



## AVIARY EXPERIENCE HAS NO EFFECT ON PREDISPOSITION OF FEMALE COMMON CANARIES (*SERINUS CANARIA*) FOR LONGER SEXY PHRASES

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**ABSTRACT.**—We tested female Common Canaries' (*Serinus canaria*) preferences for “sexy phrases” of different durations. Two groups were used: (1) females raised in acoustic isolation and (2) females raised in “normal” acoustic conditions. We presented sexy phrases to both groups and counted their copulation-solicitation displays to determine their preference for the length of these stimuli. Females of both groups gave more copulation-solicitation displays in response to the longest sexy phrases presented. Our results indicate that the duration of sexy phrases is an important acoustic cue for female Common Canaries, as is total song duration in many species; this preference can be explained by theories of sexual selection. Moreover, responses of both experienced and inexperienced females are similar, which indicates that experience does not influence the females' preference for long sexy phrases. These preferences could come from predispositions, as is the case for many acoustic parameters of sexy phrases. Received 24 May 2008, accepted 18 December 2008.

**Key words:** Common Canary, copulation-solicitation display, female preference, male song, mate choice, predisposition, *Serinus canaria*, sexual experience, song experience.

### L'expérience acquise en volière par les femelles de *Serinus canaria* n'a pas d'influence sur leurs prédispositions pour de longues phrases sexy

**RÉSUMÉ.**—Au cours de cette expérience, nous avons testé les préférences de femelles de *Serinus canaria* pour des phrases sexy de durées variables. Deux groupes ont été utilisés : (1) le premier se composait de femelles élevées en isolement acoustique et (2) le second, de femelles élevées dans des conditions acoustiques « normales ». Nous avons utilisé les postures de sollicitation à l'accouplement comme index comportemental pour déterminer les préférences de ces femelles pour la durée des stimuli. Les deux groupes ont réalisé plus de postures en réponse aux phrases sexy les plus longues proposées. Ces résultats indiquent que la durée de ces phrases est un paramètre acoustique important pour les femelles *S. canaria*, au même titre que la durée totale du chant chez d'autres espèces ; cette préférence entre ainsi dans le cadre de plusieurs théories de la sélection sexuelle. Par ailleurs, que les femelles soient élevées en isolement acoustique ou dans des conditions acoustiques « normales », leurs réponses sont similaires et indiquent la faible influence de l'expérience sur les préférences des femelles pour la durée des phrases sexy. Ces préférences sont très certainement issues de prédispositions, comme c'est le cas pour de nombreux paramètres acoustiques de ce type de phrases.

MALE SONG HAS two principal functions in songbirds: attracting and stimulating females, and defending territories (Kroodsma and Byers 1991, Catchpole and Slater 1995, Searcy and Yasukawa 1996). Studies of many species have shown that males use different types of song for each function. Longer songs generally seem to be used for intersexual relations, whereas shorter songs are more often used in intrasexual interactions (Catchpole and Slater 1995). Moreover, song-diffusion experiments have demonstrated that male and female Great Reed Warblers (*Acrocephalus arundinaceus*) behave differently toward playbacks of long and short songs (Catchpole et al. 1986). In some species, including Great Reed Warbler (Catchpole et al. 1986), Zebra Finch

(*Taeniopygia guttata*; Clayton and Pröve 1989, Balzer and Williams 1998, Neubauer 1999), White-rumped Munia (*Lonchura striata*; Clayton and Pröve 1989), White-throated Sparrow (*Zonotrichia albicollis*; Wasserman and Cigliano 1991), House Finch (*Carpodacus mexicanus*; Nolan and Hill 2004), and Blue Tit (*Parus caeruleus*; Kempenaers et al. 1997), females prefer longer songs. In Common Canary (*Serinus canaria*; hereafter “canary”), a particular category of song phrases stimulates females more than other phrases (Vallet and Kreutzer 1995, Vallet et al. 1998). These so-called “sexy phrases” are composed of two-note syllables that cover a large bandwidth and are emitted at a high rate.

