ORIGINAL ARTICLE

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Sexual preferences for songs in female domestic canaries (*Serinus canaria*): can late song exposure, without social reinforcement, influence the effects of early tutoring?

Abstract We studied the relative effects of early and late song exposure without social reinforcement on female sexual preferences in the domestic canary (*Serinus canaria*). Young female canaries were tape-tutored during their first 4 months of life with songs of either domestic or wild male canaries (DT and WT conditions). When they reached sexual maturity, these females were placed in breeding conditions and some of them were re-exposed to songs. During this "late exposure" the females, according to their experimental group, were either presented with new domestic or wild songs (DL and WL conditions) over 40 days, or were kept without song stimulation (− condition). Afterwards, we assessed the sexual preferences of all the females for domestic or wild songs using the copulation solicitation display assay. The results showed that both DT/– and DT/DL females showed a clear preference for domestic songs. However, whereas WT/WL females preferred wild songs; WT/– females did not show any preference. Finally, DT/WL and WT/DL females failed to show any preference. It appeared that a second song experience at the beginning of their first breeding season, without any social reinforcement, allowed the emergence or stabilisation of early preferences, or interfered with these early preferences depending on whether the song category used during the late exposure phase matched or not the song category used during the early tutoring phase, and also depending on which category was used during the first tutoring phase. This

behavioural plasticity could help young adult females to adjust the 'standard' they built during infancy to new environmental conditions.

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Introduction

Bird song has evolved under both intra- and inter-sexual selective pressures (Gil and Gahr 2002). Moreover, it has been established in several taxa that learning processes are involved in male song development. However, studies on female learning abilities, and their consequences on song preferences and mate choice, are rather scarce when compared with the numerous works on song learning in males (Catchpole and Slater 1995). Yet female oscines in some species are able to learn and retain songs heard early in life, and this process of song memorisation appears to guide female sexual responsiveness to the courtship songs of males (Baker et al. 1981; Baker 1983). Several laboratory studies have shown that songs heard during early life influence the females' later song preferences (see Riebel 2003 for a review). These preferences were measured with different methods like nest building activities (Spitler-Nabors and Baker 1983), approach behaviour, or time spent near a loudspeaker (Miller 1979a), and courtship displays, such as copulation solicitation displays (CSD) (Searcy 1992). Using the copulation solicitation display (CSD) assay, Nagle and Kreutzer (1997b) found that adult female domestic canaries (*Serinus canaria*) preferred a conspecific song heard during their first months of life. Using a choice test with loudspeakers, Miller (1979b) demonstrated that female zebra finches (*Taeniopygia guttata*) preferred their father's song rather than an unknown individual's dissimilar song, but did not clearly prefer their father's song to an unknown individual's similar song. More recently, Depraz et al. (2000) demonstrated that adult female domestic canaries, exposed early to songs of

domestic canaries showed sexual preferences for songs from males of their own domestic strain over songs from wild males. In their experiment, the songs played to adult females were different from the songs played during infancy. In contrast, female domestic canaries exposed early to wild songs failed to show a clear-cut preference for wild songs (Depraz et al. 2000). These results suggested that female domestic canaries have a predisposition to learn songs of their own strain rather than songs of an alien strain (Depraz et al. 2000). Some authors proposed that preferences for categories of songs heard during infancy led females to mate preferentially with males singing songs similar to those the females were exposed to when young; they argued that in species with several populations and song dialects, females assortatively mate with males producing songs of their own local (natal) dialect (Eastzer et al. 1985; Baker et al. 1987). From studies on species having various subspecies and song dialects, it has been suggested that song dialects, by facilitating assortative mating, restrict gene flow among songbird populations (Marler and Tamura 1962, 1964).

In addition, it has been found that, in some species, females disperse more than males (Morton et al. 1972; Morton 1992) and it has been hypothesised that they could have to adjust their previous pattern of preference to the small variations encountered in the songs of the males living where they settle (MacDougall-Shackleton et al. 2001).

