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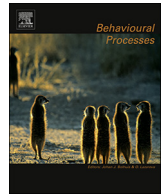
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# Consistency of female preference for male song in the domestic canary using two measures: Operant conditioning and vocal response



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## ABSTRACT

Variation of female preferences is often reported in the literature and could be related to an artefact derived from multiple different methods used. Thus, there is a need to evaluate the influence of different methods when assessing female preferences. The present study aims to compare female preferences obtained from an operant conditioning test and from female vocal responses to male song in the domestic canary (*Serinus canaria*). In an operant conditioning test, females had the possibility to choose between two keys; a peck on one key elicited a supposed very attractive canary song while a peck on the other key elicited a less attractive song. Meanwhile, female vocal responses were recorded. Our results revealed that female canaries preferred to peck on the key eliciting the attractive song and that they emitted more copulation calls in response to the attractive song compared to the less attractive song. This study shows the congruence of these two methods and further suggests that they are reliable to study female preferences in laboratory conditions.

## 1. Introduction

It is generally assumed that sexual selection operates through several mechanisms such as contests, coercion, sperm competition or mate choice (Andersson and Iwasa, 1996). Sexual selection is extensively studied but there is no consensus on how sexual selection is accurately evaluated (Fritzsche and Booksmythe, 2013). The relation between variation of a phenotypic trait and variation in reproductive success seems the most direct measure (Andersson, 1994) but measuring reproductive success is often difficult to achieve and does not allow to separate the contributions of the pre- and post-copulatory mechanisms (Fritzsche and Booksmythe, 2013). Instead, proxies of reproductive success have been used by a large number of studies which aimed at assessing female preferences for a male trait since these preferences could predict their future mate choice (Aspbury and Basolo, 2002; Cummings and Mollaghan, 2006; Lehtonen and Lindström, 2008).

Songbirds are among the most studied organisms to investigate sexual selection and there is strong evidence that male song plays a major role for female choice (e.g. Catchpole, 1987; Searcy and Yasukawa, 1996). Several methods have been used to assess female preferences in the field or in laboratory conditions such as phonotaxis in response to live males or male songs (Forstmeier and Birkhead, 2004; Holveck and Riebel, 2007), cardiac responses during song playbacks (Ikebuchi et al., 2003), the copulation solicitation display assay (King

and West, 1977; Leboucher et al., 1994) and vocal responses to song playback (Nagle et al., 2002; Amy et al., 2015). Among these, the Copulation Solicitation Display (CSD) assay is perhaps the most reliable measure of female preferences; the more a female gives copulation solicitation displays towards a male (or a song), the more she should prefer this male (or song). The CSD assay has been successfully applied in at least 20 species (See table 1 in Searcy, 1992) but this often required the use of oestradiol treatment in some species (Searcy and Marler, 1981; Searcy, 1992; Anderson, 2009). Some studies described the same pattern of females' responses to the preferred songs with vocalizations (Nagle et al., 2002; Amy et al., 2015) as the CSD assay: females emitted more vocalizations to the preferred songs.

An alternative method for testing female preferences to male songs is the operant conditioning procedure (e.g. Riebel et al., 2002). Here, male song acts as a reinforcer and females should more frequently activate the playback of their preferred song (Riebel and Slater, 1998). Operant conditioning tests can be considered reliable since females express their preferences through an active choice. Yet, operant conditioning can lead to a less direct measure of female preferences than measures of copulation solicitation (Anderson, 2009) or vocal responses. Moreover, variation of female preferences reported in the literature could be related to an artefact derived from multiple different methods used to measure the female preferences (Wagner, 1998) and there is a need to evaluate the influence of different methods when

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assessing female preferences. To our knowledge, few studies have compared operant conditioning with others methods. One study showed that female preferences were consistent across operant conditioning, phonotaxis and spatial association tests (Holveck and Riebel, 2007) while another one showed a strong congruence between the operant conditioning and the copulation solicitation display assay (Anderson, 2009). To date, we do not know if female copulation calls in birds (Amy et al., 2018) and operant conditioning lead to consistent assessment of female preferences.

