AUDITORY EXPERIENCE DOES NOT SHAPE SEXUAL PREFERENCES FOR SONGS IN FEMALE NORTHERN CARDINALS

by

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Summary

Bird song is typically used by males to attract females. As a consequence of the vocal learning process, the acoustic morphology of male songs shows marked geographic variation. Whether females use variation in male songs to choose mates has been controversial (reviewed by Catchpole & Slater, 1995). In some species, the song types that females produce when treated hormonally have been considered to be the song types they prefer in the context of mate choice. To examine this notion, I investigated the song type preferences of female northern cardinals (*Cardinalis cardinalis*) using a more direct measure, copulation solicitation display. Unlike females of many other species of songbirds in the Temperate zone, female cardinals naturally develop songs by imitating adults just as males do, allowing direct identification of when and what song types are memorized by females for vocal production. I sought to determine if the memory trace formed for vocal performance is identical with the memory trace that guides song type preference in a sexual context, and whether females truly form

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any song type preference based on auditory experience during the first year of their lives. To address these questions, audio-video playback experiments were carried out on captive-raised adult cardinals whose complete auditory history was known. The results showed that female cardinals did not come to prefer any song type based on experience; they responded equally to all conspecific song types. Thus, memory formed for vocal production in females is not equal to song type preferred in sexual context. The results suggest that variation in song types is not important for mate choice in cardinals.

Introduction

In most species of the songbirds in the temperate zone, only males sing. In many species, the acoustic morphology of songs tends to vary little among males in a local population but varies greatly between males in geographically separate populations (Marler, 1952; reviewed by Mundinger, 1982; Catchpole & Slater, 1995). Geographic variations in song, or song dialects, are considered to arise largely as a consequence of the vocal learning process during which young males learn to imitate the songs of adults, just as humans acquire speech.

One of the primary functions of male song is to attract females (Eriksson & Wallin, 1986; Johnson & Searcy, 1996). The extent to which females use acoustic variations in male songs for mate choice is not well understood. If females choose males based on their songs, the formation of any preferences that exist is likely to be dependent on experience because the exact song morphology that males produce is a consequence of their auditory experience. A juvenile female songbird hears the common song types of her natal area, and then may also be exposed to different song types when she disperses to her first breeding site. Thus, a female can potentially form a preference for a song dialect that she heard during the natal period or for a dialect that she heard after the dispersal period.

Do females prefer to mate with males that sing their natal dialect? It has been suggested that such a preference could be adaptive for females by helping them select mates that are genetically adapted to local conditions (Nottebohm, 1969, 1972; reviewed by Baker & Cunningham, 1985). However, the results of studies on this question are largely contradictory (reviewed by Catchpole & Slater, 1995). For example, female white-crowned sparrows (*Zonotrichia leucophrys*) are shown to prefer males with natal song dialect in some studies (Baker *et al.*, 1981, 1987; Baker, 1983; Tomback & Baker, 1984; Casey & Baker, 1992), but not in other studies (Baptista & Morton,

1982, 1988; Chilton *et al.*, 1990; Chilton & Lein, 1996). I present evidence here that the incongruous results obtained may partly be due to the methods used to determine the song type preference of females. Song preferences of females were sometimes deduced from song types that they themselves produced after administering testosterone (*e.g.* Baker *et al.*, 1981; Tomback & Baker, 1984). The use of this measure assumes that the song types produced were memorized by the females during their natal period, and that these songs are the song types females prefer in the context of mate choice. However, whether the timing of song acquisition in females is restricted to natal period is not known in species tested (Petrinovich & Baptista, 1987), and whether the memory formed for song production is truly identical to the memory that guides mate preference has not been systematically examined. Moreover, hormonally induced songs of females are often sufficiently degraded acoustically such that the accurate identification of song type memorized is difficult (Baker & Cunningham, 1985; Petrinovich & Baptista, 1987; Chilton & Lein, 1996).

In the present study, I have investigated whether the memory trace formed for vocal performance is identical with that used for mate choice in female northern cardinals (*Cardinalis cardinalis*). The song type preference was assessed using a direct measure, copulation solicitation display, a stereotyped posture assumed by females prior to copulation. This measure is particularly suitable to test mate choice in female cardinals because they engage in extra pair copulation (Ritchison *et al.*, 1994) so that their true preference at the time of copulation receptivity, not at the time of pair-formation, can be directly assessed. Copulation solicitation display assumed in playback situation has been shown to directly correspond to actual copulation frequency in other species (*e.g.* brown-headed cowbird; West *et al.*, 1981). Female cardinals are ideal of the purpose of the study because, unlike many female songbirds in the Temperate zone, they develop songs naturally by imitating adults (Dittus & Lemon, 1969; Yamaguchi, 1996) such that song types memorized for vocal performance could be accurately identified without any hormonal manipulation. In addition, I have examined the effect of auditory experience on the formation of song type preferences in females not only during the natal period, but also during the post-natal period prior to the first breeding season. To address these questions, I carried out an audio-video playback experiment.

