Sexual preferences for mate song in female canaries (Serinus canaria)

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SEXUAL PREFERENCES FOR MATE SONG IN FEMALE CANARIES (*SERINUS CANARIA*)

running title: MATE SONG PREFERENCES IN FEMALE CANARY

NATHALIE BEGUIN, GERARD LEBOUCHER[1)] & MICHEL KREUTZER

(Equipe Oiseaux, UPRESA CNRS 7025, Laboratoire de Psychophysiologie et Ethologie, Bâtiment H, Université de Paris X - Nanterre, 200 avenue de la république. 92001 Nanterre cedex - France)

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1) Corresponding author

Summary

Recent studies have shown that female passerine birds gave more sexual displays for songs of their mates than for songs of other males. The present study aimed to determine to what extent familiarisation with a song may account for females' song preferences. Eighteen female canaries were paired with a male during a short period and were later familiarised with songs. During the familiarisation period, females were exposed to the sight of their previous mate while they heard the song of their previous mate (M) and while they heard the song of a non-mate (non-mate reinforced, NMR). These females could also hear the song of another non-mate male without sight exposure (non-mate non-reinforced, NMNR). At the end of this familiarisation period, the sexual preferences of the females for these songs were studied : we analysed the total number of CSD elicited by each song during the whole period of sexual responsiveness. As a consequence of the method used to pair the animals, 10 of the 18 females laid fertile eggs whereas 8 females laid non fertile eggs. Fertile females displayed more for M song than for NMR or NMNR songs. Non fertile females unlike fertile females did not display preferentially for any of the 3 songs and, particularly, did not show sexual preference for their previous mate. These results strongly suggest that mate recognition is not a mere effect of familiarisation with songs but is closely associated with previous copulatory experience. When they began to display sexual responses, fertile females presented a clear preference for M song against NMR and NMNR songs. During this period, non fertile females displayed more for NMR song than for NMNR song. In contrast, before egg-laying no song preference appeared for fertile as well as for non fertile females. Just before egg-laying, the females appear to be less selective towards male stimuli. Modification of female sexual preferences might account for the emergence of extra-pair copulations observed during the reproductive cycle in wild species.

Introduction

It has been hypothesised that bird song has three principal functions in the context of sexual selection. Bird song is used (1) to repel rival males, (2) to attract and entice females and (3) to stimulate females' reproductive activity (Kroodsma & Byers, 1991 ; Baptista & Gaunt, 1994 ; Catchpole & Slater, 1995). Before laying, passerine females manifest their willingness to copulate by showing a particular courtship : the copulation solicitation display (CSD). The solicitation display assay has frequently been used to measure females' preferences to playback songs (Searcy, 1992). Results of such experiments indicate that female show sexual preferences for certain categories of conspecific songs (King & West, 1977 ; Catchpole et al., 1986) ; or for special song phrases (Vallet & Kreutzer, 1995). It has been stated that the discrimination shown by females under these laboratory conditions was important in natural conditions because these preferences were expressed in a direct mating context (Searcy, 1992 ; O'Loghlen & Beecher, 1997). Males whose songs are very stimulating are expected to gain high reproductive success.

Evidence that male vocalisations also play a major role in mate recognition has been reviewed by Falls (1982). Females are more responsive to recordings of their mates' vocalisations over vocalisations of non-mates (Mundinger, 1970 ; Miller, 1979 ; Wiley et al., 1991, Robertson, 1996), suggesting that females are able of recognising their mates' song. Field observations of Eens and Pixteen (1995) on female starlings tend to support this assumption.

Recently, O'Loghlen and Beecher (1997) demonstrated that female song sparrows (*Melospiza melodia*) gave more sexual displays and displayed more intensely for song types recorded from repertoires of their mates than for songs from other males from the local population. However, these authors pointed out that they cannot distinguish from their results whether females preferentially responded to mate song types because they recognised these types as belonging to their mates or simply because of familiarity with these song types (O'Loghlen & Beecher, 1997).