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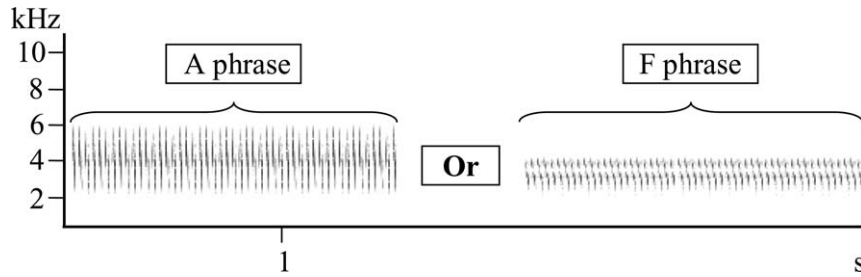


FIG. 1. Examples of A and F phrases. The A phrase has a frequency bandwidth of 4 kHz located between 2 and 6 kHz, whereas the F phrase has a frequency bandwidth of 2 kHz located between 2 and 4 kHz. These two phrases have a rate of 20 syllables  $s^{-1}$ .

Considering that females of many species prefer longer male songs and that female canaries are especially attracted to sexy phrases, we decided to test female canaries' preference for the duration of sexy phrases. Because emission of sexy phrases requires vocal motor constraints in males, they are considered honest signals for females (Vallet et al. 1997). Therefore, we predicted that female canaries would prefer longer sexy phrases, not only because females of many other species do, but because longer phrases are more difficult for males to produce. Moreover, two types of sexy phrases exist: "A" phrases, with a frequency bandwidth of 4 kHz, and "F" phrases, with a frequency bandwidth of 2 kHz (Fig. 1; Drăgănoiu et al. 2002, Pasteau et al. 2007). Previous studies have shown that A phrases provoke more copulation-solicitation displays (CSDs) in female canaries than F phrases, though the latter are also important acoustic cues (Drăgănoiu et al. 2002). Therefore, we tested females' responses to three durations of each type of sexy phrase: 1.0, 1.5, and 2.0 s. This reflects the males' natural production of sexy phrases, which last 1.5 s, on average (Vallet et al. 1998). The behavioral index used to test female preferences is the number of CSDs (King and West 1977, Searcy and Marler 1981, Kreutzer and Vallet 1991, Searcy 1992).

Finally, another peculiarity of female canaries is their predisposition for certain male songs (Drăgănoiu et al. 2002). Indeed, females discriminate individual canary song (Nagle and Kreutzer 1997a, b) and prefer certain acoustic parameters that define "sexy phrases," such as their fast rate, syllable complexity, and large bandwidth (Drăgănoiu et al. 2002; Pasteau et al. 2004, 2007, 2009). It has been observed that song diffusion during an individual's early life, adult acoustic experience, and sexual experience can independently modify such predispositions, particularly those for species song (Nagle and Kreutzer 1997a, b; Depraz et al. 2000) and frequency bandwidths of sexy phrases (Drăgănoiu et al. 2002). In addition, it has been demonstrated that female Zebra Finches prefer longer songs (Neubauer 1999). Therefore, we tested whether acoustic and sexual experiences are necessary for the expression of female canaries' preferences.

We tested two groups of females. One consisted of one-year-olds raised in acoustic isolation. These sexually inexperienced females had never heard or seen males, though they were always housed with other young and adult females and were never deprived of social contact. The second group was raised in an aviary, under "normal" acoustic conditions. These two-year-old females were housed with males and could, therefore, hear a large variety of male song. Each female had reproduced once by the time of testing.

## METHODS

**Subjects.**—We tested 18 female domestic canaries, an outbred, genetically heterogeneous form, divided into two groups. To obtain the first group (ISO group, females reared in acoustic isolation,  $n = 9$ ), we placed females in sound-attenuation chambers ( $60 \times 55 \times 80$  cm inside,  $90 \times 80 \times 110$  cm outside) for reproduction and removed males before hatching so that only the mothers reared the fledglings. Later, we removed the young males from the brood. Males were identified by their first vocalizations (subsongs) at ~30 days old. These vocalizations are very different from adult songs (Nottebohm 1993) and from the experimental stimuli we used (Pasteau et al. 2004). These females, hatched and reared in acoustic isolation, were placed in sound-attenuation chambers containing four cages, each holding two individuals ( $38 \times 26 \times 33$  cm). In these conditions, the birds were never deprived of social contact. The second group (AVI group, two-year-old female controls,  $n = 9$ ) were raised in "normal conditions." These females were chosen from a pool of 60 canaries (30 females and 30 males) that had spent one year in an aviary, each having reproduced once (for more details on female rearing conditions, see Pasteau et al. 2004). Because females are sexually mature at around one year of age and because we needed sexually experienced females for the experiment, we had to wait for the AVI females to finish their first reproductive cycle and a subsequent short-day photoperiod before we put them back on a long-day photoperiod for the experiment. Thus, the AVI females were two years old at the time of the experiment. Previous studies have shown that it is not the age of females that influences their responses, but rather their experience (Nagle and Kreutzer 1997a, b). In summary, isolated females had never heard male songs, whereas females raised in an aviary heard a large variety of these vocalizations.