I report here that female cardinals are not selective with regard to song types of males. In contrast to what has been assumed in some previous studies, the song types that female cardinals memorize for song production does not dictate what they prefer in the context of mate choice. The results suggest that female cardinals do not form a clear preference for particular conspecific song types heard during the first year of their lives. Thus, geographic variation in song types may not be important for mate choice in cardinals. In addition, this study demonstrates a novel use of audio-video playback techniques to assess females' mate preferences, a method that can be used to address other questions involving audio-visual communication in animals.

Methods

Subjects

Thirteen captive-raised female cardinals of one to two years of age were used for the experiment. Complete records were available on the auditory and vocal learning history of the subjects during the first year of their lives. The subjects in this study were a subset of birds used for another study on song learning (Yamaguchi, 1996). Females were collected from the Santa Rita Experimental Range and the Sierrita Ranch in Arizona in the Spring of 1993 and 1994 as nestlings (three to seven days of age) and hand-raised in the laboratory. When they fledged at 11 to 12 days of age, they were individually housed in sound isolation chambers, and tutored daily with a set of tape recorded adult cardinal songs beginning at 18 days of age on average. All the recordings used as tutor songs were sampled from sound libraries in the Cornell Library of Natural Sounds, the Borror Laboratory, and from recordings kindly made available by Dr. Gary Ritchison. Tutor tapes were changed periodically throughout the first year of their lives. During each tutoring period, each female heard four song types. For four females collected in 1993, the tutor set was changed every 30 days for 11 months (they heard a total of 44 song types). For the rest of the birds that were collected in 1994, the tutor set was changed every 10 days for the first 50 days, then every 60 days during the rest of the year (they heard a total of 40 song types). They were tutored twice daily, with each song type repeated 90 times, once every ten seconds during each tutoring session. The acoustic morphology of each tutor song used was distinct from every other song, so that the song imitation by the subjects could be pinpointed without ambiguity at the completion of song development. Because different song types within a cardinal's repertoire are shown to be used equally frequently in various social contexts in this species (Ritchison, 1988), it was assumed that all of the tutor songs could serve equally well as song models. Subjects were divided into separate tutor groups according to hatch date (three groups in 1993, five groups in 1994), and the order of tutor sets they heard was balanced among different tutor groups. Therefore, at a given age, birds from different groups heard different sets of songs. By one year of age, all individuals developed adult songs. Evidence of song learning was obtained spectrographically by comparing songs produced by the subjects and the tutor songs that they heard. All the subjects copied at least two tutor song

types. Their song learning period (sensitive period) was between 15 to 130 days of age, with most songs learned before 45 days of age (Yamaguchi, 1996), which corresponds to the natal period before dispersal. After completion of this song learning study, the present experiment began. Prior to the experiment, all subjects were housed in the sound isolation room as a group for several hours a day for a week, so that they became accustomed to the testing environment.

One week prior to the start of the experiment, all subjects were implanted with silastic tubes filled with estradiol (see Nelson & Marler 1993) to enhance their sexual responsiveness so that their physiological state resembled the sexually receptive stage of the adult female reproductive cycle.

Playback experiment

General

A pilot experiment revealed that auditory stimuli alone did not elicit copulation solicitation displays in this species. A visual image of a male cardinal, on the other hand, proved to be a sufficient stimulus to elicit copulation responses in some females even without estrogen treatment. I therefore used a combination of the playback song and the visual image of a male cardinal, which turned out to be a potent stimulus for eliciting sexual responses from female cardinals. The same video image of a male was dubbed with different song types as playback stimuli. The audio-video playback technique is a powerful method because the response to different auditory stimuli can be examined while holding the visual stimulus constant (Evans & Marler, 1991).

Playback stimuli

Auditory stimuli: All stimulus songs used were either recordings of male cardinals used to tutor the subjects during the first year of their lives as mentioned above, or recordings of male cardinals and blue grosbeaks made in the field (see below). The following five categories of male songs were used as playback stimuli (Fig. 1).

(1) Tutor song types that were copied for vocal production (T1): These are the song types that were acquired for song production by the subjects. T1 songs were presented to the subject females, on average, between 25 (range 15 to 38) and 40 (range 25 to 68) days of age. Because cardinals typically become independent from their parents around 45 days of age, all the songs used as T1 were heard by the subjects mostly during the natal period. Thus, T1 represents the song types that were heard during the natal period and later imitated by the subjects. In total, nine song exemplars were used as T1 stimuli.

(2) Tutor song types rejected as a model for vocal production (T2): These songs were heard by the subjects on the same days as the T1 songs, but not memorized for vocal production. Ten song exemplars were used as T2 stimuli.

(3) Tutor songs that were heard during post-dispersal period (T3): These songs were presented to the subjects between 278 (range 186-344) to 331 (range 246–396) days of age on average, corresponding to the post-dispersal period of wild birds (Smith, 1969). None of these songs were acquired by females for vocal production. Six song exemplars were used as T3 stimuli.