In studies dealing with song preferences, shifts in preferences occurred as a consequence of complex social interactions involving acoustic, visual and, sometimes, tactile interactions and social reinforcement. Several studies showed that modifications of song preferences could occur after mating. For instance, Nagle and Kreutzer (1997a) showed that adult female domestic canaries early tutored by wild songs, and displaying preferentially to their wild tutoring canary song altered their preference pattern after being paired for 6 months with a male domestic canary. The songs used during both tests were identical, and the socially and sexually experienced females showed no more preference between their wild tutoring song and two songs from the domestic strain (Nagle and Kreutzer 1997a). The consequences of early and late tutoring on males' song performance learning have also been studied in domestic canary strains (Mundinger 1995). Using phonotaxis techniques, Clayton (1988) demonstrated that young female zebra finches early tutored with a live adult male and re-exposed to another live adult tutor from 4 to 6 months of life, after the sensitive period is supposed to be completed in this species, were still capable of song discriminating learning. However, little is known about the effects of a new song exposure in early adulthood, without social reinforcement, on later females' preferences for songs in a mate choice context. Using operant techniques with zebra finches, Riebel (2000) assessed tape tutored females' preferences for tutor or unfamiliar songs, and addressed the question of whether the females' preferences were stable along time. She found that the preferences were stable only in females "normally" early tutored, while control (untutored) females changed their preferences after they experienced a new short song exposure following the three first preference tests.
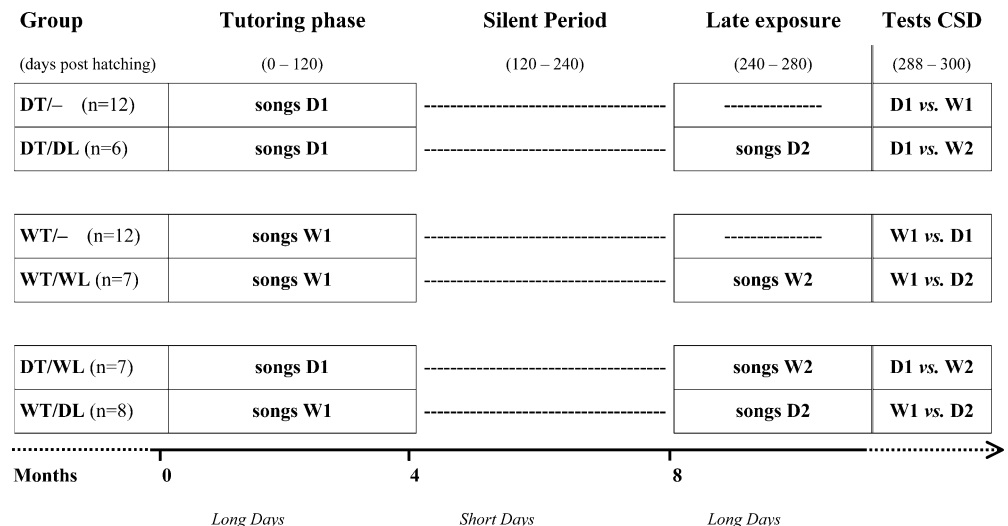
The aim of our study was to examine to what extent a late song playback exposure during the first reproductive cycles, without any social reinforcement, could stabilise or could interfere with further sexual preferences for songs in female domestic canaries.

Methods

General

In this study, 51 female domestic canaries *Serinus canaria* were raised and tested with domestic or wild canary songs between 1996 and 1999. These subjects belonged to an outbred form, of heterogeneous genetic background, of domesticated canary. Twenty-five females were raised in soundproof chambers by foster mothers and tape-tutored with domestic canary songs for 4 months (domestic tutoring: DT). Twenty-six females were tape-tutored with wild canary songs, for 4 months (wild tutoring: WT). When

Fig. 1 Outline of the experimental design. Groups: *DT/–*: females tutored with domestic songs and not exposed when adult. *WT/–*: females tutored with wild songs and not exposed when adult. *DT/DL* and *WT/WL*: females tutored and late exposed to the same category of songs (either domestic or wild). *DT/WL* and *WT/DL*: females early tutored and late exposed to songs of different categories. *n* number of females for each situation. *D1*, *W1*: domestic and wild song series used during the tutoring phase. *D2*, *W2*: domestic and wild song series used during the late exposure phase

