

# Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song

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Motor constraints on vocal production impose a trade-off between trill rate and frequency bandwidth within birdsong. We tested whether domesticated canary (*Serinus canaria*) females, reared either in acoustic isolation or in aviary conditions, had a preference for broad bandwidth songs with artificially increased syllable rates. The copulation solicitation display (CSD) was used as an index of female preference. As predicted, both naive and experienced females were especially responsive to syllables with a broad bandwidth emitted at an artificially increased rate. Female preference for supernormal stimuli provide support for the honest-signalling hypothesis and our results are consistent with recent findings indicating that production of song phrases maximizing both bandwidth and syllable rate may be a reliable indicator of male physical or behavioural qualities. We suggest that female preference for vocal emissions, which simultaneously maximize these two parameters, could be a widespread pattern within songbirds.

**Keywords:** acoustic communication; bird song; supernormal stimulus; *Serinus canaria*

## 1. INTRODUCTION

One of the main functions of male song in passerines is mate attraction (Kroodsma & Byers 1991; Catchpole & Slater 1995). This has been clearly shown by studies using song broadcasting in the field (Eriksson & Wallin 1986; Mountjoy & Lemon 1991). In several species, males can use different song types in order to attract mates or to repel rivals (Kroodsma *et al.* 1989; Spector 1991). For example, male great reed warblers (*Acrocephalus arundinaceus*) have two types of song, called long and short songs (Catchpole 1983). Females prefer long over short songs under laboratory conditions (Catchpole *et al.* 1986) and were found to choose exclusively males producing long songs in the wild (Bensch & Hasselquist 1991).

Sometimes, male ability to attract a partner is mainly explained by the presence of a particular element in the male repertoire, as shown in a field study on water pipits, *Anthus spinoletta* (Rehsteiner *et al.* 1998). Laboratory studies also reported that females may show a clear preference for precise elements of the male vocal repertoire. Thus, female common domesticated canaries, *Serinus canaria*, prefer a special phrase of male song, called 'A' phrase or 'sexy' phrase, composed by a two-note syllable with rapid frequency modulation, repeated at a high rate (Vallet & Kreutzer 1995; Vallet *et al.* 1998).

Concurrently, it has been shown that a trade-off exists in bird song (Emberizidae family) between trill rate and frequency bandwidth: maximal values of frequency bandwidth decrease with increasing trill rates (Podos 1997). Canaries are also subject to this singing pattern (figure 1), which seems to be imposed by motor constraints (Podos 1996). Indeed, the production of complex vocalizations involving the use of both sides of the syrinx (such as elements with a large frequency bandwidth) impedes on air reserve replenishing and thus generates a conflict

between the temporal and the phonetic complexity (Suthers & Goller 1997).

The 'A' phrase is a good example of vocal emission which tries to maximize these two parameters: Suthers *et al.* (2001) pointed out that production of 'A' phrases with high syllable rates (more than 16 per second) by male canaries requires the participation of both sides of the syrinx. Looking for the key factors which make this special phrase attractive to females, Vallet *et al.* (1997) found that female canaries prefer 'A' phrases with 15 syllables s<sup>-1</sup> or more, thus giving a clear indication of syllable-rate importance. Although previous work has emphasized the possible function of broad bandwidth (Vallet & Kreutzer 1995), at the present time there is no experimental evidence for this supposition.

The present study seeks to find out if females prefer songs which are characterized by a combination of trill rate and bandwidth, which breaks the trade-off relationship existing between these two factors (Podos 1997). We artificially increased the rate of naturally emitted syllables with a large bandwidth and tested female sexual responsiveness for these supernormal stimuli. We suggest that female canaries will prefer elements with an exaggerated combination of syllable rate and bandwidth because they should be difficult to produce and thus a reliable indicator of male quality, according to Zahavi's theory of honest signalling (Zahavi 1975, 1977). We also want to establish to what extent females' sexual preferences are affected by frequency bandwidth.