Female preferences for male songs are well known in the domestic canary (*Serinus canaria*) and the CSD assay was extensively used to assess these preferences. During a CSD, the female canary arches her back, crouches and simultaneously brings her head back and her tail forward, moves her wings away from the body and vibrates the wings and the cloaca (Kreutzer and Vallet, 1991). Female canaries produce more CSDs for a male canary song containing a particular phrase named “A-phrase” (or “sexy phrase”) (Vallet and Kreutzer, 1995; Vallet et al., 1998). This A-phrase contains two distinctive notes repeated at a high rate (more than 15 syllables  $s^{-1}$ ) (Vallet et al., 1997) with rapid frequency modulation and this phrase is very attractive and elicits strong sexual responses by female canaries (Vallet and Kreutzer, 1995; Vallet et al., 1998). In general, females produce more CSDs for male songs maximizing both frequency bandwidth and syllable rates (Drăgănoiu et al., 2002). Moreover, in a recent study, Amy et al. (2015) showed that females also emitted a particular vocalization named Female-Specific Trills (FST) during songs containing A-phrases and they showed a strong positive correlation between the occurrence of CSDs and the occurrence of FSTs; these FSTs are likely to function as copulation calls (Amy et al., 2015). Thereby, domestic canaries are a good model to compare the consistency of female preferences to male song by using different measures. To this end, we tested female canaries with an operant conditioning paradigm and we quantified female vocalizations in response to songs broadcast during this test. We used FSTs emitted by the female rather than CSDs for two reasons: a) because FSTs are more frequent than CSDs during repeated stimulations (Amy et al., 2015) and are thus easier to count and b) because continuous recordings of female vocalizations required less storage than continuous recordings of videos.

The operant conditioning apparatus used was analogous to those used in previous studies (Riebel and Slater, 1998; Riebel, 2000; Holveck and Riebel, 2007). Females had the possibility to choose between two keys. When they pecked on one key, a very attractive song was broadcast. When they pecked on the other key, a less attractive song was broadcast. To compare key pecks to vocal responses, we measured the copulation calls (i.e. FSTs in Amy et al., 2015) emitted by the females during the playback of song triggered by the first peck on each key each day, since female domestic canaries responded more to the first playback of song than the second playback and even more than the third playback (Amy et al., 2015). We expected that females would peck more on keys broadcasting the very attractive songs than keys broadcasting the less attractive songs and that females would emit more copulation calls for very attractive songs than for less attractive songs.

## 2. Material and method

### 2.1. Ethical note

Experimental conditions were approved under the license number APAFiS #392 by the Charles Darwin ethic committee and were in line with the guidelines of the Association for the Study of Animal Behaviour (ASAB). Before and after the experiment, females were maintained in social groups. During the experiment, females were maintained individually in sound-proof chambers. Animal caretakers and the experimenters examined the birds by sight several times a day (two times per day minimum) to avoid any sign of distress or discomfort, and to be sure of their well being.

### 2.2. Subjects, breeding conditions and general protocol

For this study, we tested 25 naïve females domestic canaries (> 10 months old at the beginning of the experiment) obtained from a breeder (Animal Diffusion). Before the experiment, all females were maintained in social groups in aviaries (118 × 50 × 50 cm), on a short-day photoperiod (8 L : 16 D) for 6 months. At the beginning of the experiment, females were placed in individual cages (38 × 22 × 26 cm), equipped with two perches, nest bowls and nesting material, in a room on a long-day photoperiod (16L:8D; Leboucher et al., 1994). Females were first tested for their sexual receptivity (see subsection 2.3). Once receptive, a female was placed in the double choice test apparatus for 12 consecutive days. This apparatus was a cage (38 × 22 × 26 cm) equipped for double choice test (see subsection 2.4.). This cage was placed in a sound-proof chamber (internal dimensions: 70 × 51 × 51 cm) on a long-day photoperiod. During the 12 days of the double choice test, females could not interact with each other. During the test for sexual receptivity and the double choice test, females were provided with water and seeds ad libitum, with breeding food twice a week, nesting material and cuttlebones as a source of calcium. After the experiments, females were moved to a common aviary.