(4) Novel songs that the subjects have never heard before (T4): Two song exemplars were used as T4 in this experiment; one recorded from a male cardinal 50 km south of where the subjects were collected, the other from a male in Baja California (by Dr. Luis Baptista), more than 500 km direct distance away from where the subjects were collected.
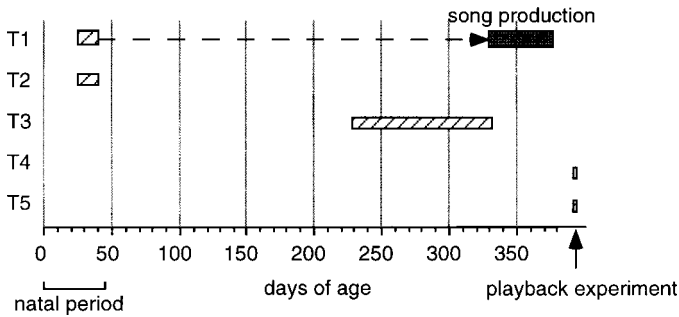
Fig. 1.   Age when subjects heard five different stimulus songs. The natal period of parental dependence ends at around 45 days of age. The arrow at the bottom indicates when the playback experiment was conducted. The hatched box indicates mean age when subjects were exposed to each stimulus tutor song during the first year of their lives. The broken arrow connecting a hatched box and a shaded box indicates that T1 songs that they heard during the natal period were used as a model for song production later in life.

(5) Heterospecific songs (T5): Songs of the blue grosbeak, a closely related sympatric species were used as stimuli in this category. Two blue grosbeak song types that were recorded 5 km away from the collection site were used.

Song stimuli were prepared using the SIGNAL sound analysis system (Engineering Design, 1987) such that the average amplitude of all songs was equalized.

I carried out acoustic analyses to examine if there were systematic acoustic differences between the song types used in the various treatment groups, that would confound the results. In order to characterize the acoustic properties of songs, I counted the number of phrases included in a song, and measured their syllable repetition accuracy (an index that indicates how stereotyped repeated syllables in a song are; see Yamaguchi, 1998), harmonic amplitude differences (an index that indicates the amplitude of harmonics in relation to the amplitude of fundamental frequency; see Yamaguchi, 1998), maximum frequency, minimum frequency, dominant frequency, and song duration. The first two parameters were measured only on conspecific songs (T1-T4) because the acoustic structure of the blue grosbeak songs differed greatly from cardinal songs, and it was not possible to make the same measurements. Syllable repetition accuracy and harmonic amplitude differences have been shown to be acoustic parameters that differ between the songs of male and female cardinals (Yamaguchi, 1998). Kruskal-Wallis tests were used to examine if these seven parameters differ among the five groups of songs. A detailed description of the terminology and the method used for the sound analyses is found elsewhere (Yamaguchi, 1998).

Visual stimulus preparation: In the wild, a male cardinal performs an elaborate courtship display to a female prior to copulation (Bent, 1968; Lemon, 1968; Yamaguchi, pers. obs.). The display involves quivering of his wings, extensive piloerection, swaying of his body from side to side, and singing. To simulate the courtship display of a male cardinal, a captive male was placed in a cage with a pane of Plexiglas on the front and his courtship display was videotaped. A video camera (Panasonic Ag-455P) recorded the image of the bird through the Plexiglas window. The size of the bird image was adjusted so that its image on the playback monitor was precisely life-sized. The display behavior of the male was edited to two minutes.
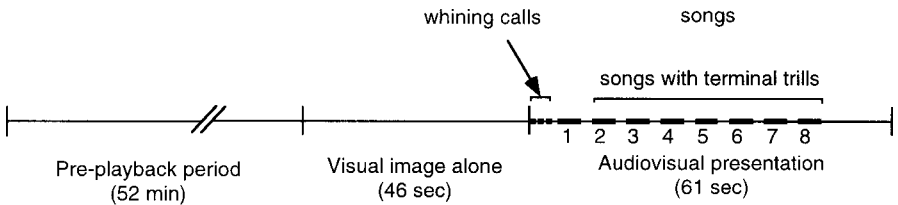
Fig. 2.   The time course of the playback experiment trial.

Combined playback stimuli: All five auditory stimuli (T1-T5) were dubbed onto the videotape of the displaying male. Each test began after the subject had spent 52 minutes in the sound isolation room exposed to the background image and noise described below. Following this acclimation period, a 2-minute playback trial was carried out. During the two minutes of playback, the visual image alone preceded the audiovisual stimuli by 46 s. During the next 61 s, a song was repeated 8 times every 7 s, which corresponds to the natural song delivery rate of courtship singing in males (Yamaguchi, pers. obs.). Two additional vocalizations, high pitched whining calls (similar to 'copulatory see' described by Lemon, 1968), and terminal trills ('rattle' described by Lemon & Scott, 1966; Lemon & Herzog, 1969) that are often emitted during courtship singing were also added both at the beginning and at the end of the audio stimuli (Fig. 2).