Group	Tutoring phase	Silent Period	Late exposure	Tests CSD
(days post hatching)	(0 – 120)	(120 – 240)	(240 – 280)	(288 – 300)
DT/– (n=12)	**songs D1**	------------------------------------	--------------	**D1 *vs.* W1**
DT/DL (n=6)	**songs D1**	------------------------------------	**songs D2**	**D1 *vs.* W2**
WT/– (n=12)	**songs W1**	------------------------------------	--------------	**W1 *vs.* D1**
WT/WL (n=7)	**songs W1**	------------------------------------	**songs W2**	**W1 *vs.* D2**
DT/WL (n=7)	**songs D1**	------------------------------------	**songs W2**	**D1 *vs.* W2**
WT/DL (n=8)	**songs W1**	------------------------------------	**songs D2**	**W1 *vs.* D2**

Months   0   4   8

Long Days   *Short Days*   *Long Days*

8 months old, these females were distributed into six groups (Fig. 1); six females underwent a late exposition to domestic songs (DT/DL females); seven females were exposed to wild songs (DT/WL females); seven females underwent a late exposition to wild songs (WT/WL females); eight females were exposed to domestic songs (WT/DL females). The late exposure period lasted 40 days. Twelve domestic tutored (DT/– females) and 12 wild tutored females (WT/– females) were kept without song stimulation.

Females' sexual preferences were then assessed by measuring the number of CSDs (King and West 1977; West et al. 1979; Searcy et al. 1981).We scored the number of complete CSDs after Kreutzer and Vallet (1991) and Leboucher et al. (1994).

During the experiment, the birds were given seeds and water daily and fresh food and vitamins twice weekly.

Experimental songs

Experimental domestic and wild songs were made with phrases extracted from the repertoires of domestic and wild males and were computer-edited at 22.05 kHz (8 bits) with the Avisoft-SASLab Pro software (Specht 1990-2002). All song stimuli were then recorded on analog tapes by means of a Marantz PMD 201 recorder.

Four series of songs were elaborated (Fig. 2): two series of five domestic songs (D1 and D2) and two series of five wild songs (W1 and W2). The D1 and W1 series were used during the tutoring phase, while the D2 and W2 series were used during the late exposure phase (Fig. 1). The phrases of songs used during the tutoring and the late exposure phase came from repertoires of separate groups of males.

Domestic songs series (D1 and D2)

Each song consisted of six different phrases (each phrase lasting 2 s) from tape-recorded (with a tape recorder Marantz PMD 201 and a L. E.M. EMU 4535 microphone) songs of males living in our aviaries, making the duration of each domestic song 12 s. A song bout (SB) was made by the repetition, eight times on end, of the same song. In a SB, two consecutive songs were separated by a pause of 9 s. To build the song tape of one series, each of the five SBs was then repeated two times according to a randomly selected order (SB1-SB2-SB3-SB4-SB5-SB1-SB4-SB2-SB5-SB3). Thus, we obtained a song tape lasting about 30 min.

Wild songs series (W1 and W2)

Each song consisted of six different phrases (lasting 1 s) from tape-recorded songs of wild males, making the duration of each WT song 6 s. Wild canaries songs were recorded on Chão Island (Madeiran archipelago, Portugal) in 1996 and 1997 by S. Leitner and C Voigt (see Leitner et al. 2001 for technical details on recording procedure). A song bout (SB) was made by eight repetitions of the same wild song. In a SB, two consecutive songs were separated by a pause of 4.5 s. To build the song tape of one series, each of the five SBs was then repeated 4 times, thus obtaining a song tape lasting about 30 min.

Early song tutoring

Three to four fertile eggs were given to females incubating alone in single cages (35×24×20 cm) placed in sound attenuation chambers (65×50×80 cm inside, 95×102×110 cm outside). In each attenuation chamber, tape tutoring began 1 week after the first egg hatched. Tutoring songs (D1 or W1 series) were played daily (from 1100 to 1330 hours and from 1500 to 1730 hours) over 4 months (Fig. 1). Songs were played from tape-recorders Panasonic RQ-P202 (50–14000 Hz) over loudspeakers Karman SB780 (100–18000 Hz) placed in the attenuation chambers. Sound attenuation chambers were closed during acoustic exposure; no sound from outside the isolation chambers could be heard. When young were 1 month old, their foster mother was removed. At the end of the tutoring phase, the lighting regime was progressively changed to short days (8:16 h light:dark). Birds were maintained in this short daylight schedule for 4 months (Fig. 1). As soon as young males emitted subsongs they were removed from the sound attenuation chambers.
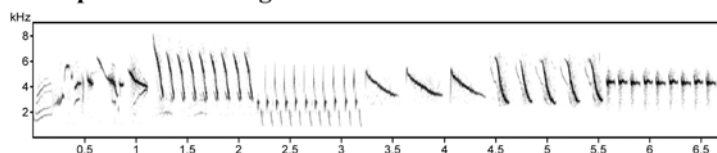
Late exposure period