Previous work has demonstrated, using different techniques, that several species of passerines have an innate recognition of conspecific song (Dooling & Searcy 1980; Nelson & Marler 1993; Whaling *et al.* 1997; Braaten & Reynolds 1999) and in one case, a predisposition to memorize songs of own subspecies has been documented (Nelson 2000). Female canaries reared in acoustic isolation were found to be especially responsive to songs containing special elements, the previously described 'A' phrase (Nagle & Kreutzer 1997a). Another research line

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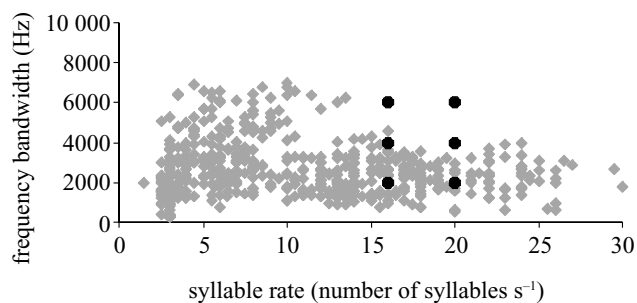


Figure 1. Relation between bandwidth and syllable rate within canary song ( $n = 547$  syllables). Dark points indicate the stimuli used in our experiment.

has proven that female sexual preferences can be affected by early tutoring (Casey & Baker 1992; Nagle & Kreutzer 1997*a,b*; Depraz *et al.* 2000). In order to distinguish the roles played by predispositions and song experiences in the establishment of females' sexual preferences, we chose to test females reared both in acoustic isolation and in aviary conditions.

## 2. MATERIAL AND METHODS

### (a) *Subjects and housing*

We used 20 domesticated common canary females belonging to an outbred form of heterogeneous genetic background, reared in our laboratory. Two groups were formed: females in the ISO Group ( $n = 10$ ) were hatched and reared in total acoustic isolation, whereas females in the AVI Group ( $n = 10$ ) were reared in aviary conditions, so they could hear a large variety of males' songs.

During the experiments, females were kept in individual cages (35 cm  $\times$  20 cm  $\times$  25 cm) and provided with daily supplies of seeds, fresh food, water and vitamins. Cages were placed in sound attenuation chambers (63 cm  $\times$  58 cm  $\times$  85.5 cm inside and 90 cm  $\times$  83 cm  $\times$  109 cm outside), with a maximum of four cages in a chamber; females could not see each other during test periods.

### (b) *Experimental songs*

Experimental songs were built using, exclusively, recordings from males in our laboratory. We selected two-note syllables with three different bandwidths (figure 2: (b) 2 kHz ('F' phrase); (c) 4 kHz ('A' phrase); and (d) 6 kHz ('G' phrase)). We used a Macintosh iMac (400 MHz) and Sound Edit software, v. 2 (Macromedia, 22 000 Hz, 16 bits) in order to create two different syllable rates: 16 and 20 syllables  $s^{-1}$  (32 and 40 notes  $s^{-1}$ , respectively). Six stimuli were thus created: F16, F20, A16, A20, G16 and G20; males can produce 'F' and 'A' phrases at these rates but elements with a large bandwidth ('G') are naturally emitted at tempos lying between 5 and 14 syllables  $s^{-1}$  (figure 1). Songs last 6 s and have a fixed structure pattern (figure 2*a*): (i) 0.75 s of introductory syllables; (ii) 1.5 s—the tested phrase; and (iii) 3.75 s—final syllables; (i) and (iii) are elements with a very low sexual value. After each song, a 14 s silence period enabled birds to resume their regular activity. Song bouts consisted of six repetitions of the same song and lasted for 2 min. Stimuli were played backed using a MD-MS701H(S)2 SHARP recorder connected to a speaker (Sony, model no. SRS-A35) placed in the attenuation chamber.

### (c) *Experimental design*

We recorded the responses of females during a 30 day period, tests being carried out twice a day. During the same day, test periods were separated by a minimum 2 h interval (the first test being carried between 08.00 and 12.00 and the second one between 12.00 and 19.00). A test period lasted for 22 min and consisted of the presentation of six song bouts (corresponding to the six stimuli being tested: 6 min  $\times$  2 min), separated by 2 min silence periods (5 min  $\times$  2 min). In order to avoid order effects due to possible habituation, each stimulus was positioned an equal number of times in 1st, 2nd, ..., 6th position ( $n = 10$ ), during the whole period test ( $n = 60$ ).

In order to avoid simple pseudoreplication (Kroodsma 1989), each stimulus was provided in five different samples (for example, F16<sub>1</sub>, ..., F16<sub>5</sub>). Thus, we measure female responses for a class of stimuli (ex: F16 class: phrases with a bandwidth of 2 kHz and a syllable rate of 16 syllables  $s^{-1}$ ) and not to only one particular stimulus (for instance, F16<sub>1</sub> alone). As we are limited to a small number of subjects (we cannot measure sexual postures for more than four females simultaneously) and stimulus samples (canaries seldom produce elements of type 'G', with a very large bandwidth), each of 10 birds was tested with the five different samples of stimuli. Sacrificial pseudoreplication arises if we pool the data within a class (for example, F16: F16<sub>1</sub>, ..., F16<sub>5</sub>). To avoid pseudoreplication in this case, statistical tests should be done with the number of stimuli within a class as sample size (McGregor *et al.* 1992). As we re-used the same signal several times, we averaged the responses to obtain a single datapoint for that particular stimulus (Kroodsma *et al.* 2001). Thus, our sample points are given by the number of different stimuli within a class and not by the number of subjects used (see also Searcy *et al.* 1997).