The present study aimed to determine to what extent familiarisation with a song may account for females' song preferences. This experiment was designed taking into consideration the results of operant conditioning studies showing that the association of visual and auditory stimuli was a strong reinforcer in birds (Delsaut & Roy, 1980). Female canaries were paired with a male during three days, and were later familiarised with their mate song and with non-mate songs. During the eight-day familiarisation period, females were daily exposed to the sight of their previous mate ; during this exposure, they could hear the song of their previous mate and the song of a non-mate. Females could also hear the song of a non-mate without sight exposure. At the end of this familiarisation period, the sexual preferences of the female for these songs were studied.

Studies in zebra finches (*Taenopygia guttata*) suggest that recent experience is a prominent factor in female sexual choice (Collins, 1995). Taking these results into account, we can hypothesise that the two songs reinforced by the sight of a male will be preferred. The alternative hypothesis states that females will memorise the features of their mate during the courtship period and will only prefer the song of their previous mate.

Females were allowed to mate only during a few days, so some females failed to lay fertile eggs. We analysed the results taking into account whether females laid fertile or non fertile eggs.

Methods

Subjects and housing

In this study, we used 23 female and 4 male domestic canaries (*Serinus canaria*). The animals were chosen from a pool of 2-3 year old canaries, raised in our laboratory. These animals (females and males) had previous reproductive experience but the females were never paired with each of the 4 males. Before the experiment, females and males were initially housed in aviaries during three months in single-sexed groups, on a short daylight schedule (LD 8 :16). Under these conditions the birds show no reproductive activity. Females and males were brought into breeding conditions by lengthening the photoperiod (LD 14 :10). The animals were housed in individual cages (38 x 33 x 26 cm), fitted with perches and nest bowls and were provided with nesting material (coconut fibbers, cotton strings). The birds were given seeds, fresh food, vitamins and water daily.

We used 4 different songs (S1, S2, S3 and S4) emitted by 4 different males (respectively M1, M2, M3 and M4) to stimulate sexual responses of the female canaries, but only two of the 4 males (M1 and M2) were paired with the females.

Experiment 1

This experiment was designed to study the effect of the 4 songs (S1, S2, S3 and S4) produced by the 4 males (M1, M2 , M3 and M4) on sexual responses of 5 females, never paired with any of these 4 males.

Females were tested for song preferences according to methods previously used in our laboratory (Kreutzer & Vallet, 1991). Female responsiveness to songs was assessed in two tests each day, one in the morning (11 :00 to 12 :00) and one in the afternoon (15 :00 to 16 :00). During song test sessions, sexually receptive females were individually placed, in a separate room, in glass-enclosed sound attenuation chambers (52 x 50 x 40 cm inside, 80 x 72 x 70 cm outside). Female canaries were presented with 4 different playback song bouts consisting of repetitions of the same song (S1, S2, S3 or S4). Each song lasted 9 s, a duration which is within the normal range for male canaries. Each song was repeated six times to build a song bout. Consecutive songs were separated by 9 s pauses which were chosen to allow the full development of all sexual displays. Stimuli were played back by a tape recorder (50 - 14000 Hz) connected to a speaker (100-18000 Hz) placed within the attenuation chamber. The degree of a female's sexual response was measured by the number of complete copulation solicitation displays (CSD). In such a complete display, the female crouched and arched her back while vibrating her wings which she held away from her body. Each complete display was scored as a unique event. Song bouts were presented at random. The females could not see any male.

Experiment 2

General

This experiment was divided into three distinct phases. During the first phase, (reproduction) , before the laying of their first clutch, females were paired with a male. During the second phase, (familiarisation and song reinforcement procedure), females which cared for young were daily exposed to the sight of their previous mate ; during this exposure, they could hear the song of their mate and the song of a non-mate. Females could also hear the song of a non-mate without sight exposure (control song). During the third phase, (song test sessions), females were tested for male song preferences, this stage occurred before the laying of the second clutch.

First phase : reproduction

Females were paired with a male for three days. We only used 2 different males M1 and M2 similar in age (2 years) and weight (25 g), but with different songs and feathers. These two males were known to have similar reproductive success in prior reproductive experiments with different females.

When a female began to place nesting material in her nest bowl, she was randomly paired with one of the two males, housed in two separate rooms. In each room, all the females - each one in her turn - were paired with the same male. This method is used by breeders to ensure the dissemination of a rare phenotype (Delille, 1974). During a pilot experiment, we used this method to pair the animals ; insofar as females were allowed to mate only during a few days, some females failed to mate and laid non fertile eggs. In the present study, this method was used to obtain females laying fertile eggs and females laying non-fertile eggs.