Each group was tested after spending six months in a short-day photoperiod (8 h light:16 h dark). Three days before the experiment began, all females were placed in a long-day photoperiod (16 h light:8 h dark). This noninvasive method (in comparison with estradiol implants) allowed us to "restart" the subjects' reproductive cycle and to synchronize their periods of receptivity (Leboucher et al. 1994). The tests lasted 30 days, during which all females were kept in soundproof chambers ( $60 \times 55 \times 80$  cm inside;  $90 \times 80 \times 110$  cm outside) containing four individual cages ( $38 \times 26 \times 33$  cm).

**Experimental songs.**—We constructed the songs in AVISOFT (Avisoft Bioacoustics, Berlin), following a pattern similar to that of conventional canary song. Each song lasted 6 s and was organized in three parts: (I) a 0.75-s part containing two introductory notes

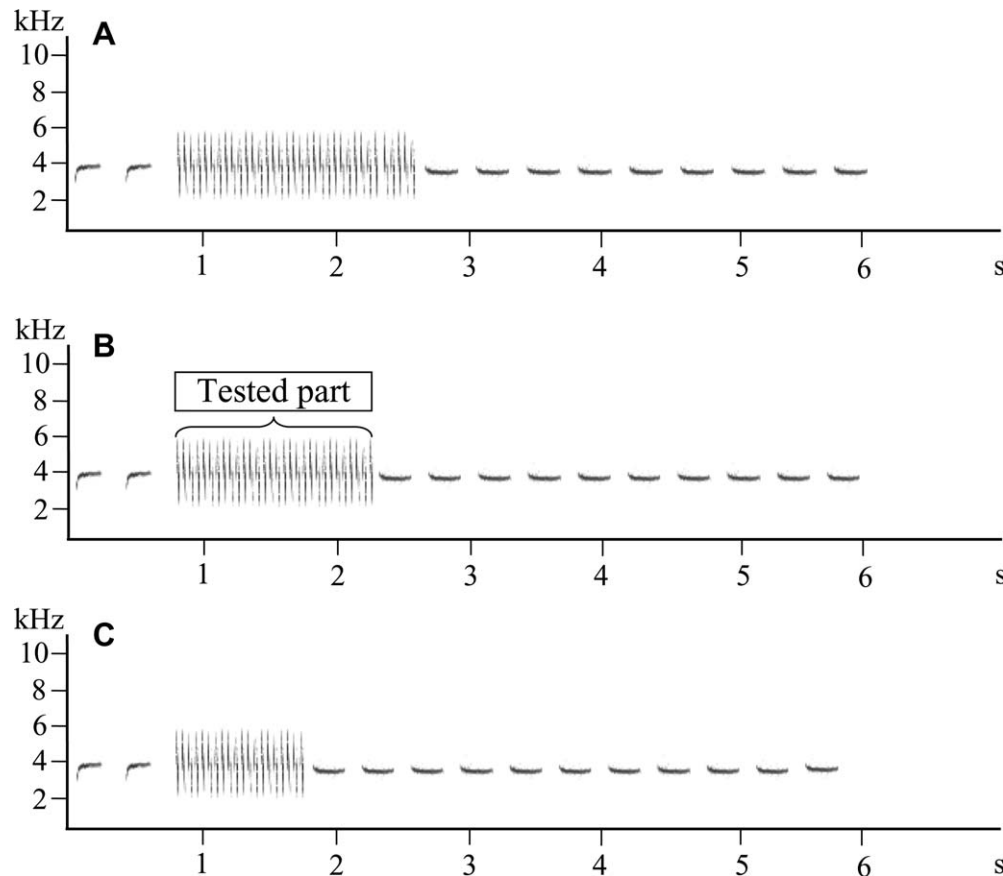


FIG. 2. Structure of song playback, with two 0.75-s introductory notes, the tested part lasting (A) 2.0 s, (B) 1.5 s, or (C) 1.0 s, and concluding notes lasting (A) 3.25 s, (B) 3.75 s, or (C) 4.25 s.