When 8 months old, females reached sexual maturity. All the subjects were then housed in individual wire cages placed in attenuation chambers and provided with nest cups and nest material (cotton strings placed in a dispenser, renewed if necessary). Each attenuation chamber contained four individual cages; with adjacent cages separated by opaque partitions so that each animal could hear but not see the other three. This device minimised social influences, but avoided complete social deprivation. The animals were stimulated to breed by exposure to a photostimulatory lighting regime: 14:10 h light:dark (Follett et al. 1973; Hinde and Steel 1976).

The birds were exposed for 40 days to one of the two different acoustic conditions. The females respectively referred to as the DT/DL and WT/DL groups were exposed to the D2 series (Fig. 1). The females referred respectively to as the DT/WL and WT/WL groups were exposed to the W2 series. During this period the females built nests and laid eggs. During an equivalent period, DT/– and WT/– females were handled in similar conditions but were not exposed to songs.

Example of 'domestic' song:
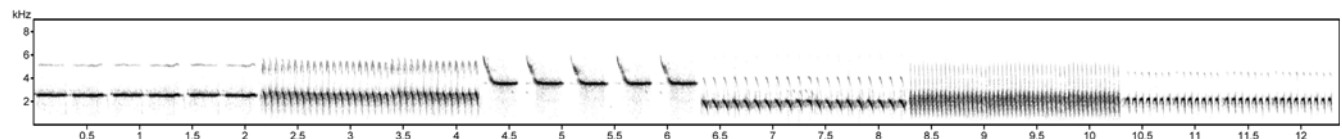
Example of 'wild' song:

Fig. 2 Examples of computer edited songs. Spectrograms were generated using a 22.05 kHz sampling rate and a 256 point FFT with Hamming windowing. See Methods for more details

Testing phase

After the 40-day late exposure phase all females were maintained in silence for 1 week. During this period, nest cups and nesting material were removed from the cages, in order to induce disruption of incubation (Goldsmith et al. 1984), then cups and nesting material were given back and females began a new reproductive cycle. Thus, the females became sexually receptive and could be tested for CSDs.

All the groups were tested according to the same general design. Two test sessions were carried out each day, between 1000 and 1800 hours (one in the morning and one in the afternoon) over 12 days, allowing a total of 24 sessions. Each song bout consisted of eight repetitions of the same song followed by a silent period of 10 s. Song bouts were separated by a 2-min delay and the order of presentation was randomised.

The songs series used for testing each group are detailed in Fig. 1.

Statistical analysis

Nonparametric statistics were used to analyse data (Siegel and Castellan 1988). Analyses were computed using statistical software (Sigmastat 2.03, SPSS Science). The females' preferences for either domestic or wild songs were evaluated with two-tailed Wilcoxon signed rank tests by comparing the number of CSDs given by each treatment group to wild and domestic songs.

Results

Data for each group are summarised in the Fig. 3. We tested separately the preferences of each group with Wilcoxon signed rank tests. The analysis indicated that DT/– females gave significantly more CSDs to domestic than to wild songs ($n=12$, $W=-66.0$, $T+=0.0$, $T-=-66.0$, $P=0.001$); females of the DT/DL group also preferred domestic to wild songs ($n=6$, $W=-21.0$, $T+=0.0$, $T-=-21.0$, $P=0.031$). In contrast, WT/WL females preferred wild songs ($n=7$, $W=-25.0$, $T+=1.5$, $T-=-26.5$, $P=0.031$) whereas WT/– females did not show a significant preference for wild songs ($n=12$, $W=28.0$, $T+=47.0$, $T-=-19.0$, $P=0.240$). In the case of DT/WL and WT/DL females, when late exposure condition did not match early condition, females failed to show any preference (DT/WL: $n=7$, $W=2.0$, $T+=11.5$, $T-=-9.5$, $P=0.844$; WT/DL: $n=8$, $W=6.0$, $T+=13.5$, $T-=-7.5$, $P=0.563$).

