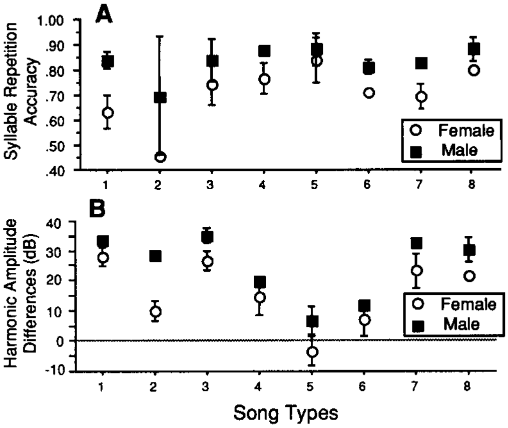

FIGURE 3. (A) Scatter plot of Syllable Repetition Accuracy ± SE of the two sexes separated by song types. SRAs are similar among different song types, and males consistently have significantly higher SRAs than females do. (B) Scatter plot of Harmonic Amplitude Difference ± SE of the two sexes separated by song types. HADs vary significantly among song types, but female songs contain significantly larger HADs than male songs do regardless of song types.

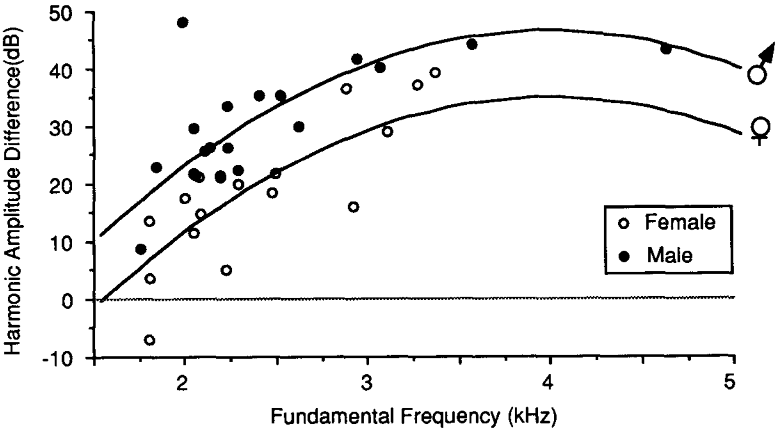

FIGURE 4. The relationship between the fundamental frequency, sex, and the harmonic amplitude difference (HAD). The harmonic amplitude difference increase asymptotically along with increased fundamental frequency, and male songs always have larger HADs than female songs do within the 5 kHz analysis range.

less smooth in female than in male syllables, and the shapes of the repeated female syllables are more irregular in comparison to those of repeated male syllables. Typically, in male songbirds, the vocal output progresses from a less stereotyped (plastic song) to a highly stereotyped form (crystallized song) during the sensorimotor phase of song development (Marler and Peters 1982, Podos et al. 1995). Male cardinals also show the characteristic increase in vocal stereotypy prior to song crystallization. The lower degree of syllable stereotypy in songs of adult female cardinals suggests that perhaps females never fully crystallize their songs.

The other sexually dimorphic trait I found in this study is the relative amplitude of harmonics; female songs contain relatively louder harmonics than male songs do. Nowicki and his colleagues have shown that in songbirds, harmonics are generated at the syringeal sound source, and are efficiently filtered out by the coordinated activity of the syrinx and vocal tract movement; the result is a concentration of energy in the fundamental frequency that gives songs a pure-tonal quality in many species of songbirds (Nowicki and Capranica 1986, Nowicki 1987). Female cardinals are sometimes observed to sing without opening their beak in contrast to males that sing with their beaks flared (Yamaguchi, pers. observ.). This difference in singing posture probably affects the amplitude of harmonics in songs of the two sexes. Recently, Podos et al. (1995) showed that plastic songs of immature male Song Sparrows *Melospiza melodia* contain louder harmonics than crystallized adult songs, and that the suppression of harmonic amplitude is a skill that emerges during the course of vocal motor development. It is likely that male cardinals follow a similar developmental trajectory, enhancing the tonal quality of songs during the sensorimotor phase. The relative amplitude of harmonics contained in adult female songs resembles that in plastic songs of male cardinals. Therefore, the acoustic morphology of a female song may be viewed as a neotenic form of the crystallized male song.

Sex differences in the level of syllable stereotypy and harmonic amplitude may be ascribable to hormonal differences in the two sexes. Previous studies have reported that testosterone is necessary for song crystallization in male songbirds (Marler et al. 1987, Marler et al. 1989). In a separate study of the endocrinological basis of song development in cardinals, I found that females maintain low basal levels of testosterone throughout song development, whereas males have elevated levels coinciding both with the sensorimotor period of song learning and with the song production period in adulthood (Yamaguchi 1996). Thus, differences in the circulating levels of testosterone between the two sexes may account for the sex difference in syllable stereotypy and harmonic amplitude. If this hypothesis is correct, then I predict that administration of testosterone to a female in the later stages of song development should masculinize her songs by increasing syllable stereotypy and suppressing harmonic amplitude. The target sites of testosterone are likely to be both peripheral and central. Testosterone is shown to act as a trophic factor and increase the weight of syrinx (Luine et al. 1980). It is conceivable that the sex difference in the syringeal muscle mass at the time of song production leads to difference in sound quality. In addition, testosterone may act on the central nervous system and elicit changes in motor patterns including posture assumed while singing and the coordinated movement of trachea such that harmonic structure of the songs become different in the two sexes.

One of the acoustical differences of songs described here, the harmonic amplitude difference, may be related to the functional differences of songs in the two sexes. Male cardinals, as in many other species of oscines, sing mainly to defend their territories and to attract females (Laskey 1944). Female cardinals, in contrast, use their songs for intra-pair communication within a territory (Ritchison 1988, Halkin 1997) and in female-female agonistic interactions when a strange female intrudes into a territory already occupied by a female (Ritchison 1988, Yamaguchi, pers. observ.). Thus, the male's song is a long range signal that must be loud to reach its audience, whereas the female's song is a short range signal that can be soft. Peters and Nowicki (1996) suggest that it may be easier for birds to produce loud sounds if the sound is a pure tone. The prediction derived from this hypothesis, a tight coupling between higher sound amplitude and pure-tonal quality of sound, is prevalent in birdsong in general. Males of monogamous territorial species such as Song Sparrows and cardinals (i.e., long range signalers) tend to produce pure-tonal songs, whereas males of nonterritorial breeders (i.e., short range signalers) such as Zebra Finches (*Taeniopygia guttata*) produce songs with significant harmonic overtones. Therefore, the differential amplitude requirement of male and female songs may have led to the evolution of sexual dimorphism in harmonic amplitude in cardinals.

I have demonstrated the presence of predictable and reliable sexual dimorphism in a learned vocalization. I conclude that acoustic dimorphism of cardinal song can be viewed as a difference in the completeness of song development in the two sexes, and it may reflect sex differences in the circulating levels of testosterone at later stages of song development. The dimorphism is sufficiently stable and predictable that it probably explains acoustic sex recognition as exhibited by cardinals in a previous study (Yamaguchi, in press).

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