As in other video playback experiments (C. Evans, pers. comm.), birds tended to give a startle response when an image of a male appeared suddenly from a previously blank screen. To reduce startle response, I presented the image of an empty cage with a background sound of cage noise prior to the stimulus presentation. The image of the empty cage was the backdrop of the footage of the displaying male. The background cage noise was recorded from 5 caged cardinals housed in a room making pecking and hopping noises along with sporadic calls, but with no songs.

Experimental procedures

The experiment was conducted in July and August 1995, a period that coincides with breeding season in the wild. All subjects were presented with all five stimuli, one trial per day. The order of stimulus presentation differed for each subject to minimize the influence of order effects on the result.

For the experimental trials (Fig. 3), each subject was placed in a cage ($25 \times 30 \times 45$ cm) in a walk-in sound isolation room (IAC 403-A, $2.2 \times 2.3 \times 2.3$ m). The TV monitor (Panasonic BT-S901Y, resolution; 525 line / 60 fields) with two speakers (Realistic Autosound Speakers 12-1704) attached to both sides was placed 25 cm away from the subject's cage, and the responses of the subjects along with the image on the stimulus monitor and stimulus songs were recorded on videotapes (Panasonic Ag-455P and Panasonic AG7650). The location of the stimulation unit (*i.e.* a TV monitor and speakers) was changed from one side of the subjects' cage to the other between trials in order to minimize the habituation of the subjects to the monitor. Stimulus presentation was controlled from outside the isolation room. The stimulus video tape was played on a Panasonic AG7650 video deck, and the auditory stimulus tape was played on a tape deck (Nakamichi Cassette Deck 2) and amplified with an amplifier (Realistic Integrated Stereo Amplifier SA150). The volume of the speaker was adjusted so that the average amplitude of all songs was approximately 65 dB in the center of subjects' cage.
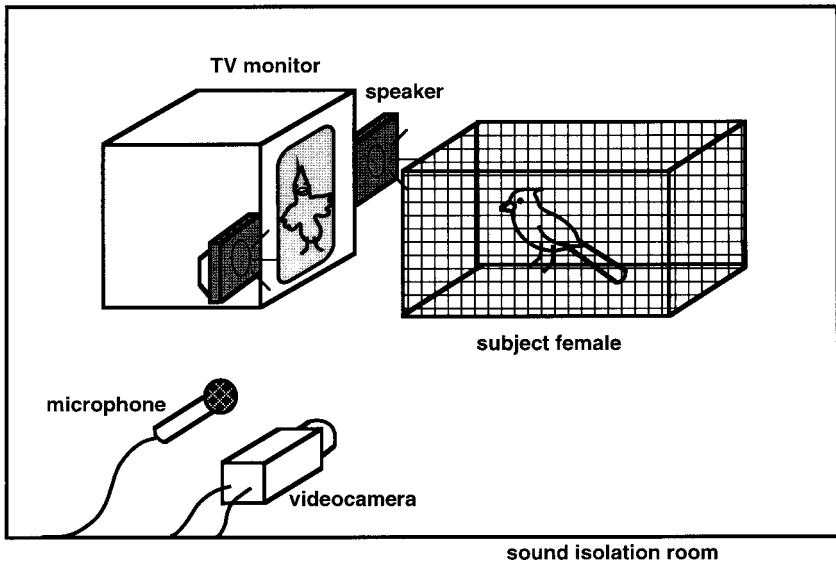
Fig. 3.   The playback experiment setup.

Response

In a natural setting, when a female accepts a courting male, she carries out a copulation solicitation display involving crouching, quivering her wings, and raising her tail (Lemon, 1968; Yamaguchi, pers. obs.). I used the duration of this copulation solicitation display to assess the female song preference.

The duration of the display was defined as the time between when a subject raised her tail and beak and became motionless, and when she started moving her head to look at the monitor again. Some subjects displayed in response to the visual stimuli that preceded the audiovisual stimuli. In these cases, the duration of copulation solicitation displays that took place in response to visual stimulation alone was considered as the baseline response, and subtracted from the response that took place during the audiovisual stimulus presentation.

Statistical analysis

I used Wilcoxon's signed rank test to determine whether the duration of displays elicited differed in the four comparisons listed below. When comparisons involved more than two treatment groups (*i.e.* responses from more than one trial), the means of the treatment groups were taken. The family confidence interval for the four comparisons was set at 90% with a sequential Bonferroni adjustment for each variable (*i.e.* significant p-values necessary to reject H_0 are set at 0.025, 0.033. 0.05, 0.1 for the most significant to the least significant four comparisons; Rice, 1989; Wright, 1992).

Comparison between responses to heterospecific song vs novel conspecific song (T5 vs T4):
Both classes of songs were novel to the subjects, but they differed in species identity. This comparison was designed to test the validity of the experimental paradigm that was used to

assess the song preference by females. Female cardinals do not show receptive response to the songs of closely related sympatric species such as the blue grosbeak in the wild, and were not expected to do so in the laboratory if the experimental paradigm created was an adequate simulation of the circumstances that accompany courtship in the wild.