Ten females were paired with male M1, and eight females with male M2. Females were alone to incubate and rear their young. Eight days after being laid, eggs of the first clutch were candled to determine whether they were fertile or not. Females which laid non fertile were given foster young when their eggs were supposed to be at the onset of hatching period.

For logistic reasons, one half of females for each male was first exposed to photostimulation and the remaining half was exposed to photostimulation two months later.

Second phase : familiarisation and song reinforcement procedure

This phase began when nestlings were 9 days old until they were 17 days old. Twice a day each female was separated from her young during 50 minutes and subjected to the familiarisation and song reinforcement procedure. The females were placed in a cage within the glass-enclosed sound attenuation chambers. A tape recorder (50-14000 Hz) connected to a speaker (100-18000 Hz) diffused songs to females in the sound-attenuation chamber. Females were submitted to the playback of three different tape-recorded songs (presented at random and separated by one minute) : the mate song, the song of a non-mate reinforced by the sight of the mate, the song of a non-mate non reinforced by the sight of the mate.

The mate song (M) was a song frequently emitted by their previous sexual partner (song S1 for male M1 or song S2 for male M2). The hearing of this song was reinforced by the sight of their mate. The mate was housed in a separate cage placed 1.5m in front of the sound-attenuation chamber. Females who were mated with male M1 could see M1 when hearing song S1, females who were mated with male M2 could see M2 when hearing song S2.

The song of a non-mate reinforced by the sight of the mate (NMR) was a song emitted by a non-mate male (song S3 of male M3 and song S4 of male M4). The hearing of this song was reinforced by the sight of their mate. Females who were mated with male M1 could see M1 when hearing song S3, females who were mated with male M2 could see M2 when hearing song S4.

The song of a non-mate non reinforced by the sight of the mate (NMNR) was a control song emitted by a non-mate male. The hearing of this song was not reinforced by the sight of their mate. Females who were mated with male M1 heard song S2, females who were mated with male M2 heard song S1.

Each song (duration 9s) was repeated six times to build a song bout ; in a song bout, two consecutive songs were separated by a pause of 9 s. The song bout was played-back during 15 min.

Third phase : song test sessions

At the end of the second phase, when young were 19 days old, females were tested for song preferences. Previous experiments in our laboratory showed that female canary began to regain sexual activity when their young were 20 days old (Nagle et al., 1993). Female responsiveness to songs was assessed in two song test sessions each day, one in the morning (11 :00 to 12 :00) and one in the afternoon (15 :00 to 16 :00), as previously described (see Experiment 1). During song test sessions, females were temporarily separated from their young ; individual cages were placed, in a separate room, in sound attenuation chambers. Female canaries were presented with M (S1 or S2), NMR (S3 or S4) and NMNR (S1 or S2) playback songs.

Data analysis

Experiment 1

Female preferences were analysed using the CSD displayed during song test sessions. To estimate female preferences we analysed the total number of CSD elicited by each song during the whole period of sexual responsiveness (Total number of CSD). After log transformation of data, parametric statistics were used (Winer, 1971). One way ANOVA for repeated measures, followed by post-hoc multiple comparisons tests (Newman-Keuls) was used to analyse the total number of CSD for the 3 songs.

Experiment 2

Female preferences were analysed using the CSD displayed during song test sessions. Two variables were taken into account to analyse data on CSD : (a) the 3 different songs (M, NMR, NMNR) and (b) the fertility of females (fertile, non fertile). To estimate female preferences we analysed the total number of CSD elicited by each song during the whole period of sexual responsiveness (Total number of CSD).

Moreover, we analysed female preferences taking into account the development of female responsiveness. The number of CSD elicited during the first 2 days of sexual responsiveness (CSD at the beginning of sexual responsiveness) and during the two days preceding the formation of the first egg of the second clutch (CSD before egg-laying) were taken into account.

After log transformation of data, parametric statistics were used. Two-way ANOVA for repeated measures, followed by post-hoc multiple comparisons tests (Newman-Keuls) was used to analyse the number of CSD for the 3 songs. Moreover, t-tests were used to compare 2 independent measures.