Each sample within a class was used an equal number of times ( $n = 12$ ) during the 60 tests we carried. Within a sample, each stimulus was positioned an equal number of times in 1st, 2nd, ..., 6th position ( $n = 2$ ).

### (d) *Sexual responses and song discrimination*

Copulation Solicitation Display or CSD (King & West 1977; Searcy & Marler 1981; Searcy 1992) was used as an index of females' preferences. During a complete CSD a female crouches, arches her back, brings her tail forward and tosses back her head. This posture is associated with wing vibration and spreading of the feathers surrounding the cloacal region. Incomplete CSD may occur with lack of wing vibration and complete tail movement. We scored the responses, awarding 0 for no display, 0.5 for an incomplete display and 1 for a complete display (Kreutzer & Vallet 1991). Generally, wild birds need oestradiol implants in order to perform CSDs in captivity (Searcy 1992). We used a non-invasive method, based on photoperiod change and originally described for domestic canaries in our laboratory (Nagle *et al.* 1993; Leboucher *et al.* 1994). Three days before the beginning of the experiments, we changed the photoperiod from short days (8 L : 16 D) to long days (15 L : 9 D) and we provided females with nest bowls (10 cm in diameter) and nest material (coconut fibres, shredded linen), enhancing their reproductive activity. Birds reach a maximal responsiveness during days  $-2$  to  $+2$ , where 0 is the day where the first egg was laid. Nests were removed from cages 3–8 days after clutch completion and a second reproductive cycle started after a 4–7 day period.

One may ask if birds were able to perceive the entire frequency range of phrases used in our experiments and the syllable rates