Comparison between responses to copied songs (T1) vs rejected songs (T2):   This contrast was designed to test if the memory formed by a female for vocal production is equivalent to memory used in the context of mate choice. Both T1 and T2 were heard by the subjects at the same time during the natal period, but one was used as a model for song production and the other was not. If songs learned for vocal production by females were the song types they preferred their mates to have, as assumed in previous studies (Konishi, 1965; Tomback & Baker, 1984), I expected to see greater responsiveness to T1 than to T2.

Comparison between responses to pre-dispersal (T1 and T2) vs post-dispersal songs (T3): In this comparison, the two classes of songs were heard at different times; before and after the normal dispersal age. In the previous comparison, T1 and T2 proved to be similar in eliciting response in females (see results). Thus, T1 and T2 were combined in this comparison to illustrate the overall response of females to songs heard during the pre-dispersal period. The comparison was designed to test if songs heard during the natal period are more preferred than songs heard later in life.

Comparison between responses to familiar songs (T1, 2 and 3) and novel songs (T4):   In this contrast, one class had been previously heard by the subjects during the first year of their lives and the other had not. Since the previous comparison showed that the subjects responded no differently both to pre- and post-dispersal songs (see results), all three classes of songs, T1, T2, and T3 were combined to represent familiar songs. This comparison was designed to test if prior familiarity with songs influences sexual responsiveness to them.

In addition to these four planned comparisons, I tested whether each class of familiar songs -T1, T2, and T3- elicited different responses from those evoked by the novel songs (*i.e.* three comparisons; T1 *vs* T4, T2 *vs* T4, T3 *vs* T4). The potency of copied songs and postnatal songs was also compared (*i.e.* T1 *vs* T3). The family confidence interval for these four post hoc comparisons was also set at 90% with sequential Bonferroni adjustment for each variable (see above for significant *p*-values).

Results

Sound analyses of song stimuli

None of the seven acoustic parameters differed among the song types included in the five different treatment groups (Table 1, Fig. 4). I conclude that the acoustic properties of the groups of song types used as stimuli did not differ systematically in ways that could have influenced results of the preference tests.

TABLE 1. *The result of six Kruskal-Wallis tests to examine if acoustic variables differed among songs used as different treatment groups in the playback experiment*

Parameters	df	H	p-value
Number of phrases	3	4.08	0.14
Syllable repetition accuracy	3	0.88	0.83
Harmonic amplitude difference	3	6.61	0.08
Maximum frequency	4	7.25	0.12
Minimum frequency	4	6.40	0.17
Dominant frequency	4	4.01	0.41
Song duration	4	3.11	0.54

None of the parameters differed significantly.

Playback responses

Five subjects did not respond to any stimuli. Therefore, further analyses on the intensity of response were based on the remaining eight subjects. Only one subject responded to heterospecific songs, while seven, four, five, and six individuals responded to the T1, T2, T3, and T4 respectively. The lone individual that responded to heterospecific song solicited after hearing a terminal trill, a conspecific vocalization, that followed the blue grosbeak songs (see playback stimuli in method section); this was the only subject to solicit to all five song types. One of the subjects started displaying to the visual stimuli before the onset of audio-visual stimuli in all five trials. In four of the trials with conspecific songs, this subject continued responding for various periods of time when the auditory stimuli were played, but in the trial with heterospecific songs, the subject immediately stopped responding when the song was played. This observation may suggest that heterospecific songs have an aversive effect in females. The planned comparisons of the response intensity measured by the duration of response yielded the following results:

T5 *vs* T4

Subjects spent a significantly longer time displaying in response to conspecific songs than to heterospecific songs ($z = -2.366$, $p = 0.018$, Fig. 5). Females clearly distinguished conspecific songs from heterospecific songs even though they had never heard either song before. They showed almost no response to heterospecific songs despite the presence of the visual stim-
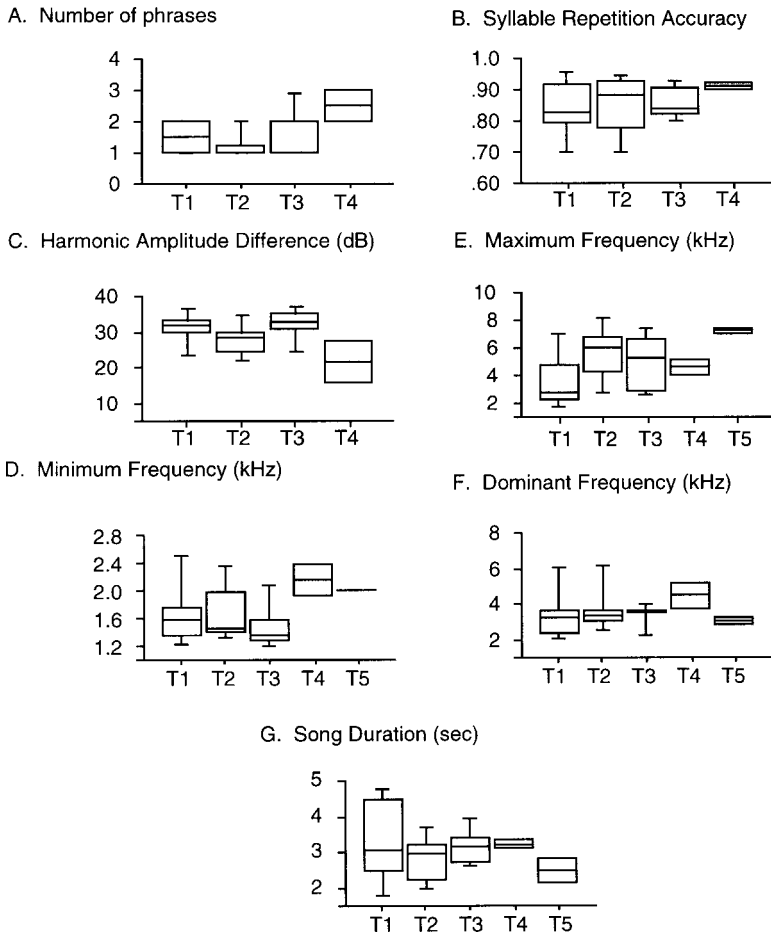
Fig. 4. Acoustic parameters of songs used as stimuli in the playback experiment. T1 = learned songs, T2 = rejected songs, T3 = post-natal songs, T4 = novel songs, T5 = heterospecific songs. The middle bar within a box indicates the median, the top and bottom of the box indicate the 75 percentile, and the end of the error bars indicates 90 and 10 percentile of the data set.