Discussion

Our data indicate that exposure to tape-recorded songs affects song preference exhibited later in a sexual context, and are consistent with several earlier works on other songbirds showing that female song preferences are influenced by acoustic experience (Baker 1983; Baker et al. 1987; Casey and Baker 1992). Moreover, the different early and late tutoring treatments of our experiment produced different effects upon female preference for domestic (D) or wild (W) song categories.

Both groups of domestic female canaries early tutored with D songs, and re-exposed when adult to songs of the same category (DT/DL) or not re-exposed (DT/–) showed a significant preference for their tutoring songs (Fig. 3a).
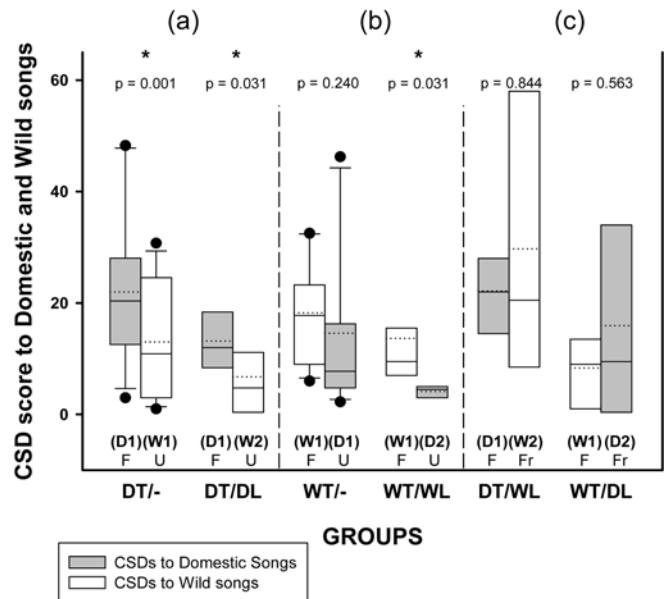
Fig. 3a–c Effect of early tutoring and late exposure to songs on sexual preferences. In the *box plots*, the *solid* and *dotted horizontal bars* denote respectively the median and mean number of CSDs given by females of the different groups to domestic and wild songs, the *box* denotes upper and lower quartiles, *vertical bars* indicate the interquartiles and *black dots* indicate the outliers. *D1, W1, D2* and *W2* in brackets beneath the boxes indicate the series of songs used for testing. *F* and *U* indicate if the test songs are familiar or unfamiliar. *Fr* indicates that the test song was familiar, but was heard more recently than the other one (see Fig. 1 and Methods). Statistical analysis: for each group: CSDs scores were compared with Wilcoxon signed rank tests; *P* are given with * indicating a significant difference

This result matches previous results of song tutoring experiments in female domestic canaries (Nagle and Kreutzer 1997a, 1997b; Depraz et al. 2000). It should be noted that these results were rather expected, because in this first part of our experiment, females were given a choice between familiar songs of domestic canaries and unfamiliar songs of wild canaries. Consequently, we might rationally suppose that females only exposed to one kind of song, domestic or wild, would prefer the familiar type. So it should also be expected that females of both the WT/– and WT/WL groups would prefer their familiar wild tutoring songs (W1) to unfamiliar songs (D1, D2). Our data partially failed to confirm such an expectation. Females early tutored with songs of the wild category and re-exposed to other songs of the same category (WT/WL) showed a significant preference for their tutoring songs. However, WT/– females did not show any preference (Fig. 3b). This result is comparable to a previous one, obtained in closely related experimental conditions (Depraz et al. 2000). In that study, females exposed early to wild songs failed, when adult, to choose between wild and domestic canary songs whether the songs were familiar or not (Depraz et al. 2000). In the present study, the result of the WT/WL females (Fig. 3b) suggests that females early tutored with a song category differing from the songs produced by the males of their own strain need a subsequent re-exposure with new

specimens of songs of the 'alien' strain in order to become able to discriminate between them and unfamiliar songs belonging to their own strain. However, it remains possible that a longer exposure at the beginning of their life or an exposure to more various songs specimens would result in more clear-cut preferences