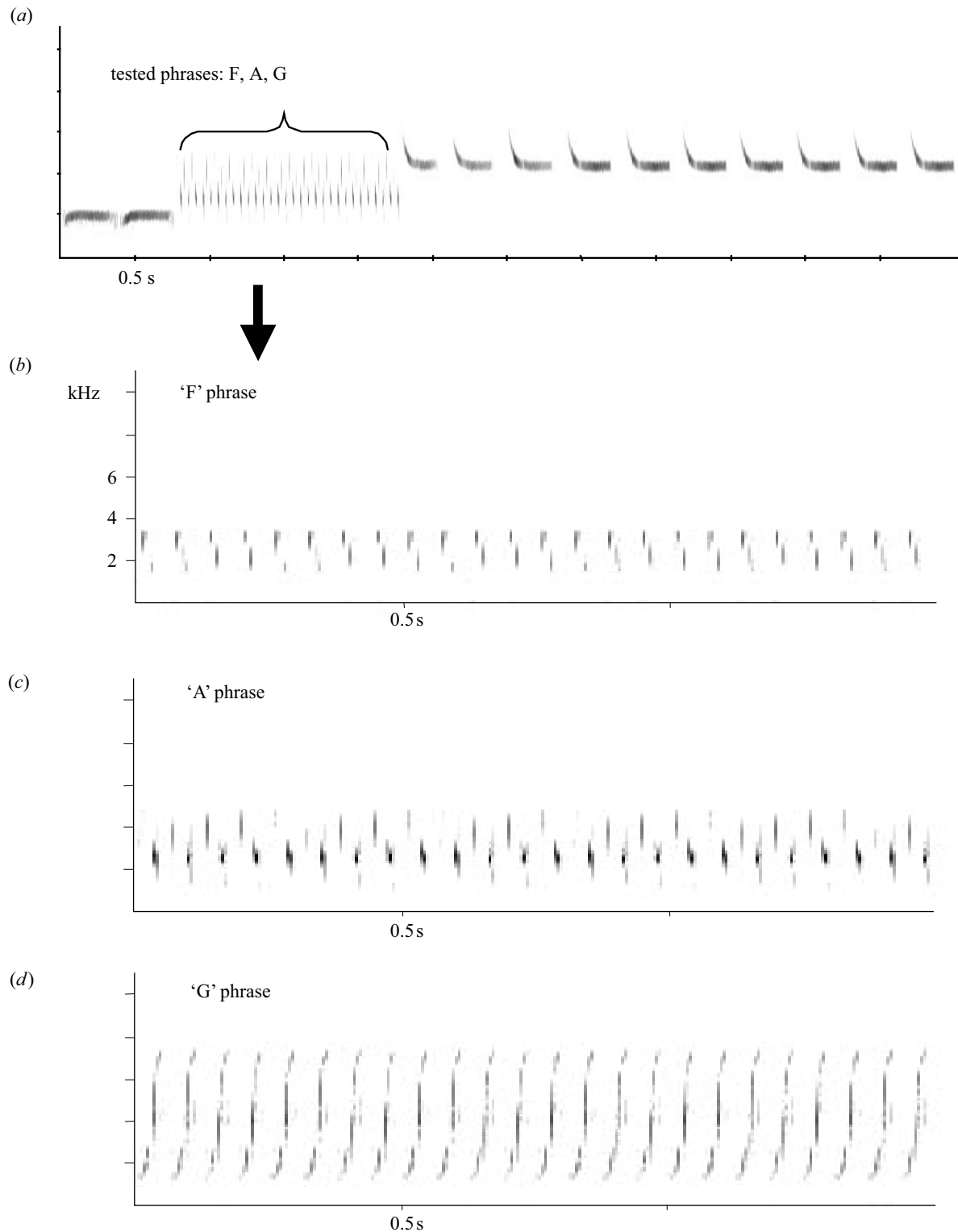


Figure 2. (a) Structure of a played-back song: (i) introductory syllables: 0.75 s; (ii) tested phrase: 1.5 s; (iii) final syllables: 3.75 s. (b–d) Examples of tested phrases with a narrow (b) ('F': 2 kHz), medium (c) ('A': 4 kHz) and large (d) ('G': 6 kHz) bandwidth; rate is 16 syllables  $s^{-1}$ .

we chose to test. In canaries, high-frequency sensitivity is related to the highest frequencies contained in the species song and, generally, there is a good correspondence between hearing sensitivity and the vocalization power spectra (Dooling *et al.* 1971; Dooling 1980). Concerning syllable rate, Dooling suggests in his review of auditory perception in birds that intersyllable intervals of less than 2–3 ms may not be perceived by birds (Dooling

1980); but in our test phrases, silences between syllables had a minimum length of 3 ms. In view of these results we believe that females were able to accurately perceive the different stimuli used in our experiment.

Scores for the different songs for both groups of females were compared and tested for significance using the Friedman two-way analysis of variance ( $F$ ), followed by Student–Newman–

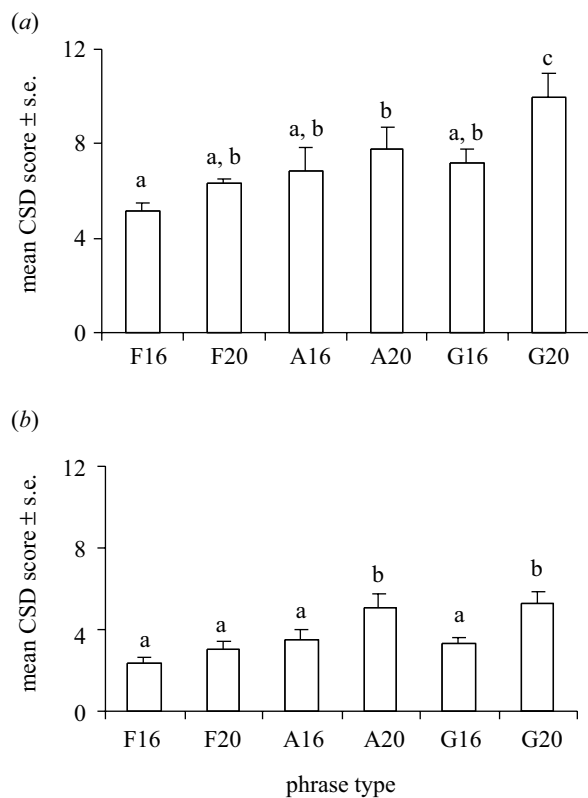


Figure 3. Mean  $\pm$  s.e. number of copulation solicitation displays (CSD) given by female canaries reared in acoustic isolation (a) ISO group ( $n=10$ ) and (b) in AVI group ( $n=10$ ) to the six tested phrases: F16, F20, A16, A20, G16 and G20 ('F': 2 kHz, 'A': 4 kHz, 'G': 6 kHz; 16 and 20 = 16 and 20 syllables  $s^{-1}$ ). Five different samples of stimuli were used and statistical analysis was performed by sample rather than by subject. Mean values represent responses per female per sample and are illustrative only as all statistics were non-parametric. The presence of a same letter above bars indicates a non-significant difference between the two stimuli.