### 2.3. Test for sexual receptivity

Every morning, between 10:00 and 11:00 am, females were exposed to one minute of male songs repeated two times with two minutes of silence between the repetitions. These male songs contained several G-phrases (referring to scale categories of increasing bandwidth; Drăgănoiu et al., 2002; Pasteau et al., 2007), but no A-phrase, broadcasted with a loudspeaker (Ultimate Ears Boom 2) connected to a digital audio player able to play WAV files (Philips Gogear). Responses of females were recorded through webcams (Logitech Carl Zeiss Tessar HD 1080p) and videos were monitored to assess females’ sexual receptivity. When a female exhibited a CSD, we considered her as a receptive female, and we placed her in an operant conditioning apparatus. Only 18 females showed sexual receptivity and were therefore tested in the operant conditioning apparatus (double choice test; see subsection 2.4). Eleven out of these eighteen females built a nest and laid at least one egg during the experimental phase.

### 2.4. Double choice test apparatus

Two red response keys (1 cm in diameter) were mounted on one side of the cage. The female could peck on one or the other key only from the first perch or the fourth perch (see Fig. 1). The pecking on the keys triggered the playback of the song assigned to the key. A loudspeaker (Elipson Mini Horus Sat), amplified by a stereo amplifier (Pioneer A-209R), was placed in front of the cage in the middle of these two response keys. A webcam (Logitech Carl Zeiss Tessar HD 1080p), placed in a corner of the sound-proof chamber allowed the observers to record and to watch the behaviour of the tested bird without disturbing her. A

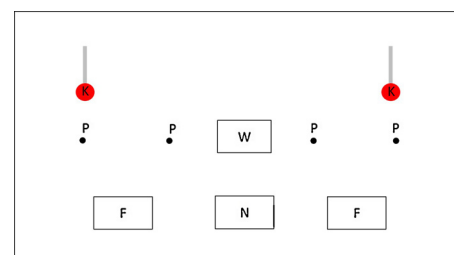


Fig. 1. Schematic representation (side view) of the operant conditioning apparatus. The two keys, the four perches and the water were mounted on the back side of the cage. The two feeders and the nest were mounted on the front side of the cage. K: key, P: perch, W: water, F: feeder, N: nest.

microphone (Behringer C-2), was located above the loudspeaker and recorded the vocalizations of the tested bird continuously. All cages were symmetric. See Fig. 1.

All apparatus were controlled individually and automatically by a computer (HP Compaq Elite 8300 Convertible Microtower working under Windows 7), using SAP (Sound Analysis Pro 2011; Ofer Tchernichovski, Elena Kashtelyan & David Swigger) and My SQL. SAP was used to play the song assigned to the key through the loudspeaker in each sound-proof chamber and to continuously record the vocalizations of the tested bird through the microphone. Data (time of key peck, ID of the key pecked) were saved in My SQL tables.

## 2.5. Stimuli

We used two types of stimuli: A20 song types containing a very attractive phrase with two distinctive notes repeated at a rhythm of 20 syllables  $s^{-1}$  (A20) and A10 song types containing a moderately attractive phrase with two distinctive notes repeated at a rhythm of 10 syllables  $s^{-1}$  (A10) (Amy et al., 2015). Sixteen songs of male canaries were recorded during the preceding years in our laboratory. The digitalization and construction of the song files was done with Avisoft SASLAB-PRO software (Raimund Specht, Berlin, Germany) with a sample frequency of 22,050 Hz. From these sixteen canary songs, we constructed A20 song types as follows: the song lasted 6 s with two introductory notes (0.75 s), then one very attractive phrase with two distinctive notes repeated at a rhythm of 20 syllables  $s^{-1}$  (1.50 s) and six conclusive notes (3.75 s). Then we used these sixteen A20 song types to generate sixteen A10 song types with a moderately attractive phrase with two distinctive notes repeated at a rhythm of 10 syllables  $s^{-1}$  (with the same frequency bandwidth as A20 song types). See Fig. 2 for sonograms. All songs were passed through a band pass filter (0.8–8 KHz) and adjusted to the same amplitude; each song was manually standardized to the same amplitude by using amplitude envelope. All songs were played back at the standardized level of 65 dB (measured with a Ro-LINE SPL meter 1, using A-weighting, at the typical position of the test bird, 30 cm from the loudspeaker). Finally, a A20 song and a A10 song were assigned to each bird and the combination of the A20

song and the A10 song was different for each female. For each tested bird, the A20 song and the A10 song were not built from the same original song.