Results

Experiment 1

The one-way ANOVA for repeated measures revealed no significant effect of songs for the total number of CSD (df=3, F = 0.29 , p = 0.83). The five females did not appear to prefer any of the 4 songs (Fig. 1).

Experiment 2

As a consequence of the method used to pair the animals, 10 of the 18 females laid fertile eggs whereas 8 females laid non fertile eggs. Six females paired with M1 and 4 females paired with M2 laid fertile eggs ; 4 females paired with M1 and 4 females paired with M2 laid non fertile eggs. Eight of the 10 fertile females had been paired at least one day before laying the first egg of the clutch whereas only 3 of the 8 non fertile females had been paired before the first egg. The remaining females (2 fertile and 5 non fertile females) had been paired the day they laid the first egg.

Fertile females laid 4.5 ± 0.22 eggs and non fertile females laid 4.38 + 0.32 eggs (t-test, p = 0.75). Females raised one or two young (1.6 ± 0.22 for fertile females *vs*. 1.13 ± 0.13 for non fertile females ; t-test, p = 0.1).

During the third phase of the experiment (song test sessions), females began to display CSD about seven days before laying the first egg of the second clutch (7.11 ± 1 days before the first egg). The end of sexual responsiveness occurred just after the laying of the first egg (0.33 ± 0.51 day after the first egg).

The two-way ANOVA for repeated measures revealed a significant effect of songs and a significant interaction between songs and fertility factors for the total number of CSD and for the number of CSD at the beginning of sexual responsiveness (Table 1). These results indicate that the effect of different songs depended on whether females laid fertile or non fertile eggs. Cell comparisons were used instead of main effect analysis. For the total number of CSD and for the CSD at the beginning of sexual responsiveness, fertile females displayed more for M song than for NMR or NMNR songs (Fig. 2 A & B). For non fertile females no difference was found between songs when considering the total number of CSD ; in contrast analysis of the CSD at the beginning of sexual responsiveness indicates that non fertile female gave more CSD for NMR than for NMNR songs (Fig. 2 B). Moreover, non fertile females displayed more for NMR than fertile females when considering the total number of CSD (Newman-Keuls, $p < 0.05$) or when considering the CSD at the beginning of sexual responsiveness (Newman-Keuls, $p < 0.01$).

The two-way ANOVA for repeated measures revealed no significant effects of songs or fertility and no significant interaction between songs and fertility factors for the CSD before egg-laying (Table 1).

Discussion

Pairing and fertility of the females

In the second experiment, ten of the 18 females laid fertile eggs whereas 8 females laid non fertile eggs. Insofar as females had previous reproductive experience and laid fertile eggs in previous reproductive cycles, we can assume that non fertile females failed to copulate or, at least, failed to copulate repeatedly with their sexual partner. Several studies have pointed out that multiple mating with the same male could ensure fertilisation (Martin et al,. 1974 ; Birkhead, 1988 ; Møller & Birkhead, 1992 ; Whittingham et al., 1994). The timing of pairing may account, partly, for this result. Most fertile females (8 on 10) were paired at least one day before laying their first egg, in contrast, most of non fertile females (5 on 8) were paired the day they laid their first egg. Paired animals were not systematically observed ; however, empirical observations carried out during the present experiment or during a pilot experiment indicated that copulation did not occur during the first few hours of pairing even if females were fully receptive : a familiarisation period between the two sexual partners seemed to be necessary. In a previous study (Leboucher et al,. 1994) we observed that C.S.D to tape-recorded songs were displayed mainly between nest-building and egg-laying and disappeared progressively thereafter ; moreover during the third phase of the second experiment (song test sessions) the end of sexual responsiveness occurred just after the laying of the first egg of the second clutch (0.33 ± 0.51 days after the first egg). It is likely that during the first phase of the experiment, the majority of the non fertile females were belatedly paired and consequently rejected most copulation attempts.