not stimulating to females; (II) a part containing a sexy phrase, A or F (lasting 2, 1.5, or 1 s); and (III) a part containing concluding notes (lasting 3.25, 3.75, or 4.25 s), also nonstimulating to females (Fig. 2). Each 6-s song was followed by 14 s of silence and was repeated six times to make up a “song bout” ( $6 \times [6 \text{ s song} + 14 \text{ s silence}]$ ), and each song bout was followed by 2 min of silence.

To limit pseudoreplication (Kroodsma 1989), we collected 20 introductory notes, 20 A phrases, 20 F phrases, and 20 concluding notes from 20 male repertoires. With each element collected from a single male, combinations resulted in 20 exemplars of two types of song with the three parts: the first song type contained an A phrase, and the second an F phrase.

Our experiment involved changing the duration of the sexy phrase (part II). As mentioned above, we used 20 A phrases (with a frequency bandwidth of 4 kHz located between 2 and 6 kHz) and 20 F phrases (with a frequency bandwidth of 2 kHz located between 2 and 4 kHz). For each type of sexy phrases, the duration was modified to obtain 20 samples of six phrases:  $2 \times 20$  phrases that lasted 2.0 s ( $20 A^{(2.0)}$  and  $20 F^{(2.0)}$ ; Fig. 2A),  $2 \times 20$  phrases that lasted 1.5 s ( $20 A^{(1.5)}$  and  $20 F^{(1.5)}$ ; Fig. 2B), and  $2 \times 20$  phrases that lasted 1.0 s ( $20 A^{(1.0)}$  and  $20 F^{(1.0)}$ ; Fig. 2C).

**Testing.**—Copulation-solicitation displays (King and West 1977, Searcy and Marler 1981, Searcy 1992) were used as behavioral indexes

for female preferences. A CSD consists of a female crouching, wings spread, back arched, bringing her head and tail to a near-vertical position. An observer, placed behind a one-way mirror, scored the response as 0 (no display) or 1 (display) (Kreutzer and Vallet 1991).

We conducted the experiment for 30 days, performing the tests twice a day. A test session corresponded to a sample diffusion, and test sessions were separated by an interval of  $\geq 2$  h (Table 1). For example, in the morning of day 1, all females heard sample<sub>1</sub> ( $A^{(2.0)}$ ,  $A^{(1.5)}$ ,  $A^{(1.0)}$ ,  $F^{(2.0)}$ ,  $F^{(1.5)}$ ,  $F^{(1.0)}$ ), and in the afternoon of day 1, these same females heard sample<sub>20</sub> ( $A^{(2.0)}$ ,  $A^{(1.5)}$ ,  $A^{(1.0)}$ ,  $F^{(2.0)}$ ,  $F^{(1.5)}$ ,  $F^{(1.0)}$ ). In the morning of day 2, all females heard sample<sub>6</sub>, and, in the afternoon, sample<sub>15</sub>, and so on (Table 1). In this way, each female was subjected to 60 test sessions and heard each sample three times. The diffusion order of samples ( $n = 20$ ) and of the song types they comprised ( $n = 6$ ) was randomized. Thus, we can assume that any preferences that our groups showed are a consequence of the song type and not of the particular sample. Songs were diffused at 30 cm from the cage with an ARCHOS Gmini XS hard-disc player and a SONY SRS A 202 speaker.

**Statistical analysis.**—We analyzed each group’s results by using the total number of CSDs but, as is conventionally done, we represent only the mean ( $\pm$  SE) CSD value obtained per female for each stimulus in Figure 3.

TABLE 1. Example of test sessions that each female of both groups heard separately. During 30 days, each female was subjected to 60 test sessions (tests being performed twice a day). A test session corresponds to a sample diffusion. A sample corresponds to the six stimuli used. The order of samples and stimuli is random.