## 2.6. Double choice test and analyses

The double choice test lasted 12 consecutive days. Song types were switched between keys daily to control for a possible side bias. The first day, ten seeds were scotch-taped on each key to attract the female towards the keys. If the female pecked the keys 6 times (Houx et ten Cate, 1999) within the first two days, seeds were removed from the keys. If not, we continued to scotch-tape seeds on each key and the female was trained for 15 min between 14:00 and 16:00. During this training, the female was observed through the webcam in the sound-proof chamber and the experimenter played the song assigned to the key each time the female approached, explored or touched the key. The key pecks during trainings were not included in the total number of key pecks. This training method was similar to that used in previous studies (Houx and ten Cate, 1999; Holveck and Riebel, 2007). The training lasted for a maximum of 4 consecutive days until the female willingly pecked on a key during a training session.

At the end of the 12 consecutive days of test, female canaries pecked  $4624 \pm 1070$  (mean  $\pm$  se) times on keys. In order to analyse the preferences of the females, we extracted the number of key pecks for each side and for each type of song and we calculated 1) the preference ratio per female for a song type: total number of the key pecks for the A20 song divided by the total number of pecks on the two keys, 2) the preference ratio per female for a key-side: total number of pecking on the right key divided by the total number of pecks on the two keys. Then, for the eighteen females, we calculated the mean of preference ratios for 1) the A20 song type and 2) the right key. We compared these means of preference ratios as a deviation from 0.5 using a one sample *t*-test. Data analysis was done using R v. 2.7.1 (R Development Core Team 2008).

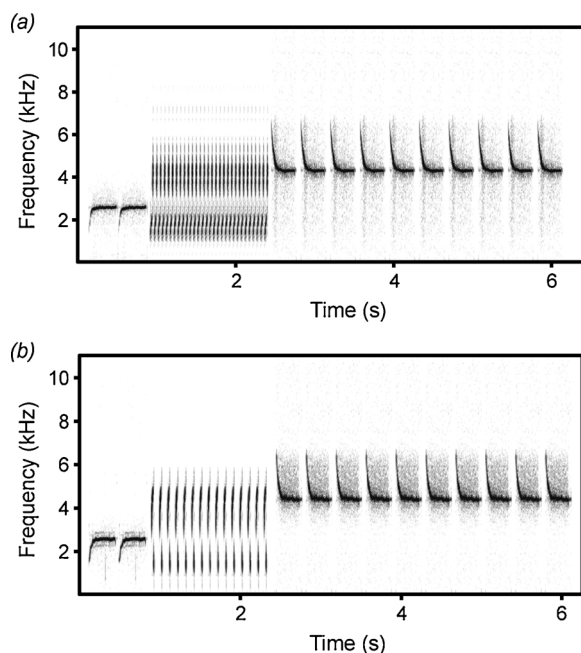
Using visual inspection of sound spectrograms (Avisoft SASLAB-PRO software; Raimund Specht, Berlin, Germany), we measured the number of copulation calls (i.e. FSTs described in Amy et al., 2015) emitted by the female during the first playback of each song type each day. We compared the total number of FSTs given by the females to the A20 songs to the total number of FSTs given to the A10 songs using a paired *t*-test. Then, to assess if the operant conditioning test truly reflects a preference for the A20 songs, and is not skewed by spatial preferences, we compared the total number of FSTs given after having pecked on the left key to the total number of FSTs given after having pecked on the right key, using a paired *t*-test. Data analysis was done using R v. 2.7.1 (R Development Core Team 2008). At last, to assess if the uttering of copulation call was related to the motivation to peck on the keys associated with the different songs, we tested the relationships between a) the number of key pecks on the A20 songs and the number of FSTs given in response to the A20 songs and b) the number of key pecks on the A10 songs and the number of FSTs given in response to the A10 songs, with Spearman correlations.