ulus of conspecific male. Thus, I concluded that the experimental paradigm used in this study yielded a valid measure of song preference in females.
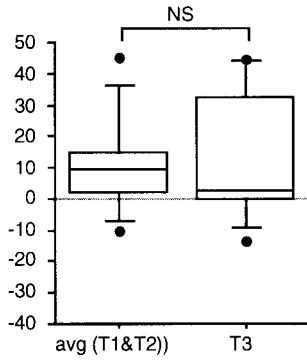
T1 *vs* T2

The duration of displays assumed were similar in response to songs accepted or rejected for imitation ($z = -1.183$, $p = 0.237$, Fig. 5). Further, the subjects responded similarly to T1 and to T3 ($z = -0.338$, $p = 0.735$,
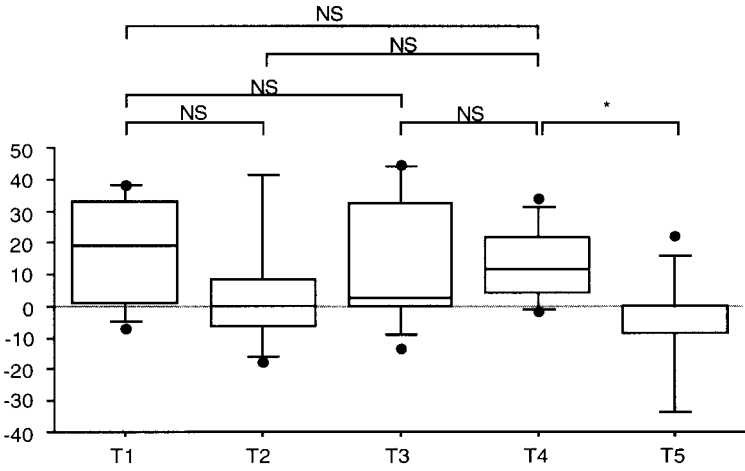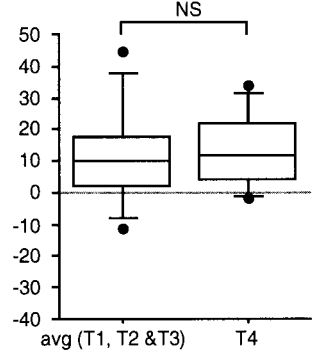
Fig. 5.   A. Box plots showing the total duration of displays elicited by five different classes of songs. Each box indicates 10, 25, 50, 75, and 90 percentile of the data set. An asterisk indicates a statistically significant difference, and NS indicates that difference is statistically insignificant. B. Box plots comparing the average of T1 and T2 to T3. C. Box plot comparing the average of T1, T2, and T3 to T4.

Fig. 5) or to T4 ($z = -0.420$, $p = 0.674$, Fig. 5). Therefore, songs learned as models for song production are no more potent in eliciting sexual responses

from females than the songs that they heard at the same time but did not learn, or songs they were hearing as adults for the first time.

T1 and T2 *vs* T3

Subjects showed similar duration of displays in response to pre-dispersal and post-dispersal songs ($z = -0.338$, $p = 0.735$, Fig. 5). I conclude here that the exposure to songs during the natal period does not differentially enhance sexual responsiveness to them as compared to the exposure to songs later in life.

T4 *vs* T1, T2 and T3

Subjects responded similarly to novel songs and to familiar songs ($z = -1.4$, $p = 0.161$, Fig. 5). The result was the same when I compared each class of familiar songs to the novel songs ($z = -0.42, -1.40, -0.70$, $p = 0.674, 0.161, 0.484$ for T1 *vs* T4, T2 *vs* T4, T3 *vs* T4 comparisons respectively). Thus, I conclude that familiarity with songs does not enhance sexual responsiveness of female cardinals to them.