Total number of CSD displayed by fertile and non fertile females

During the first experiment, females without previous sexual experience with the males which emitted the songs failed to display song preferences (Fig . 1) ; this result indicates that the four songs used in the two experiments (S1, S2, S3 and S4) had the same sexual value. In contrast, during the second experiment, fertile females displayed more for M song (S1 or S2) than for NMR (S3 or S4) or NMNR (S1 or S2) songs (Fig. 2 A). Mate recognition on the basis of song is widespread in bird species (Mundinger, 1970 ; Miller, 1979 ; Wiley et al., 1991 ; Robertson, 1996). As previously stated (see Introduction), O'Loghlen & Beecher (1997) demonstrated that female song sparrows (*Melospiza melodia*) were more readily stimulated to perform sexual displays when presented with song types from repertoires of their mates than songs from other males in the local population. These authors failed to distinguish from their results whether females preferentially responded to mate song types because they recognised these types as belonging to their mates or simply because of familiarity with these song types (O'Loghlen and Beecher ; 1997). The present study clearly shows that mate recognition is not a mere effect of familiarisation with songs : fertile female displayed more for the mate song than for the two non mate songs despite one of the non-mate songs was reinforced by the sight of the mate like the mate song during the recent period of familiarisation.

Non fertile females unlike fertile females did not display preferentially for any of the 3 songs (Fig. 2 A), and particularly, did not show sexual preference for their previous mate. In our experiment, females with non fertile eggs were given foster young to adopt. Consequently, it is unlikely that the lack of egg fertilisation could be a salient cue used to weight mate versus non-mate songs. This result strongly suggest that mate song preference is closely associated with previous copulatory experience. As far as we know, similar results have not yet been reported. However, previous studies showed that in female birds, the divorce rate was negatively correlated with reproductive success during the previous breeding (Lindén, 1991 ; Choudhury, 1995).

Development of song preferences in fertile and non fertile females

When they began to display sexual responses, fertile females presented a clear preference for M song against NMR and NMNR songs (Fig. 2 B). During this period, non fertile females tended to display more for M and NMR songs than for NMNR song (number of CSD are respectively : 3.38 ± 1.85, 4.00 ± 1.71 and 1.5 ± 0.95) (Fig. 2 B). This result suggest that the female choice was affected by their recent experience (Collins, 1995), namely, the familiarisation and reinforcement period ; however the difference between M and NMNR songs did not reach statistical significance (p = 0.1).

In contrast, before egg-laying no song preference appeared for fertile as well as for non fertile females (Table 1, Fig. 2 C). So, just before egg-laying, females seemed to be less selective towards male stimuli. In mammals, T-maze experiments indicated that gilts were less selective towards male stimuli when sexual motivation was high, during the fertile and receptive period, and more selective before and after the receptive period (de Jonge et al., 1994). As far as we know, variation in sexual selectivity during the reproductive cycle of female birds have not been yet evidenced. The causal bases for perceptive or cognitive variations during the course of the reproductive cycle are still unknown. However, neurophysiological studies of Brenowitz (1991) on female canaries indicated that the forebrain nucleus HVC, played a role in specific song recognition. More recent studies, in our laboratory (Del Negro et al., 1998) showed that chemical lesion of the HVC reduced discrimination between two conspecific songs in female canaries. Estrogen receptors were found in the region of the HVC in male as well as in female canaries (Fusani et al., 1996 ; Gahr et al., 1987). So, it is not unlikely that the variations in estradiol concentrations during the reproductive cycle mediate female selectivity through hormonal effects on the HVC. (Breutel et al., 1997)

Field studies indicate that a non negligible proportion of young in broods of female birds are the outcome of extra-pair copulations (Wagner, 1991 ; Dunn & Lifjeld, 1994 ; Kempenaers et al., 1995 ; Whittingham & Lifjeld, 1995). These extra-pair copulations could be an important component of the reproductive success of female (Birkhead & Møller ,1992). There are also increasing evidence that females initiate, not just resist or accept extra-pair courtship (Sheldon 1994 ; Gray, 1996). We have no information about the distribution of extra-pair copulations during the reproductive cycle in female canaries ; particularly, we don't know if females solicit for extra-pair copulations just before egg-laying when their sexual selectivity is low. In other species, like red-winged blackbirds (*Agelaius phoeniceus*), extra-pairs copulations reach a peak two days before egg-laying (Gray, 1996). Likewise, female chaffinches (*Fringilla coelebs*) solicit for extra-pair copulations at a particularly high rate in the days immediately before laying (Sheldon, 1994). Modification of female sexual preferences may account for the emergence of extra-pair copulations observed during the reproductive cycle in wild species.