Keuls (SNK) for multiple comparisons (Winer 1971). Relative response levels were compared between ISO Group and AVI Group using  $z$ -tests. All tests were performed using SIGMASTAT (v. 2.0) statistical software.

### 3. RESULTS

There was a significant heterogeneity in the response to the six different phrases for the number of copulation solicitation displays in both groups (Friedman- $F$  two-way analysis of variance, ISO group  $\chi^2_5 = 14.486$ ,  $p = 0.013$ ; AVI group  $\chi^2_5 = 17.114$ ,  $p = 0.004$ ).

#### (a) ISO group

Females reared in acoustic isolation gave significantly more responses to the G20 phrase (6 kHz and 20 syllables  $s^{-1}$ ) than to all other phrase types (SNK two-tailed,  $n=5$ ,  $p < 0.05$ ; figure 3a). With one exception (A20 phrase triggered significantly more responses than F16 phrase, SNK two-tailed,  $n=5$ ,  $p < 0.05$ ), responses to other phrases were not significantly different. Despite this, we observed that response level invariably increases for phrases with larger bandwidths and higher syllable rates.

#### (b) AVI group

Females reared in aviary conditions displayed a similar number of sexual postures to phrases with a medium or large bandwidth emitted at a high syllable rate (A20 and G20; figure 3b). The response level for A20 and G20 was significantly superior to the response level for all other phrases (SNK two-tailed,  $n=5$ ,  $p < 0.05$ ) and no other significant differences were found.

If we rank the different stimuli within each group according to female preference, we find that both groups of females strongly agreed in their preferences (Spearman's  $r$ :  $r = 0.943$ ,  $n = 6$ ,  $p = 0.016$ ). Generally, the absolute response level for females reared in acoustic isolation was twofold when compared with that of AVI group females. When we compared relative response level (ratio between the number of CSDs for a particular stimulus and the total number of CSDs within a group) between the two groups, females in the AVI group gave significantly more responses to A20 phrase than females in ISO group ( $z = 2.918$ ;  $p = 0.004$ ). All other differences were non-significant (F16:  $z = 1.095$ ;  $p = 0.273$ ; F20:  $z = 0.851$ ;  $p = 0.395$ ; A16:  $z = 0.144$ ;  $p = 0.855$ ; G16:  $z = 1.458$ ;  $p = 0.145$ ; G20:  $z = 0.266$ ;  $p = 0.79$ ).

### 4. DISCUSSION

Our main results (figure 3) indicate that both females reared in acoustic isolation and females reared in aviary conditions prefer an exaggerated male trait (phrase G20), beyond the limits of vocal production. Moreover, a good concordance exists between groups in preference for different phrases.

Females reared in acoustic isolation gave significantly more responses to G20 phrase than to all other phrase types. This is a phrase with a large bandwidth (6 kHz) and an artificially increased rate (20 syllables  $s^{-1}$ ), which is not naturally produced by male canaries. We generally observe a preference for phrases with a larger bandwidth and a greater syllable rate. Thus, for the same bandwidth, birds always gave more responses to phrases with a greater syllable rate. Likewise, for the same number of syllables per time unit, they generally preferred phrases with a larger bandwidth (G20 > A20 > F20 and G16 > A16 > F16, with an almost similar response level for G16 and A16). This response pattern suggests that female canaries have an innate directional preference for phrases with a greater syllable rate and a greater bandwidth. In a previous study, we found that naive females had a sexual preference for songs containing 'A' phrases, comparable with those used in the actual experiment (Nagle & Kreutzer 1997a). Our results give a supplementary cue concerning this perceptual predisposition, emphasizing the role of trill rate and bandwidth.

Work by Vallet *et al.* (1997) has already demonstrated the role of syllable rate, and this is consistent with the fact that females use song rate in order to choose their mates (for a review, see Catchpole & Slater 1995; Gil & Gahr 2002). This study confirms previous findings: for the same bandwidth, elements with a higher tempo always triggered more responses. It indicates, at the same time, that high syllable rate is a quality necessary but not sufficient to trigger a very high level of sexual responses: for a given syllable rate, females generally gave more CSDs in response

to elements with a larger bandwidth. This suggests that female canaries use at least two cues of males' vocal production in order to assess the quality of their future partner. Other passerine species also use multiple cues during the mate choice process; Buchanan & Catchpole (1997) have shown that female sedge warblers, *Acrocephalus scoenobaenus*, pay attention both to males' repertoire size and to the time they spend singing during flight. Unlike sedge warblers, canaries seem to operate at a different level, which is the song unit.