Taken together, subjects responded more to conspecific songs than to heterospecific songs. However, within the class of conspecific songs, song types the subjects acquired for song production, the ones they heard during natal period, the ones they heard during the first year of their lives prior to the first breeding season, or the song types they have never heard before elicited sexual responses equally well.

Discussion

The results show that in the presence of a video image of a displaying conspecific male, cardinal females responded selectively to conspecific songs, by soliciting longer to cardinal songs than to heterospecific songs. However, all types of conspecific songs tested elicited similar sexual responsiveness. The lack of response to the heterospecific songs shows that estradiol-treated females were not responding to all auditory stimuli indiscriminately. Instead, they distinguished between biologically relevant auditory stimuli (conspecific songs) and irrelevant ones (heterospecific songs), and responded only to the former. In this sense, the similarity of subjects' responses to all classes

of conspecific songs presented is in fact meaningful. This suggests that geographic variation in songs does not play a role in mate choice in cardinals.

The use of negative data to infer the absence of a phenomenon has always been difficult, because the failure to reject a null hypothesis cannot be taken as an evidence to support the null hypothesis. One might argue that the absence of a song type preference shown in this study may be due to the low statistical power resulting from a relatively small sample size. A future experiment using larger sample sizes might, in fact, reveal a difference in responsiveness of females to different song types. However, the significance of such differential response would probably be minor, given the tendency of female cardinals to respond to all conspecific song types as shown in this study. Thus, even if there were males with less preferred song types, they would still be able to elicit copulation solicitation responses from a proportion of females in a population.

It may also be argued that inferences made from this study have poor external validity because of the use of captive-raised animals. Subjects may not have develop song preferences because some factors that were crucial for the formation of song type preference were absent in captivity. While this concern may be valid, it was necessary to conduct the present experiment in a controlled acoustic environment, because one goal was to test whether auditory experience leads to the formation of song type preference. It is impossible to document the complete auditory experience of a bird in the wild, but it will be important to test whether wild-caught adult females are also unselective in their responsiveness to male song types in the context of mate choice. Meanwhile, the fact that the subjects in this study developed fully normal songs by imitating tape recordings shows that one type of developmental process that involves auditory experience is intact in captivity. If the formation of song preferences was under a firm genetic control and expressed during a defined developmental period, as in song development, such a process might well be observed even in captivity. Taken together, I tentatively conclude that female cardinals do not show song type preference based on their auditory experience during the first year of their lives.

Song memorization for vocal production and song type preference

Song types copied by females for their own vocal production are not necessarily preferred more in a sexual context than other song types. This finding

contradicts the prevalent assumption that the same memory trace formed for song production in females serves dual function and guide mate selection (*e.g.* Tomback & Baker, 1984). This assumption has not been previously subjected to vigorous examination, mainly because of the difficulties in tutoring captive females (Baptista & Petrinovich, 1986; Petrinovich & Baptista, 1987), and in determining unambiguously the memory trace acquired by females for vocal performance (Baker & Cunningham, 1985). By using cardinal females, which naturally produce stereotyped songs that are comparable to those of males, I found that the memory for song acquisition is not equivalent to the memory used for sexual song preference.

The lack of a female preference for males that share her own song types might lead to the prediction that the members of a mated pair do not necessarily share song types. However, field observations show that song types are largely shared within a breeding pair as well as among individuals breeding in one location (Ritchison, 1988; Halkin, 1990; Yamaguchi, pers. obs.). At least three explanations may account for the observed song matching within pairs. First, the majority of both male and female cardinals disperse only limited distances from the natal area (Smith, 1969). Therefore, pairs may share song types because the two sexes learn, and settle, only within the area of their natal dialect. Second, males may learn additional song types at the time of pair formation so that song types of the members of a pair eventually converge. This is a definite possibility because male cardinals have been shown to learn songs during the first Spring both in captivity and in the field (Lemon & Scott, 1965, Dittus & Lemon, 1969; Yamaguchi, 1996). Third, a female may prefer a male that has the same song types as hers at the time of pair formation, and then become less selective with regard to male's song types as she becomes sexually receptive. The second and the third possibilities would lead female that are long-distance dispersers to pair with males that do not sing song types that are shared by members of the breeding population. However, pair-specific song types that are not shared by other individuals in the geographic population have not been commonly observed (Halkin, 1990; Yamaguchi, pers. obs.). Thus, limited dispersal appears to be the most likely explanation of the song matching between the members of a pair. I conclude that song matching in wild cardinal pairs does not contradict the lack of song type preference revealed in the present study. Moreover, the discusssion suggests that the field observation of song matching within pairs in other species cannot necessarily be taken as an evidence of a female's song preference for the song types within her own vocal repertoire.