## 3. Results

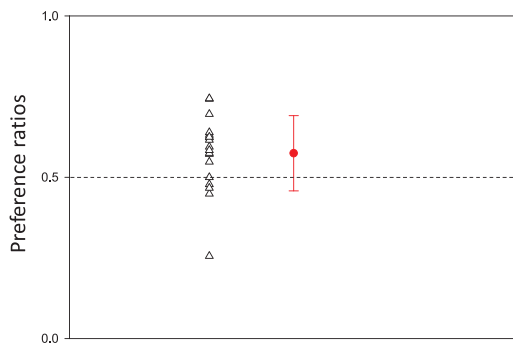
Females pecked significantly more often on the key eliciting an A20-song (mean preference ratios  $\pm$  se =  $0.57 \pm 0.03$ ) than on the key eliciting a A10-song: the overall number of key pecks on A20 song was significantly greater than chance (one sample *t*-test;  $t = 2.711$ ;  $p = 0.015$ ;  $n = 18$ ). (Fig. 3)

Females pecked significantly more often on the right key (mean preference ratios  $\pm$  se =  $0.61 \pm 0.05$ ) than on the left key: the overall number of key pecks on the right key was significantly greater than chance (one sample *t*-test;  $p = 0.038$ ;  $t = 2.255$ ;  $n = 18$ ). (Fig. 4)

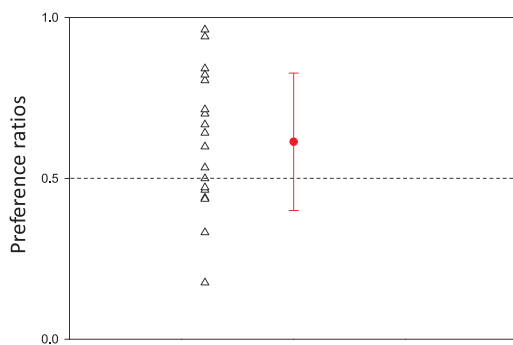
Fifteen out of 18 females emitted at least one copulation call in response to the first playback of each song type during the 12



**Fig. 2.** Sonograms of different types of broadcasted songs. Sonograms of a canary song containing an attractive phrase with two distinctive notes repeated at a rhythm of (a) 20 syllables  $s^{-1}$  (A20) and (b) 10 syllables  $s^{-1}$  (A10). A20 and A10 syllables covered the same frequency bandwidth.



**Fig. 3.** Preference ratio for A20-songs over A10-songs. Triangles represent each female preference ratio; the red circle represents the mean preference ratio. Mean preference ratio was significantly different from a 0.5 (dashed line) preference ratio (one sample t-test,  $p < 0.05$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



**Fig. 4.** Preference ratio for the right key over the left key. Triangles represent each female preference ratio; the red circle represents the mean preference ratio. Mean preference ratio was significantly different from a 0.5 (dashed line) preference ratio (one sample t-test,  $p < 0.05$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

consecutive days spent in the double choice test. Females emitted significantly more copulation calls during the playback of the A20 song type than to the A10 song type (paired t-test;  $p = 0.012$ ;  $t = 2.832$ ;  $n = 18$ ). (Fig. 5a). Females did not emit significantly more copulation calls after having pecked on the left key compared to the right key (paired t-test;  $p = 0.469$ ;  $t = -0.741$ ;  $n = 18$ ). (Fig. 5b).

There was a positive correlation between the number of key pecks for the A20 songs and the number of FSTs given to the A20 songs ( $r = 0.60$ ;  $p < 0.01$ ;  $n = 18$ ) (Fig. 6a) and between the number of key pecks for the A10 songs and the number of FSTs given to the A10 songs