Day 1		Day 2		Day 30	
Test 1 (am)	Test 2 (pm)	Test 3 (am)	Test 4 (pm)	Test 59 (am)	Test 60 (pm)
Sample <sub>1</sub> :	Sample <sub>20</sub> :	Sample <sub>6</sub> :	Sample <sub>15</sub> :	Sample <sub>11</sub> :	Sample <sub>2</sub> :
A <sup>(1.5)</sup> <sub>1</sub>	F <sup>(1.0)</sup> <sub>20</sub>	F <sup>(1.5)</sup> <sub>6</sub>	F <sup>(2.0)</sup> <sub>15</sub>	A <sup>(1.0)</sup> <sub>11</sub>	A <sup>(2.0)</sup> <sub>2</sub>
F <sup>(1.0)</sup> <sub>1</sub>	A <sup>(1.5)</sup> <sub>20</sub>	A <sup>(2.0)</sup> <sub>6</sub>	A <sup>(1.0)</sup> <sub>15</sub>	F <sup>(1.5)</sup> <sub>11</sub>	F <sup>(2.0)</sup> <sub>2</sub>
A <sup>(1.0)</sup> <sub>1</sub>	F <sup>(2.0)</sup> <sub>20</sub>	A <sup>(1.5)</sup> <sub>6</sub>	F <sup>(1.5)</sup> <sub>15</sub>	A <sup>(2.0)</sup> <sub>11</sub>	F <sup>(1.0)</sup> <sub>2</sub>
F <sup>(2.0)</sup> <sub>1</sub>	F <sup>(1.5)</sup> <sub>20</sub>	A <sup>(1.0)</sup> <sub>6</sub>	A <sup>(2.0)</sup> <sub>15</sub>	F <sup>(1.0)</sup> <sub>11</sub>	A <sup>(1.5)</sup> <sub>2</sub>
F <sup>(1.5)</sup> <sub>1</sub>	A <sup>(2.0)</sup> <sub>20</sub>	F <sup>(2.0)</sup> <sub>6</sub>	F <sup>(1.0)</sup> <sub>15</sub>	A <sup>(1.5)</sup> <sub>11</sub>	A <sup>(1.0)</sup> <sub>2</sub>
A <sup>(2.0)</sup> <sub>1</sub>	A <sup>(1.0)</sup> <sub>20</sub>	F <sup>(1.0)</sup> <sub>6</sub>	A <sup>(1.5)</sup> <sub>15</sub>	F <sup>(2.0)</sup> <sub>11</sub>	F <sup>(1.5)</sup> <sub>2</sub>

Responses to a stimulus were treated with a two-way repeated-measures analysis of variance (ANOVA) with factor A (stimulus types A<sup>(2.0)</sup>, A<sup>(1.5)</sup>, A<sup>(1.0)</sup>, F<sup>(2.0)</sup>, F<sup>(1.5)</sup>, and F<sup>(1.0)</sup>) and factor B (group types ISO and AVI). Multiple comparisons were done with a Student-Newman-Keuls *post-hoc* test. We considered tests significant when  $\alpha = 0.05$ .

## RESULTS

Female responses were affected by the different stimulus types (two-way repeated-measures ANOVA, factor A:  $F = 19.884$ ,  $df = 5$ ,  $P < 0.001$ ). However, the group type (ISO or AVI) had no effect on these responses: both groups strongly agreed in their responses (two-way repeated-measures ANOVA, factor B:  $F = 1.073$ ,  $df = 1$ ,  $P = 0.327$ ), and there was no significant interaction between stimulus types and group types (two-way repeated-measures ANOVA, factor A  $\times$  factor B:  $F = 2.362$ ,  $df = 5$ ,  $P = 0.055$ ).

Within the ISO group, the following stimulus types elicited CSDs from females (in order from most to least CSDs produced): A<sup>(2.0)</sup>, F<sup>(2.0)</sup>, A<sup>(1.5)</sup>, A<sup>(1.0)</sup>, F<sup>(1.5)</sup>, and F<sup>(1.0)</sup>. Multiple comparisons indicated no significant difference in the ISO group between F<sup>(2.0)</sup>, A<sup>(1.5)</sup>, and A<sup>(1.0)</sup> phrases or between F<sup>(1.5)</sup> and F<sup>(1.0)</sup> phrases, but there were significant differences among all the other stimuli (Student-Newman-Keuls test, two-tailed,  $P < 0.05$ ,  $n = 9$ ; Fig. 3A).

