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

running title: MATE SONG PREFERENCES IN FEMALE CANARY

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1 **Summary**

2

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

29

1 Introduction

2

3 It has been hypothesised that bird song has three principal functions in the context of
4 sexual selection. Bird song is used (1) to repel rival males, (2) to attract and entice
5 females and (3) to stimulate females' reproductive activity (Kroodsma & Byers,
6 1991 ; Baptista & Gaunt, 1994 ; Catchpole & Slater, 1995). Before laying, passerine
7 females manifest their willingness to copulate by showing a particular courtship : the
8 copulation solicitation display (CSD). The solicitation display assay has frequently
9 been used to measure females' preferences to playback songs (Searcy, 1992).
10 Results of such experiments indicate that female show sexual preferences for certain
11 categories of conspecific songs (King & West, 1977 ; Catchpole et al., 1986) ; or for
12 special song phrases (Vallet & Kreutzer, 1995). It has been stated that the
13 discrimination shown by females under these laboratory conditions was important in
14 natural conditions because these preferences were expressed in a direct mating
15 context (Searcy, 1992 ; O'Loughlen & Beecher, 1997). Males whose songs are very
16 stimulating are expected to gain high reproductive success.

17 Evidence that male vocalisations also play a major role in mate recognition
18 has been reviewed by Falls (1982). Females are more responsive to recordings of
19 their mates' vocalisations over vocalisations of non-mates (Mundinger, 1970 ; Miller,
20 1979 ; Wiley et al., 1991, Robertson, 1996), suggesting that females are able of
21 recognising their mates' song. Field observations of Eens and Piteen (1995) on
22 female starlings tend to support this assumption.

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

30 The present study aimed to determine to what extent familiarisation with a
31 song may account for females' song preferences. This experiment was designed
32 taking into consideration the results of operant conditioning studies showing that the
33 association of visual and auditory stimuli was a strong reinforcer in birds (Delsaut &
34 Roy, 1980). Female canaries were paired with a male during three days, and were

1 later familiarised with their mate song and with non-mate songs. During the eight-day
2 familiarisation period, females were daily exposed to the sight of their previous
3 mate ; during this exposure, they could hear the song of their previous mate and the
4 song of a non-mate. Females could also hear the song of a non-mate without sight
5 exposure. At the end of this familiarisation period, the sexual preferences of the
6 female for these songs were studied.

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

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

16

1 **Methods**

2

3

4 **Subjects and housing**

5

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

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

20

21

22 **Experiment 1**

23

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

27 Females were tested for song preferences according to methods previously
28 used in our laboratory (Kreutzer & Vallet, 1991). Female responsiveness to songs
29 was assessed in two tests each day, one in the morning (11 :00 to 12 :00) and one in
30 the afternoon (15 :00 to 16 :00). During song test sessions, sexually receptive
31 females were individually placed, in a separate room, in glass-enclosed sound
32 attenuation chambers (52 x 50 x 40 cm inside, 80 x 72 x 70 cm outside). Female
33 canaries were presented with 4 different playback song bouts consisting of
34 repetitions of the same song (S1, S2, S3 or S4). Each song lasted 9 s, a duration

1 which is within the normal range for male canaries. Each song was repeated six
2 times to build a song bout. Consecutive songs were separated by 9 s pauses which
3 were chosen to allow the full development of all sexual displays. Stimuli were played
4 back by a tape recorder (50 - 14000 Hz) connected to a speaker (100-18000 Hz)
5 placed within the attenuation chamber. The degree of a female's sexual response
6 was measured by the number of complete copulation solicitation displays (CSD). In
7 such a complete display, the female crouched and arched her back while vibrating
8 her wings which she held away from her body. Each complete display was scored
9 as a unique event. Song bouts were presented at random. The females could not
10 see any male.

11

12 Experiment 2

13

14 General

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

23

24 First phase : reproduction

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

29 When a female began to place nesting material in her nest bowl, she was
30 randomly paired with one of the two males, housed in two separate rooms. In each
31 room, all the females - each one in her turn - were paired with the same male. This
32 method is used by breeders to ensure the dissemination of a rare phenotype (Delille,
33 1974). During a pilot experiment, we used this method to pair the animals ; insofar as
34 females were allowed to mate only during a few days, some females failed to mate

1 and laid non fertile eggs. In the present study, this method was used to obtain
2 females laying fertile eggs and females laying non-fertile eggs.

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

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

11
12 Second phase : familiarisation and song reinforcement procedure
13 This phase began when nestlings were 9 days old until they were 17 days old. Twice
14 a day each female was separated from her young during 50 minutes and subjected
15 to the familiarisation and song reinforcement procedure. The females were placed in
16 a cage within the glass-enclosed sound attenuation chambers. A tape recorder (50-
17 14000 Hz) connected to a speaker (100-18000 Hz) diffused songs to females in the
18 sound-attenuation chamber. Females were submitted to the playback of three
19 different tape-recorded songs (presented at random and separated by one minute) :
20 the mate song, the song of a non-mate reinforced by the sight of the mate, the song
21 of a non-mate non reinforced by the sight of the mate.