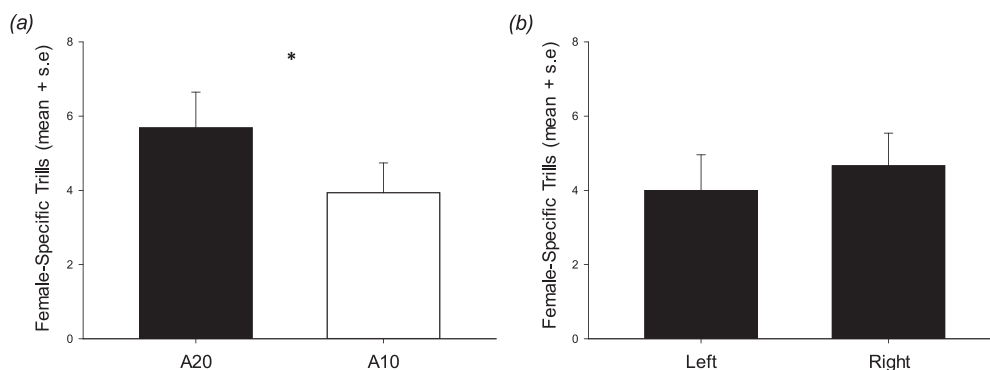
( $r = 0.74$ ;  $p < 0.001$ ;  $n = 18$ ) (Fig. 6b) during the first daily pecks.

#### 4. Discussion

Between-study differences in female mating preferences could be related to an artefact derived from multiple different methods used to access female preferences (Wagner, 1998) and a comparison of different methods was needed. In the present study, female domestic canaries showed a clear preference for A20 songs compared to A10 songs regardless of whether this preference was measured with the number of copulation calls or with the number of key pecks though most females showed a side bias in the double choice test. Moreover, there was a positive correlation between the number of key pecks and the number of FSTs emitted during the first daily song playback, regardless of the song type.

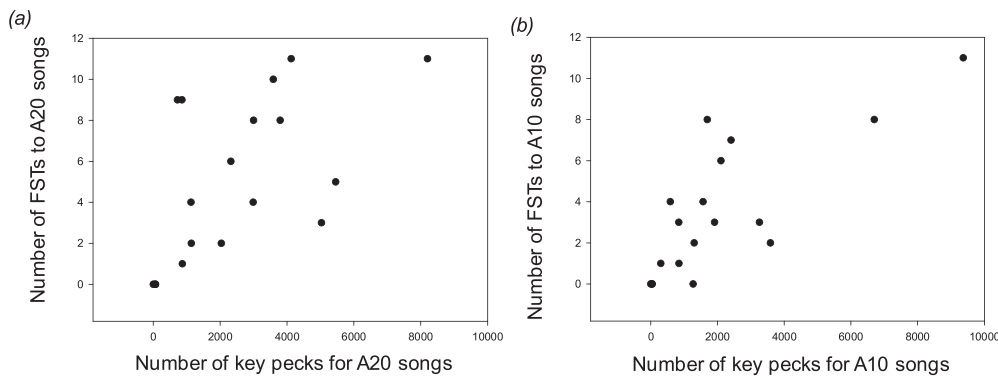
Female domestic canaries strongly prefer particular elements of male song: a phrase consisting of the sustained repetition of a two-notes syllable with a large frequency bandwidth (i.e. ‘A-phrase’ or ‘sexy-phrase’; Vallet and Kreutzer, 1995; Vallet et al., 1998). These preferences were historically discovered by the use of the copulation solicitation assay and this method was subsequently used to study female canaries’ preferences for male song (e.g. Pasteau et al., 2009a, b; Pasteau et al., 2007). Besides, alternative methods were consistent with the copulation solicitation assay such as the analysis of female vocalizations (Nagle et al., 2002; Amy et al., 2015). Amy and collaborators (2015) showed that female canaries often combine a display and a call to solicit copulation and that these copulation calls (i.e. FST in Amy et al., 2015) were expressed similarly to CSDs: both of them were more emitted in response to the A20-song type than in response to the A10-song type. In the present study, females emitted more copulation calls to A20-songs compared to A10-songs and it thus confirms that female canaries express their preferences with copulation calls. In addition, our experiment further shows that operant conditioning (here a double choice test) reveals the same preferences as female canaries pecked more on the key eliciting the A20-song than on the key eliciting the A10-song. Though the two measures (number of key pecks and number of copulation solicitation calls) were not completely independent from each other, as females triggered their own response, we are confident that operant conditioning could be a suitable tool to assess female preferences in domestic canaries.