As predicted, females preferred supernormal stimuli, maximizing both the syllable rate and the bandwidth. Preference for an exaggerated stimulus is a pattern that was found for different characteristics of acoustic (call rate, sound intensity) or visual (tail length, body size) signals (reviewed by Ryan & Keddy-Hector 1992). Our results are consistent with the honest-signalling hypothesis, which states that females choose males with exaggerated traits, as they reflect potential direct or indirect benefits (Zahavi 1975, 1977). Nevertheless, we cannot reject the sensory exploitation hypothesis (Basolo 1990; Ryan 1990; Ryan *et al.* 1990), which states that male traits have evolved in order to exploit a certain bias existing in females' sensory system. Indeed, both hypotheses predict females' preference for exaggerated male traits (Ryan & Keddy-Hector 1992). According to Endler & Basolo (1998), four criteria should be met in order to confirm the sensory exploitation hypothesis: (i) the species has the trait, a preference for the trait and the trait is used in mate choice; (ii) the trait is absent (or in a primitive form) in ancestors; (iii) preference for the trait is ancestral; (iv) there is a bias in the sensory system or brain that accurately and specifically predicts the direction of preferences. In our case, only two of these criteria are met: the first (Vallet & Kreutzer 1995) and the last (Nagle & Kreutzer 1997a; present results). Only further research, considering the phylogeny of *Serinus* genus (Arnaiz-Villena *et al.* 1999) could sustain the sensory exploitation hypothesis.

We observe that the response level is twofold in the ISO group when compared with the AVI group (figure 3). One possible explanation is that females reared in an aviary associated song production with male presence; we can imagine that playback alone is no longer sufficient to trigger off a high-response level.

Females reared in aviary conditions responded equally to song phrases 'A' (4 kHz) and 'G' (6 kHz), produced at a high rate (20 syllables  $s^{-1}$ ; figure 3b). When compared with ISO group females, they privileged a song phrase that they could have heard earlier during their lives (A20). Other phrases that could have been heard by females before the experiments (F16, F20, A16) did not trigger a greater relative response level when compared with the ISO group. A possible explanation is that these types of phrases are not costly and that their production does not enable females to extract valuable information about males' quality. On the contrary, A20 phrase may be a vocal element difficult to emit and females could associate the production of a particular song phrase (A20) with physical or behavioural male qualities. There are several arguments that lend support to this interpretation.

First, if we look at the illustration of the trade-off relationship between trill rate and bandwidth (figure 1) we notice that A20 is situated on the hypotenuse and puta-

tively amongst the most difficult to produce vocalizations. Experimental studies with other passerine species indicate that elements that maximize both parameters should be difficult to produce. Thus, young male swamp sparrows (*Melospiza georgiana*) tutored with conspecific song at an artificially increased rate (comparable with our G20 stimulus) were not able to produce accurate copies of tutor song and to sustain the syllable rate at the same time (Podos 1996), the author attributing this result to motor constraints on vocal production. Second, recent research by Suthers *et al.* (2001) has shown that male canaries need both sides of their syrinx in order to emit 'A' type syllables with a bandwidth larger than 3 kHz. Their production could therefore be a good indicator of males' phonatory abilities. Last, this special phrase emission also seems to be related to social status, with dominant males emitting 'A' phrases at a higher tempo than subordinates (Lusiantifitri 2001).

It appears that the 'A' phrase is a message that males address to females but also to other males: the presence of a conspecific (male or female) induced the production of phrases that included longer strings of 'A' phrases when compared with males singing alone (Kreutzer *et al.* 1999). Comparable results were found for water pipits (Rehsteiner *et al.* 1998). In this species, the presence of a particular element (the 'Snarr') in males' song is the best predictor of their mating status and seems, at the same time, to signal dominance in males (territory overlap is lower in males with high 'Snarr' scores). The element has a 'broad frequency band' (close to 4 kHz) and a 'rapid repetition of notes' (Rehsteiner *et al.* 1998), seeming to share the same characteristics with the 'A' phrase. This is consistent with the honest-signal hypothesis, which implies that an exaggerated male trait should serve both to attract females and to deter other males (Zahavi & Zahavi 1997).