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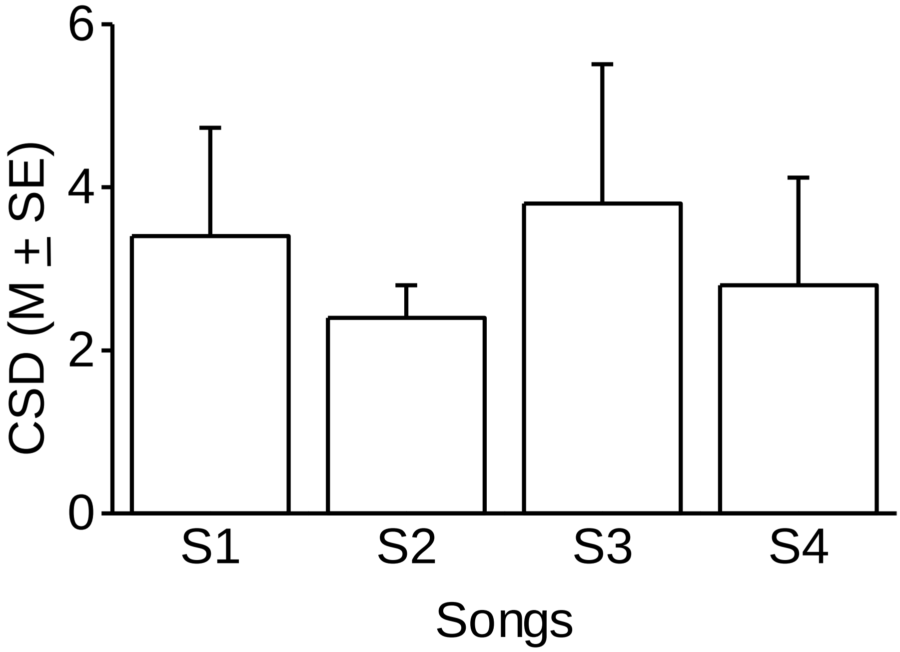
Fig. 1. Effects of 4 tape-recorded songs, S1, S2, S3, S4 on the total number of CSD showed by females (N = 5) never paired with any of the 4 males which emitted these songs. Statistical analysis: one-way ANOVA for repeated measures (df = 3, F = 0.29 , p = 0.83).

Fig. 2 Effect of the mate song (M), the song of a non-mate reinforced by the sight of the mate (NMR) the song of a non-mate non reinforced by the sight of the mate (NMNR) on (A) the total number of CSD, (B) the number of CSD at the beginning of sexual responsiveness and (C) the number of CSD before egg-laying, of fertile (N = 10) and non fertile females (N = 8). Statistical analyses : two-way ANOVA for repeated measures, see Table 1 ; post hoc analyses, Newman-Keuls tests, a : indicates a significant difference with M song, b : indicates a significant difference with NMR song, * : p < 0.05 and ** : p < 0.01.


6
4
2
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CSD (M ± SE)
S1
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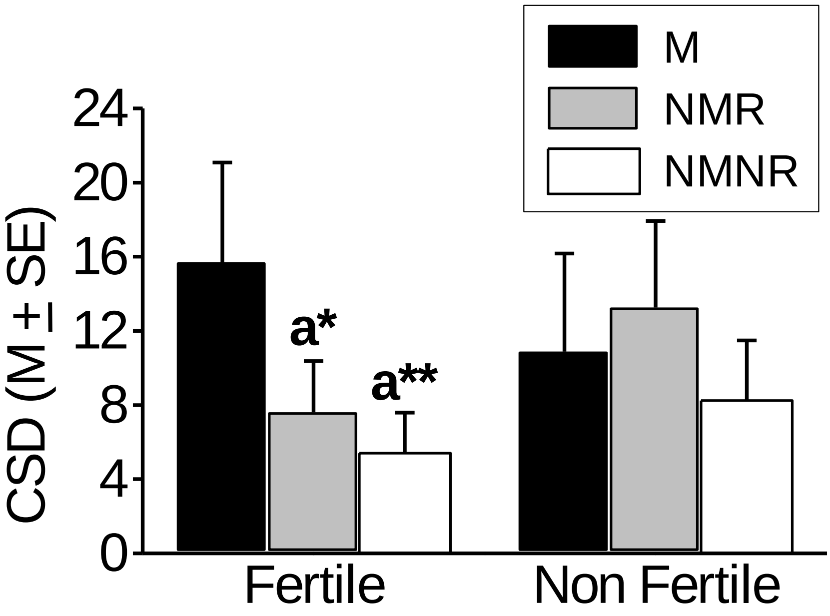
S3
S4
Songs