Natal auditory experience and song type preference

Songs heard during the natal period (up to 45 days of age) were not necessarily preferred over other song types. This result suggests that a female cardinal does not distinguish sexually between conspecific males that sing her father's song types from males that sing other song types. This lack of natal song preference in mate selection is inconsistent with some studies (Baker et al., 1981, 1987; Baker, 1983; Tomback & Baker, 1984; Casey & Baker, 1992), and agrees with others (Baptista & Morton, 1982, 1988; Payne *et al.*, 1987; Chilton *et al.*, 1990; Chilton & Lein, 1996). These results have a bearing on the hypothesis originally proposed by Nottebohm (1969, 1972) that female may gain advantage by choosing a male that sings her father's song types, because the male is likely to have been born in the same area as she was and possesses a set of genes that is adapted to the microenvironment in which they reside. However, as in some other species (Kroodsma, 1974; Payne, 1981; Beecher *et al.*, 1994), a male cardinal can learn songs both at his natal area, and at the breeding site where he has settled (Dittus & Lemon, 1966; Yamaguchi, 1996). Therefore, his song types do not necessarily indicate either his birthplace or his population membership. It may be that female cardinals lack a preference for song types heard during the natal period because they do not gain any genetic advantage by choosing males that sing their fathers' songs.

Familiarity with songs and the song type preference

Female cardinals did not discriminate conspecific songs they have heard before from those they have never heard before. Is this lack of a song type preference for mate choice in cardinals exceptional among songbirds? Adult wild-caught females of at least six species exhibit a sexual preference for the home dialect over alien dialects, as measured by the copulation solicitation display (King *et al.*, 1980; Baker *et al.*, 1981, 1987; Baker, 1983; Clayton & Pröve, 1989; Searcy, 1990; Searcy *et al.*, 1997). While preference for home over alien dialect shown in these studies may be confounded by familiarity with song, the results suggest that females of these species prefer song types that they have heard at least from the time they settle into their first breeding site (most studies refer to song types heard in the collection site of adult female subjects as 'home' dialect). Although it is not clear how prevalent the home dialect preference is among songbirds, perhaps in

part because negative results are seldom published, the difference found in cardinals may be explained by some unusual features of cardinal behavior. The sexual display of male cardinals involves a strong visual component, more exaggerated than in other species (Laskey, 1944; Bent, 1968; Lemon, 1968; Yamaguchi, pers. obs.). The fact that the visual image of a male is a necessary and sufficient stimulus to elicit sexual responses in some females, as observed in my preliminary experiment, also suggests that female cardinals may place less importance on song types in comparison to other species.

It has been shown that territorial cardinal males respond more aggressively to the home dialect than to the alien dialect during the breeding season (Lemon, 1967). This suggests that variation in song types may have different meanings to male and female cardinals. It has been hypothesized previously that the song types a male acquires are more important in the context of intrasexual selection than in inter-sexual selection (Payne, 1983a). A few studies that support the first half of the hypothesis by showing that the song types a male acquires correlate with the males' ability to establish territories (Payne, 1981; Beecher *et al.*, 1994). The results of my study, along with other studies (Payne, 1983a, b; Baptista & Morton, 1982, 1988; Payne *et al.*, 1987; Chilton *et al.*, 1990; Payne & Payne, 1993a, b, 1996; Chilton & Lein, 1996) can be taken as evidence to support the last half of the hypothesis, namely that song types are of lesser importance for mate choice.

Species recognition

The subjects responded more to novel conspecific songs than to novel heterospecific songs. The ability of female passerines to recognize conspecific songs, as measured by the copulation solicitation display, has been shown in more than ten species, (reviewed by Searcy, 1992). It appears that songs, in general, play an important role in species identification in the context of copulation. Female cardinals, as in other species studied, identified conspecific songs solely on the basis of their acoustic properties, and did so without prior experience of them. The perceptual mechanism underlying this conspecific recognition ability may be identical to the mechanism presumed to guide selective song acquisition in naive young male songbirds (Marler & Peters, 1977, 1989).

The failure of female cardinals to respond to the heterospecific songs despite the presence of visually correct species information shows an interesting interaction of information coming into different sensory channels. As mentioned earlier, visual images of a courting male are sometimes sufficient to elicit a sexual response in certain individuals, but auditory song stimuli alone are not. When appropriate auditory stimuli (conspecific songs) are added to visual stimuli, responsiveness is strongly enhanced. If, on the other hand, inappropriate auditory stimuli (heterospecific songs) are added to the visual stimuli, any initial responsiveness to the visual stimuli becomes inhibited, as evident in one individual mentioned above. It would appear that all available pieces of information arriving in different sensory channels must be congruent with species-characteristic norms to elicit copulatory displays in female cardinals.

Whether female songbirds choose males based on their song types has been controversial. The results reported here supports the argument that females do not form any clear preference for particular song types based on their auditory experience. In addition, the study rejected the assumption that song types memorized by females for vocal performance also guides song type preference in the context of mate choice. Thus, in comparison to other features of male phenotypes (*e.g.* repertoire size: Searcy, 1984) and the amount of resources that males hold (Alatalo *et al.*, 1988), the variation in song types probably plays a minor role in mate choice.

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