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

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

33 The song of a non-mate non reinforced by the sight of the mate (NMNR) was
34 a control song emitted by a non-mate male. The hearing of this song was not

1 reinforced by the sight of their mate. Females who were mated with male M1 heard
2 song S2, females who were mated with male M2 heard song S1.

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

6

7 Third phase : song test sessions

8 At the end of the second phase, when young were 19 days old, females were tested
9 for song preferences. Previous experiments in our laboratory showed that female
10 canary began to regain sexual activity when their young were 20 days old (Nagle et
11 al., 1993). Female responsiveness to songs was assessed in two song test sessions
12 each day, one in the morning (11 :00 to 12 :00) and one in the afternoon (15 :00 to
13 16 :00), as previously described (see Experiment 1). During song test sessions,
14 females were temporarily separated from their young ; individual cages were placed,
15 in a separate room, in sound attenuation chambers. Female canaries were
16 presented with M (S1 or S2), NMR (S3 or S4) and NMNR (S1 or S2) playback songs.

17

18 Data analysis

19

20 Experiment 1

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

28

29 Experiment 2

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

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

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

10

1 **Results**

2

3

4 Experiment 1

5

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

9

10

11 Experiment 2

12

13 As a consequence of the method used to pair the animals, 10 of the 18 females laid
14 fertile eggs whereas 8 females laid non fertile eggs. Six females paired with M1 and
15 4 females paired with M2 laid fertile eggs ; 4 females paired with M1 and 4 females
16 paired with M2 laid non fertile eggs. Eight of the 10 fertile females had been paired at
17 least one day before laying the first egg of the clutch whereas only 3 of the 8 non
18 fertile females had been paired before the first egg. The remaining females (2 fertile
19 and 5 non fertile females) had been paired the day they laid the first egg.

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

23 During the third phase of the experiment (song test sessions), females began
24 to display CSD about seven days before laying the first egg of the second clutch
25 (7.11 ± 1 days before the first egg). The end of sexual responsiveness occurred just
26 after the laying of the first egg (0.33 ± 0.51 day after the first egg).

27 The two-way ANOVA for repeated measures revealed a significant effect of
28 songs and a significant interaction between songs and fertility factors for the total
29 number of CSD and for the number of CSD at the beginning of sexual
30 responsiveness (Table 1). These results indicate that the effect of different songs
31 depended on whether females laid fertile or non fertile eggs. Cell comparisons were
32 used instead of main effect analysis. For the total number of CSD and for the CSD at
33 the beginning of sexual responsiveness, fertile females displayed more for M song
34 than for NMR or NMNR songs (Fig. 2 A & B). For non fertile females no difference

1 was found between songs when considering the total number of CSD ; in contrast
2 analysis of the CSD at the beginning of sexual responsiveness indicates that non
3 fertile female gave more CSD for NMR than for NMNR songs (Fig. 2 B). Moreover,
4 non fertile females displayed more for NMR than fertile females when considering
5 the total number of CSD (Newman-Keuls, $p < 0.05$) or when considering the CSD at
6 the beginning of sexual responsiveness (Newman-Keuls, $p < 0.01$).

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

10

1 **Discussion**

2

3

4 Pairing and fertility of the females

5

6 In the second experiment, ten of the 18 females laid fertile eggs whereas 8 females
7 laid non fertile eggs. Insofar as females had previous reproductive experience and
8 laid fertile eggs in previous reproductive cycles, we can assume that non fertile
9 females failed to copulate or, at least, failed to copulate repeatedly with their sexual
10 partner. Several studies have pointed out that multiple mating with the same male
11 could ensure fertilisation (Martin et al., 1974 ; Birkhead, 1988 ; Møller & Birkhead,
12 1992 ; Whittingham et al., 1994). The timing of pairing may account, partly, for this
13 result. Most fertile females (8 on 10) were paired at least one day before laying their
14 first egg, in contrast, most of non fertile females (5 on 8) were paired the day they
15 laid their first egg. Paired animals were not systematically observed ; however,
16 empirical observations carried out during the present experiment or during a pilot
17 experiment indicated that copulation did not occur during the first few hours of pairing
18 even if females were fully receptive : a familiarisation period between the two sexual
19 partners seemed to be necessary. In a previous study (Leboucher et al., 1994) we
20 observed that C.S.D to tape-recorded songs were displayed mainly between nest-
21 building and egg-laying and disappeared progressively thereafter ; moreover during
22 the third phase of the second experiment (song test sessions) the end of sexual
23 responsiveness occurred just after the laying of the first egg of the second clutch
24 (0.33 ± 0.51 days after the first egg). It is likely that during the first phase of the
25 experiment, the majority of the non fertile females were belatedly paired and
26 consequently rejected most copulation attempts.