In conclusion, responses of females raised in aviary conditions are consistent with responses of females raised in acoustic isolation. The same rules seem to guide sexual preferences of females with or without previous experience of own-species song: birds in both groups show a clear preference for broad-bandwidth song phrases emitted at an artificially increased syllable rate. Taken as a whole, our results show that female domesticated canaries prefer an exaggerated feature of males' song and may support the idea that canary vocal productions that simultaneously maximize bandwidth and syllable rate are a reliable index of males' quality. Furthermore, we suggest that the use by females of these vocal emissions as a criterion to evaluate future partners could be a more widespread pattern in songbirds.

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## REFERENCES

- Arnaiz-Villena, A., Alvarez-Tejado, M., Ruiz-del-Valle, V., Garcia-de-la-Torre, C., Varela, P., Recio, M. J., Ferre, S. &

- Martinez-Laso, J. 1999 Rapid radiation of canaries (genus *Serinus*). *Mol. Biol. Evol.* **16**, 2–11.
- Basolo, A. L. 1990 Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808–810.
- Bensch, S. & Hasselquist, D. 1991 Evidence for active female choice in a polygynous warbler. *Anim. Behav.* **44**, 301–311.
- Braaten, R. F. & Reynolds, K. 1999 Auditory preference for conspecific song in isolation-reared zebra finches. *Anim. Behav.* **58**, 105–111.
- Buchanan, K. L. & Catchpole, C. K. 1997 Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. *Proc. R. Soc. Lond. B* **264**, 521–526. (DOI 10.1098/rspb.1997.0074.)
- Casey, R. M. & Baker, M. C. 1992 Early social tutoring influences female sexual response in white-crowned sparrows. *Anim. Behav.* **44**, 983–986.
- Catchpole, C. K. 1983 Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. *Anim. Behav.* **31**, 1217–1225.
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird song—biological themes and variations*. Cambridge University Press.
- Catchpole, C. K., Leisler, B. & Dittami, J. 1986 Sexual differences in the response of captive great reed warblers (*Acrocephalus arundinaceus*) to variation in song structure and repertoire size. *Ethology* **73**, 69–77.
- Depraz, V., Leboucher, G. & Kreutzer, M. L. 2000 Early tutoring and adult reproductive behaviour in female domestic canary (*Serinus canaria*). *Anim. Cogn.* **3**, 45–51.
- Dooling, R. J. 1980 Auditory perception in birds. In *Acoustic communication in birds*, vol. 1 (ed. D. E. Kroodsma & E. H. Miller), pp. 95–130. New York: Academic.
- Dooling, R. J. & Searcy, M. 1980 Early perceptual selectivity in the swamp sparrow. *Dev. Psychobiol.* **13**, 499–506.
- Dooling, R. J., Mulligan, J. & Miller, J. 1971 Auditory sensitivity and song spectrum of the common Canary (*Serinus canarius*). *J. Acoust. Soc. Am.* **50**, 700–709.
- Endler, J. A. & Basolo, A. L. 1998 Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* **10**, 415–420.
- Eriksson, D. & Wallin, L. 1986 Male bird song attracts females—a field experiment. *Behav. Ecol. Sociobiol.* **19**, 297–299.
- Gil, D. & Gahr, M. 2002 The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* **17**, 133–140.
- King, A. P. & West, M. J. 1977 Species identification in the North American cowbird: appropriate responses to abnormal song. *Science* **195**, 1002–1004.
- Kreutzer, M. L. & Vallet, E. M. 1991 Differences in the response of captive female canaries to variation in conspecific and heterospecific songs. *Behaviour* **117**, 106–116.
- Kreutzer, M., Beme, I., Vallet, E. & Kiosseva, L. 1999 Social stimulation modulates the use of the 'A' phrase in male canary songs. *Behaviour* **136**, 1325–1334.
- Kroodsma, D. E. 1989 Suggested experimental designs for song playbacks. *Anim. Behav.* **37**, 600–609.
- Kroodsma, D. E. & Byers, B. E. 1991 The functions(s) of bird song. *Am. Zool.* **31**, 318–328.
- Kroodsma, D. E., Bereson, R. C., Byers, B. E. & Minear, E. 1989 Use of song types by the chestnut-sided warbler: evidence for both intra- and inter-sexual functions. *Can. J. Zool.* **67**, 447–456.
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W. C. 2001 Pseudoreplication in playback experiments, revisited a decade later. *Anim. Behav.* **61**, 1029–1033.