Within the AVI group, the following stimulus types elicited CSDs from females (in order from most to least CSDs produced): A<sup>(2.0)</sup>, A<sup>(1.5)</sup>, F<sup>(2.0)</sup>, A<sup>(1.0)</sup>, F<sup>(1.5)</sup>, and F<sup>(1.0)</sup>. *Post-hoc* tests indicated a significant difference between A<sup>(2.0)</sup> and all other stimuli except A<sup>(1.5)</sup> and between A<sup>(1.5)</sup> and all other stimuli except F<sup>(2.0)</sup>. There was no significant difference between A<sup>(2.0)</sup> and A<sup>(1.5)</sup>, between A<sup>(1.5)</sup> and F<sup>(2.0)</sup>, or between F<sup>(2.0)</sup>, A<sup>(1.0)</sup>, F<sup>(1.5)</sup>, and F<sup>(1.0)</sup> (Student-Newman-Keuls test, two-tailed,  $P < 0.05$ ,  $n = 9$ ; Fig. 3B).

## DISCUSSION

Our results indicate that both experienced and inexperienced females prefer longer sexy phrases. More specifically, 2-s A phrases (A<sup>(2.0)</sup>) obtained more responses than all the other stimuli, except in the AVI group, in which females did not differentiate between these phrases and 1.5-s A phrases (A<sup>(1.5)</sup>). Females preferred 2-s F phrases (F<sup>(2.0)</sup>) and A phrases that lasted  $< 2$  s (A<sup>(1.5)</sup> and A<sup>(1.0)</sup>). Finally, females responded less to F phrases that lasted  $< 2$  s (F<sup>(1.5)</sup> and F<sup>(1.0)</sup>). It is important to recall in this context that previous studies (see above) have already proved that A phrases provoke more CSDs in female canaries than F phrases because the frequency of their bandwidths differs, and our results affirm this. Their duration being equal, A phrases are more stimulating for females than F phrases. However, the duration of sexy phrases can offset the

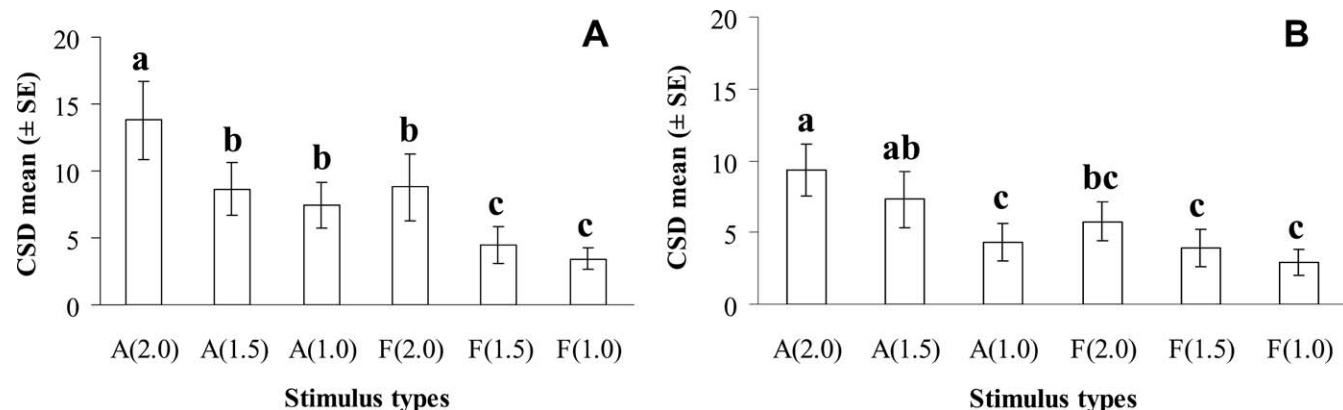


FIG. 3. Mean number ( $\pm$  SE) of copulation-solicitation displays (CSDs) per female in response to 20 samples: (A) ISO group ( $n = 9$ ) and (B) AVI group ( $n = 9$ ). Different letters indicate a significant difference (Student-Newman-Keuls test, two-tailed,  $P < 0.05$ ,  $n = 9$ ). There was no significant difference between the two groups for each analysis.



frequency bandwidth:  $F^{(2,0)}$  phrases are more stimulating than  $A^{(1,0)}$  phrases.