M
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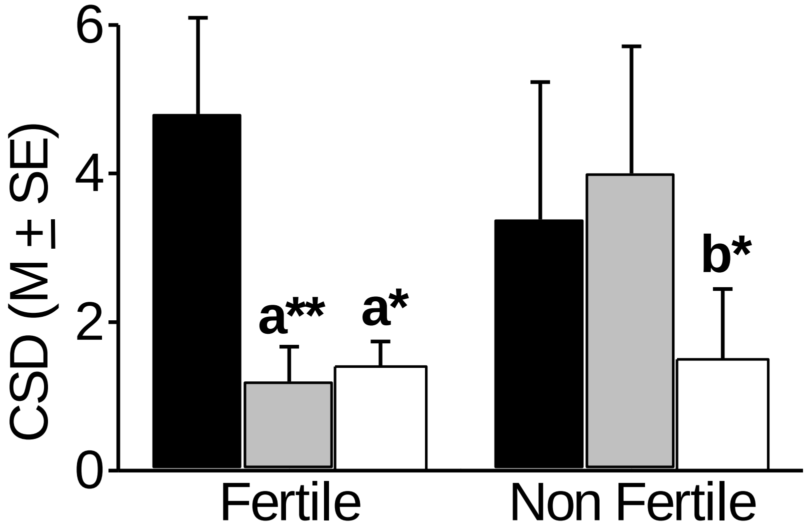
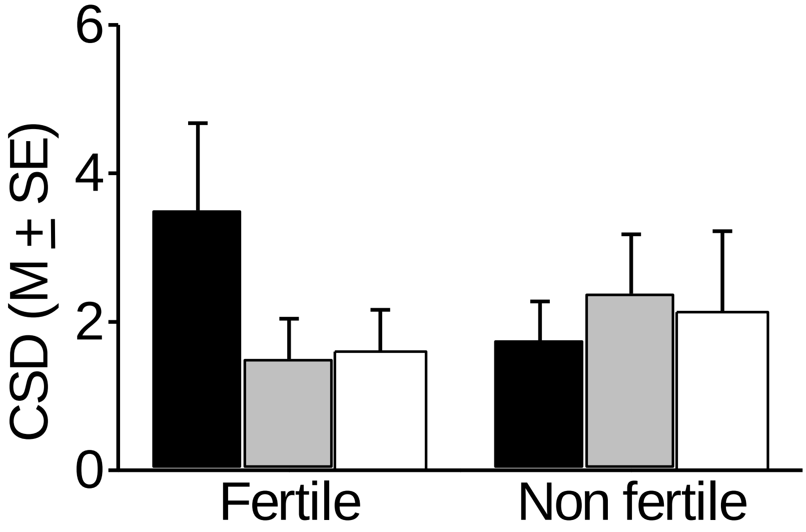
NMNR
CSD (M + SE)
24
20
16
12
8
4
0
a*
a**
Fertile
Non Fertile

A


CSD (M + SE)
6
4
2
0
a**
a*
b*
Fertile
Non Fertile

B


CSD (M + SE)
6
4
2
0
Fertile
Non fertile

C

TABLE 1. *Experiment 2 : results of the two-way ANOVA for repeated measures (df = 2,1,2).*

	Songs (Mate, Non Mate Reinforced, Non Mate Non Reinforced)		Fertility (Fertile, Non Fertile)		Interaction	
	f	p	f	p	f	p
Total number of CSD	5.84	0.007	0.28	0.60	4.63	0.017
CSD at the beginning of sexual responsiveness	7.48	0.002	0.02	0.90	7.49	0.002
CSD before egg-laying	1.23	0.30	0.01	0.92	1.93	0.16