- Leboucher, G., Kreutzer, M. L. & Dittami, J. 1994 Copulation-solicitation displays in female canaries (*Serinus canaria*): are oestradiol implants necessary? *Ethology* **97**, 190–197.
- Lusianti-Fitri, L. 2001 Les chants des canaris domestiques: leurs relations avec des caractéristiques physiologiques et le statut social des mâles émetteurs. PhD thesis, University Paris X, Nanterre.
- McGregor, P. K. (and 16 others) 1992 Design of playback experiments: the Thornbridge Hall Nato ARW consensus. In *Playback and studies of animal communication* (ed. P. K. McGregor), pp. 1–9. New York: Plenum Press.
- Mountjoy, D. J. & Lemon, R. E. 1991 Song as an attractant for male and female European starlings, and the influence of song complexity on their response. *Behav. Ecol. Sociobiol.* **28**, 97–100.
- Nagle, L. & Kreutzer, M. L. 1997a Song tutoring influences song preferences in domesticated canaries. *Behaviour* **134**, 89–104.
- Nagle, L. & Kreutzer, M. L. 1997b Adult female domesticated canaries can modify their song preferences. *Can. J. Zool.* **75**, 1346–1350.
- Nagle, L., Kreutzer, M. L. & Vallet, E. M. 1993 Obtaining copulation solicitation displays in female canaries without estradiol implants. *Experientia* **49**, 1022–1023.
- Nelson, D. A. 2000 A preference for own-subspecies' song guides vocal learning in a songbird. *Proc. Natl Acad. Sci. USA* **97**, 13 348–13 353.
- Nelson, D. A. & Marler, P. 1993 Innate recognition of song in white-crowned sparrow: a role in selective vocal learning? *Anim. Behav.* **46**, 806–808.
- Podos, J. 1996 Motor constraints on vocal development in a songbird. *Anim. Behav.* **51**, 1061–1070.
- Podos, J. 1997 A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* **51**, 537–551.
- Rehsteiner, U., Geisser, H. & Reyer, H. U. 1998 Singing and mating status success in water pipits: one specific song element makes all the difference. *Anim. Behav.* **55**, 1471–1481.
- Ryan, M. J. 1990 Sensory systems, sexual selection and sensory exploitation. *Oxf. Surv. Evol. Biol.* **7**, 157–195.
- Ryan, M. J. & Keddy-Hector, A. 1992 Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* **139**, S4–S35.
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. 1990 Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* **343**, 66–67.
- Searcy, W. A. 1992 Measuring responses of female birds to male song. In *Playback and studies of animal communication* (ed. P. K. McGregor), pp. 175–189. New York: Plenum Press.
- Searcy, W. A. & Marler, P. 1981 A test for responsiveness to song structure and programming in female sparrows. *Science* **213**, 926–928.
- Searcy, W. A., Nowicki, S. & Hughes, M. 1997 The response of male and female song sparrows to geographic variation in song. *Condor* **99**, 651–657.
- Spector, D. A. 1991 The singing behaviour of yellow warblers. *Behaviour* **117**, 29–52.
- Suthers, R. A. & Goller, F. 1997 Motor correlates of vocal diversity in songbirds. *Curr. Ornithol.* **14**, 235–288.
- Suthers, R. A., Vallet, E. M. & Kreutzer, M. L. 2001 Bilateral song production in domestic canaries. In *Neuro-Ethology Congr.*, Bonn, Germany.
- Vallet, E. M. & Kreutzer, M. L. 1995 Female canaries are sexually responsive to special song phrases. *Anim. Behav.* **49**, 1603–1610.
- Vallet, E. M., Kreutzer, M. L., Beme, I. & Kiosseva, L. 1997 'Sexy' syllables in male canary songs: honest signals of motor constraints on male vocal production? *Adv. Ethol.* **32**, 132.
- Vallet, E. M., Beme, I. & Kreutzer, M. L. 1998 Two-note syllables in canary songs elicit high levels of sexual display. *Anim. Behav.* **55**, 291–297.

- Whaling, C. S., Solis, M. M., Doupe, A. J., Soha, J. A. & Marler, P. 1997 Acoustic and neural bases for innate recognition of song. *Proc. Natl Acad. Sci. USA* **94**, 12 694–12 698.
- Winer, B. J. 1971 *Statistical principles in experimental design*. London: McGraw-Hill.
- Zahavi, A. 1975 Mate selection: a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.
- Zahavi, A. 1977 The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* **67**, 603–605.
- Zahavi, A. & Zahavi, A. 1997 *The handicap principle: a missing piece of Darwin's puzzle*. Oxford University Press.

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