The preference of female canaries for longer sexy phrases in the present study corroborates results obtained in other species in laboratory and natural conditions (Clayton and Pröve 1989, Wasserman and Cigliano 1991, Kempnaers et al. 1997, Balzer and Williams 1998, Neubauer 1999, Nolan and Hill 2004, Nowicki and Searcy 2005). Song duration is an acoustic parameter, like tempo and complexity, that is often correlated with morphological and physiological conditions of males. In Blue Tit, song duration is positively correlated with male tarsus length, and females choose males with longer songs than their social mates' for extra-pair copulation (Kempnaers et al. 1997). In the same way, in Indigo Bunting (*Passerina cyanea*), male size is positively correlated with song duration (J. Mountjoy et al. unpubl. data). These two examples indicate that song duration could be an indicator of male quality and, especially, of male size and could thus constitute an honest signal for females (Zahavi 1975, 1977; Andersson 1994). This hypothesis is strengthened by results obtained by Balzer and Williams (1998) in Zebra Finch: females invested more in reproduction when their mates sang longer songs by laying significantly more eggs. Moreover, song duration can also be an indicator of male testosterone level. In Redwing (*Turdus iliacus*), Wood Warbler (*Phylloscopus sibilatrix*), and Pied Flycatcher (*Ficedula hypoleuca*), duration of male song decreases after reproduction, when plasma testosterone level is low (Temrin 1986, Lampe and Espmark 1987, Espmark and Lampe 1993), to prepare males for parental care (Wingfield et al. 1990, Béguin et al. 1998). Leitner et al. (2001) demonstrated that duration of male song in wild canaries decreased in proportion to male testosterone levels in short-day photoperiod, and Rybak and Gahr (2004) demonstrated that song duration could be testosterone-dependent in the canary. In light of this, song duration can reflect male testosterone level and morphological traits. Therefore, females can benefit from choosing males that emit long songs.

However, can female canaries obtain these same benefits when they choose males that emit longer sexy phrases? We can assume so, because such phrases may constitute an honest signal (Vallet et al. 1997, Suthers et al. 2004). Production of longer phrases requires an excellent motor ability and coordination and imposes respiratory and muscular constraints on the syrinx (Podos 1996, Suthers et al. 2004, Vallet et al. 2006). Moreover, Kreutzer et al. (1999) demonstrated that male canaries sing longer sexy phrases when facing a congener than when alone. This result reveals that production of longer sexy phrases is reserved and limited to social interactions. Therefore, we can postulate that, like total song duration in many species, duration of sexy phrases in the canary may be a good indicator of male quality and may constitute an honest signal (Zahavi 1975, 1977; Andersson 1994).

In addition, there was no significant difference in preferences between the two groups. Although the AVI group tended to be slightly less discriminative than the ISO group, both strongly agreed in their responses. The preference of female canaries for longer sexy phrases seems to be determined by a predisposition and was not affected by social experience with males, experience of male song, or sexual experience. This is in accordance with results we have obtained previously showing that female canaries prefer low-frequency (Pasteau et al. 2007) and high-intensity (Pasteau

et al. 2009) sexy phrases. However, the preferences of female canaries seem to have a certain plasticity. Studies have demonstrated that predispositions can be modified either by early song diffusion (Nagle and Kreutzer 1997a, b) or by acoustic and sexual experience in adulthood (Nagle and Kreutzer 1997a, b; Drăgănoiu et al. 2002). In general, it seems that female canaries' predispositions are more plastic with regard to species recognition than when they concern natural variation in male song. In addition, these results are in accordance with those obtained in Zebra Finch, which showed that females are predisposed to prefer longer male songs (Neubauer 1999). However, in that species, females rarely express innate predispositions for particular songs or phrases and generally need a song pattern (live or broadcast) to develop song preferences (Riebel 2000, 2003). The agreement of our results with those obtained in the Zebra Finch is particularly interesting.

The present study permits a better understanding of female preferences for song parameters and of the developmental processes that guide these preferences. We have demonstrated that female canaries prefer longer sexy phrases. A complementary study of mate choice could confirm whether females use this preference when choosing a partner. If so, a long sexy phrase could be considered an honest signal for females. Moreover, females raised in acoustic isolation present the same preferences as females raised in normal acoustic conditions, which indicates that acoustic and sexual experiences are not necessary for developing this type of preference.

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