27

28 Total number of CSD displayed by fertile and non fertile females

29

30 During the first experiment, females without previous sexual experience with the
31 males which emitted the songs failed to display song preferences (Fig . 1) ; this
32 result indicates that the four songs used in the two experiments (S1, S2, S3 and S4)
33 had the same sexual value. In contrast, during the second experiment, fertile females
34 displayed more for M song (S1 or S2) than for NMR (S3 or S4) or NMNR (S1 or S2)

1 songs (Fig. 2 A). Mate recognition on the basis of song is widespread in bird species
2 (Mundinger, 1970 ; Miller, 1979 ; Wiley et al., 1991 ; Robertson, 1996). As previously
3 stated (see Introduction), O’Loghlen & Beecher (1997) demonstrated that female
4 song sparrows (*Melospiza melodia*) were more readily stimulated to perform sexual
5 displays when presented with song types from repertoires of their mates than songs
6 from other males in the local population. These authors failed to distinguish from
7 their results whether females preferentially responded to mate song types because
8 they recognised these types as belonging to their mates or simply because of
9 familiarity with these song types (O’Loghlen and Beecher ; 1997). The present study
10 clearly shows that mate recognition is not a mere effect of familiarisation with songs :
11 fertile female displayed more for the mate song than for the two non mate songs
12 despite one of the non-mate songs was reinforced by the sight of the mate like the
13 mate song during the recent period of familiarisation.

14 Non fertile females unlike fertile females did not display preferentially for any
15 of the 3 songs (Fig. 2 A), and particularly, did not show sexual preference for their
16 previous mate. In our experiment, females with non fertile eggs were given foster
17 young to adopt. Consequently, it is unlikely that the lack of egg fertilisation could be a
18 salient cue used to weight mate versus non-mate songs. This result strongly suggest
19 that mate song preference is closely associated with previous copulatory experience.
20 As far as we know, similar results have not yet been reported. However, previous
21 studies showed that in female birds, the divorce rate was negatively correlated with
22 reproductive success during the previous breeding (Lindén, 1991 ; Choudhury,
23 1995).

24

25 Development of song preferences in fertile and non fertile females

26

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

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

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

33

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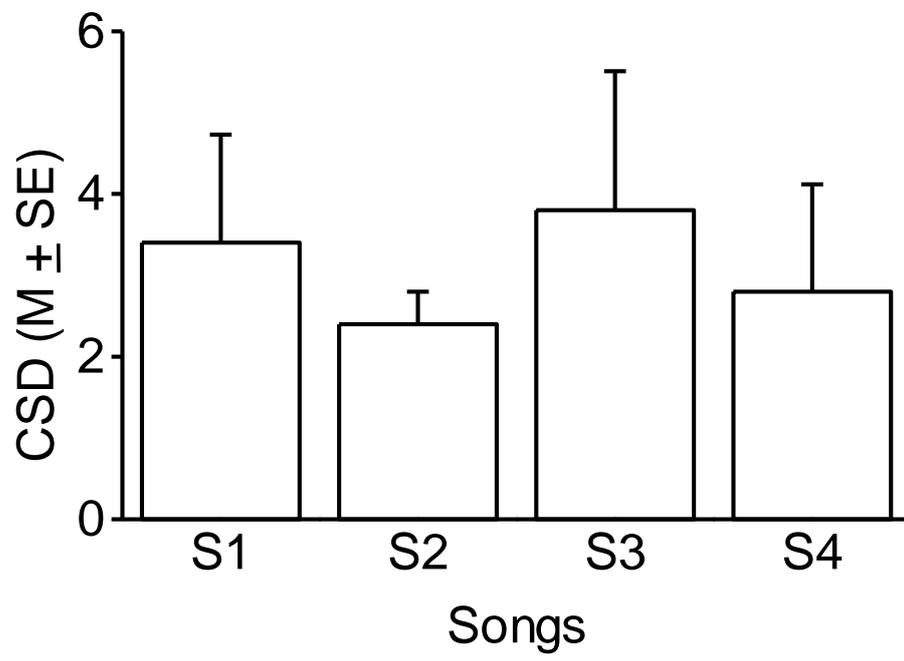
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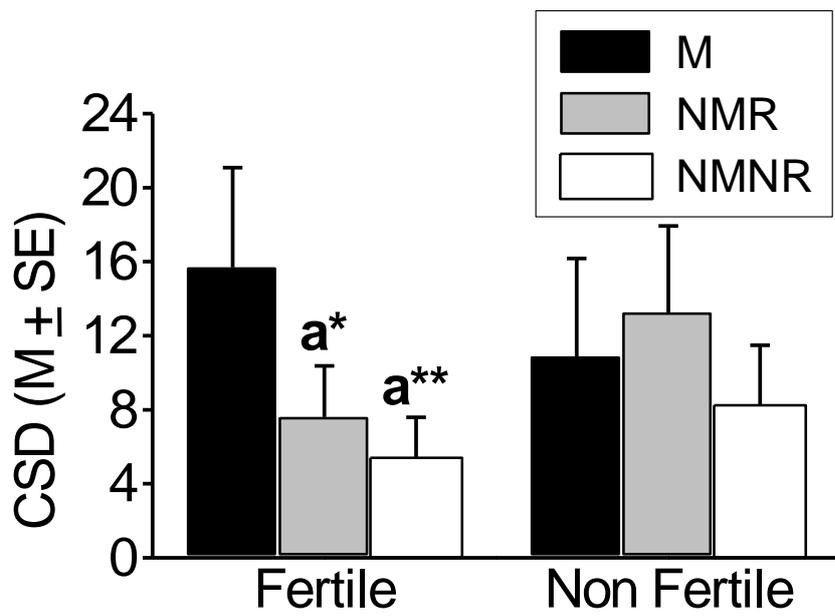
1 Fig. 1. Effects of 4 tape-recorded songs, S1, S2, S3, S4 on the total number of CSD
2 showed by females (N = 5) never paired with any of the 4 males which emitted these
3 songs. Statistical analysis: one-way ANOVA for repeated measures (df = 3,
4 F = 0.29 , p = 0.83).