Our experiment also assessed the effect of a 4-month early tutoring with songs belonging to one category, followed by a 40-day late exposure at early adulthood with songs of the other category. It also addressed the question of whether the exposure order (D then W or W then D) could influence females' subsequent preferences. In this case, our data indicate that whatever the exposure order, females whose songs used during early tutoring and late exposure phases belonged to different categories failed to choose between songs heard during their infancy and songs they had recently heard (Fig. 3c). The failure of the WT/DL group in choosing was expected, since earlier results have already indicated that females tutored with songs of an alien strain were unable to show later a sexual preference (Depraz et al. 2000; this study: group WT/–). However, the females of the DT/WL group, early tutored with songs of their own strain and re-exposed, when adult, to W songs, failed to show any preference. In this case, the early 'adequate' exposure to songs of their own strain failed to crystallise the females' subsequent preferences. Moreover, we should bear in mind that the canary is an open-ended learner species, in terms of song performance learning. This ability in adult male canaries would probably correspond to plasticity in female discriminating song learning. One may suppose that, even if all their test songs were familiar, females' responses should have been influenced by a recency effect, but our experiment was not designed to test this hypothesis. Moreover, some findings in the field of song preferences and mate choice suggest that processes different from familiarisation are implied in the determination of song preferences in adult female canaries (e.g. Béguin et al. 1998). Thus, further work is required to confirm or discard the hypothesis of a recency effect.

In addition to the familiarity and recency effects, our study could not control for all possible differential and social influences during early song tutoring, such as mother and sibling effects, known to be a possible confounding factor in sexual imprinting in zebra finches (ten Cate 1982, 1984, 1994; Kruijt et al. 1983 ten Cate and Mug 1984). It must also be pointed out that our 'wild' song stimuli are representative only of a part of the population of the Madeiran archipelago and not of the whole wild species, in which some differences occur from one archipelago to another (Mundinger 1999). Reciprocal experiments with young Island (wild) female canaries, representative of the whole population, and experiments using cross-fostering and siblings could help in understanding the mechanisms underlying the ontogenesis of female sexual preferences for songs.

As a whole, our results indicate that late exposure at the beginning of the first breeding season allows stabilisation or emergence of preferences or, in contrast, can interfere with these early preferences, depending on whether the song category used during the late exposure phase matched or not that used during the early tutoring phase. Our results are also consistent with data recently obtained by MacDougall-Shackleton et al. (2001). They studied the effect of early song learning on behavioural responses to song in adulthood in female mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*). In their experiment, juvenile females were captured before they had dispersed from their natal region. When they were 1 year old, natal-dialect song, foreign-dialect song, and heterospecific song were played back to the birds during photostimulation. Later on, when the birds were 2 years old, behavioural responses (CSDs) to the same songs were measured. The birds showed a clear preference for natal-dialect song, exhibiting more displays to natal-dialect song than to foreign-dialect or heterospecific song. However, the authors found that this effect was attenuated in birds that had heard heterospecific or foreign-dialect song when they were 1 year old (MacDougall-Shackleton et al. 2001). The authors suggested that the song playback during the late exposure would correspond to a female sparrow's first breeding season. They added that female white-crowned sparrows disperse farther than males do (Morton et al. 1972; Morton 1992) and that it is likely that an adaptive mechanism allows females who settle in non-natal dialect song areas to learn during their first breeding season and modify their song preferences (MacDougall-Shackleton et al. 2001). Canaries could follow the same pattern of dispersal, since females of the closest species in the genus *Serinus* (Arnaiz-Villena et al. 1999), the common serin (*S. serinus*), seem also to disperse more than males (Mota 1995).

In addition, Collins (1995) reported that the lone recent visual experience affected female preference for a male in zebra finches. She suggested that females had an internal standard for a particular choice criterion with which males are compared; this standard might be adjusted with respect to the recent experience of the females. This behavioural plasticity could help young adult females to adjust the standard built during infancy to changing environmental conditions such as dispersal or adaptation to males' shifts in song repertoire (Nottebohm et al. 1986).

Recent studies in the field of behavioural ecology have demonstrated that females may adjust their sexual preferences, including acoustic preferences, according to their reproductive experience (O'Loghlen and Beecher 1999). Likewise, adult female canaries were found to modify their sexual preferences for conspecific songs: Béguin et al. (1998) also established that reproductive experience affected adult sexual preferences for one individual's song. Nagle and Kreutzer (1997a) showed that adult female canaries early tutored with a wild canary song, and showing a clear preference for this song, enlarged their preferences after being paired for 6 months with a male domestic canary. However, in the present study, in contrast to the former ones, changes in females' preferences occurred without any social reinforcement,

further to the lone acoustic stimulation occurring at the beginning of the females' first breeding season.

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