Our results are in line with previous studies investigating the reliability of operant conditioning as a tool for measuring female preferences. In the zebra finch (*Taeniopygia guttata*), female preferences revealed by the operant conditioning test were consistent with those of a phonotaxis test as well as an association test (Holveck and Riebel, 2007). In the swamp sparrow (*Melospiza georgiana*), the operant conditioning test revealed the same female preferences as the copulation solicitation assay (Anderson, 2009). Combined with these two studies, our experiment adds to the growing evidence of the reliability and the



**Fig. 5.** Female-Specific Trills in response to a) the playback of A20- and A10-song types and b) the peck on the left and the right keys, triggered by the first peck on each key each day. Paired t-test, \*  $p < 0.05$ .





**Fig. 6.** Relationships between the number of key pecks for the different types of songs and the number of FSTs given in response to these songs. (a) Positive correlation between the number of key pecks for the A20 songs and the number of FSTs given to the A20 songs (Spearman correlation,  $p < 0.01$ ;  $n = 18$ ). (b) Positive correlation between the number of key pecks for the A10 songs and the number of FSTs given to the A10 songs (Spearman correlation,  $p < 0.001$ ;  $n = 18$ ) during the first daily pecks.

congruence of the methods used in laboratory conditions to study female preferences.

Operant conditioning presents several advantages. First, the female preferences could be measured without video and/or sound recordings and, thereby, without analysis of copulation solicitation displays and/or vocalizations as required in other methods (e.g. Nagle et al., 2002; Drăgănoiu et al., 2002; Amy et al., 2008, 2015). In addition, Anderson (2009) demonstrated that some females that did not perform CSD did respond in the operant conditioning assay and showed preferences for the same song type than other females. Even if the current experiment did not test unreceptive females, operant conditioning could be further used to assess preferences of unresponsive female canaries such as females being out of a reproductive cycle or before sexual maturity. Lastly, females make an active choice continually rewarded by a song in an operant conditioning test (Stevenson, 1967) while they are mainly passive in other methods. In our experiment, female canaries were highly motivated to listen to male song as shown by the amount of key-pecks, especially because the amount of key-pecks was correlated with the number of copulation calls (FSTs) regardless of the song type. Hence, their preferences revealed by the operant conditioning seem reliable and these results confirmed that songs functioned as a reinforcer (Stevenson, 1967).

Our experiment also revealed that almost all females showed a preference for one or the other key-side (though they generally pecked more on the right key) but copulation calls were not emitted more often after having pecked on the right or on the left key. Other studies in songbirds have reported side biases in double choice tests such as in female chaffinches (*Fringilla coelebs*; Riebel and Slater, 1998) or in Cape sugarbirds (*Promerops cafer*) and in lesser double-collared sunbirds (*Nectarinia chalybea*) (Jackson and Nicolson, 1998). Side biases in motor behaviour or perception could be related to a lateralization bias of the brain (Rogers, 2002a). To our knowledge, there is no research on lateralization biases in the domestic canary, except for the lateralization of the song production which is well documented (see review Nottebohm, 1980; Hartley and Suthers, 1990; Suthers et al., 2004). Yet, lateralization biases are widespread in vertebrates (see review Rogers, 2002b) and, in birds, a lateralization bias has been reported in several types of tasks (Fersen and Güntürkün, 1990; Prior et al., 2004) as well as in motor patterns (Rogers and Workman, 1993; Casey and Martino, 2000; Dharmaretnam et al., 2002) which may be influenced by prenatal visual experience (Casey and Karpinski, 1999) and by postnatal lateralized eye preferences (Casey, 2005). Despite the side bias in our experiment, the female canaries clearly preferred the A20 song type over the A10 song type. However, these two stimuli were well contrasted and further researches are needed to determine if a side bias could mask female preferences to less contrasted stimuli.

To conclude, this study shows the congruence of two measures when assessing preferences of female canaries; operant conditioning and vocal response both revealed that female canaries prefer songs with the higher repetition rate of the ‘sexy syllable’ (Drăgănoiu et al., 2002). Both measures seem reliable to study female preferences in laboratory

conditions.

#### Declarations of interest

None.

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