5

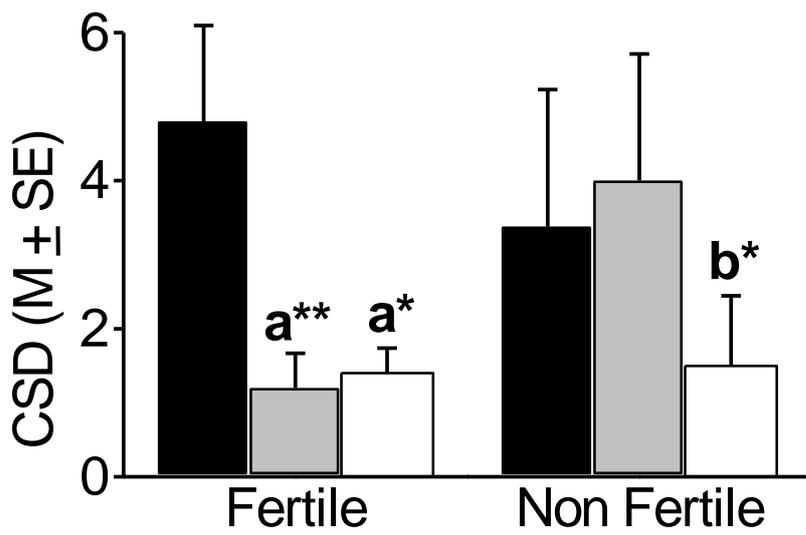
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7 Fig. 2 Effect of the mate song (M), the song of a non-mate reinforced by the sight of
8 the mate (NMR) the song of a non-mate non reinforced by the sight of the mate
9 (NMNR) on (A) the total number of CSD, (B) the number of CSD at the beginning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

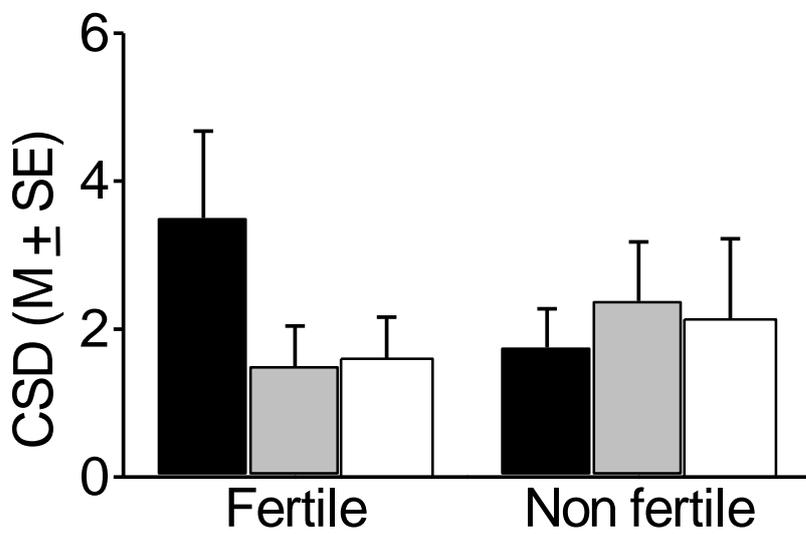




A



B



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