Available online at www.sciencedirect.com

ScienceDirect

ELSEVIER

BEHAVIOURAL PROCESSES

Mate recognition by female zebra finch: Analysis of individuality in male call and first investigations on female decoding process

Clémentine Vignal [a], Nicolas Mathevon [a,b,*], Stéphane Mottin [c]

[a] *Université Jean Monnet, Laboratoire 'Ecologie & Neuro-Ethologie Sensorielles', EA3988, 23 rue Michelon, 42023 Saint-Etienne Cedex 02, France*
[b] *Université Paris-XI, The BioAcoustics Team, NAMC CNRS UMR 8620, Orsay, France*
[c] *Université Jean Monnet, Laboratoire Hubert Curien, CNRS UMR 5516, Saint-Etienne, France*

Abstract

Zebra finches are monogamous birds living in large assemblies, which represent a source of confusion for recognition between mates. Because the members of a pair use distance calls to remain in contact, call-based mate recognition is highly probable in this species. Whereas it had been previously demonstrated in males [Vignal, C., Mathevon, N., Mottin, S., 2004. Audience drives male songbird response to mate's voice. Nature 430, 448–451], call-based mate recognition remained to be shown in females. By analysing the acoustic structure of male calls, we investigated the existence of an individual signature and identified the involved acoustic cues. We tested to see if females can identify their mates on the basis of their calls alone, and performed preliminary experiments using modified signals to investigate the acoustic basis of this recognition. Playback tests carried on six individuals showed that a female zebra finch is able to perform the call-based recognition of its mate. Our experiments suggested that the female uses both the energy spectrum and the frequency modulation of the male signal. More experiments are now needed to decipher precisely which acoustic cues are used by females for recognition.
© 2007 Elsevier B.V. All rights reserved.

Keywords: Acoustic communication; Individual recognition; Mate; Songbird; Zebra finch

1. Introduction

In flock-forming monogamous birds, mate recognition has to be performed at short as well as long ranges. Indeed, mate recognition may occur without site attachment when the flock is foraging or feeding. Since acoustic cues are efficient over short and long distances, individual vocal recognition seems to be a key component of pair-bond maintenance in birds (Beer, 1970; Clayton, 1990; Marzluff, 1988; Robertson, 1996). Zebra finches (*Taeniopygia guttata castanotis*) are gregarious songbirds of subarid regions of Australia, which form life-long pair bonds and breed in loose colonies (Butterfield, 1970; Zann, 1996). Among the number of different vocalizations produced by this species, distance calls are the most frequently emitted by both sexes. Male and female use distance calls to remain in contact espe-

cially when the birds are visually isolated from their mate during flock foraging (Zann, 1996). Distance calls are known to impart information on species, subspecies and geographical origins as well as sexual and individual identity (Zann, 1984; Okanoya and Dooling, 1991; Vicario et al., 2001). Contrary to females (Zann, 1996), males learn their call through a process of vocal imitation, which explains that the calls of different males are acoustically distinct (Zann, 1984; Simpson and Vicario, 1990; Vicario et al., 2001). In spite of their unlearned origin, female distance calls have been shown to be clearly individualized and used by males for mate recognition (Vignal et al., 2004). On the contrary, no experiment has demonstrated that the learned distance calls of male zebra finches can support mate recognition by females, which is thought to rely on male song (Miller, 1979). There is a lack of playback experiments testing whether female zebra finches use call-based mate recognition and how the individual signature of male calls is used by females.

A songbird vocalization may support individual recognition if it shows a highly individualized acoustic structure allowing accurate discrimination from the remaining conspecifics. In order to encode individual identity, an acoustic cue needs

---

* Corresponding author at: Université Jean Monnet, Laboratoire 'Ecologie & Neuro-Ethologie Sensorielles', EA3988, 23 rue Michelon, 42023 Saint-Etienne Cedex 02, France. Tel.: +33 4 77 48 50 22.
E-mail address: mathevon@univ-st-etienne.fr (N. Mathevon).

thus to present variation within individuals smaller than variation among individuals (Robisson et al., 1993; Mathevon, 1996; Charrier et al., 2002; Bloomfield et al., 2004; Charrier et al., 2004). In numerous colonial bird species, individual vocal signature is known to rely on the temporal pattern of frequency modulation and/or on the energy spectrum (Okanoya and Dooling, 1991; Jouventin et al., 1999; Lengagne et al., 2000, 2001; Charrier et al., 2001; Aubin and Jouventin, 2002; Aubin, 2004; Aubin et al., 2007). As the distance call of male zebra finches is a complex sound, typically a frequency modulated downsweep of a fundamental frequency and several associated harmonics (Zann, 1984; Simpson and Vicario, 1990), it may contain various acoustic cues capable of supporting individual identity.

The present study aimed first to investigate which acoustic parameters in the male distance call are likely to be involved in individual identity coding. Second, we tested to see whether females can identify their mates on the basis of their calls alone. Finally, we performed preliminary experiments using modified signals to investigate which acoustic cues are used in mate recognition.

2. Materials and methods

2.1. Subjects

Adult zebra finches *Taeniopygia guttata castanotis* ($n = 6$ pairs, i.e., six males and six females) served as the subjects for this study and were naïve to all testing procedures. These birds were bred in an aviary of 60 birds (12L/12D photoperiod); food and water was provided *ad libitum* and temperature was maintained between 23 and 25 °C. All birds were paired for several months, in separate pair-cages allowing visual and acoustic contact with all the birds in the aviary. Before the tests, each pair raised at least one brood (brood size = 2.33 ± 0.47 chicks). All experiments occurred between 0900 and 1200 h. During testing periods, temperature, food and water conditions were the same as in the aviary. The experimental protocols were approved by the Jean Monnet University's animal care committee.

2.2. Recording of male calls and analysis of acoustic parameters

The six male zebra finches were recorded for analysis of male distance calls. Each male was isolated from its mate and 7–10 distance calls were recorded with a Sennheiser MD42 microphone, placed 0.3 m above the cage, connected to a Marantz PMD690/W1B recorder with 22,050 Hz sampling rate. We analysed a total of 55 male distance calls using Syntana software (Aubin, 1994) and Praat version 4.0.19 (http://www.praat.org). We defined 18 spectral, temporal and amplitude acoustic cues to describe the calls' acoustic structure.

The zebra finch distance call is a complex sound with a fundamental frequency associated with several harmonics (Fig. 1a). This sound is frequency and amplitude modulated. The male distance call has an elevated fundamental frequency (600–1000 Hz) compared to the female one (400–500 Hz). It is

typically a frequency-modulated downsweep of around 100 ms (Zann, 1984; Simpson and Vicario, 1990; Vicario et al., 2001). In our population of zebra finches, the typical male distance call can be divided into two segments of different durations (Fig. 1a): a first segment composed by an initial rapid ascending frequency modulation of low amplitude followed by a short stable part (the tonal component defined by Zann (1984)), and a second segment defined by a long and loud descending frequency modulation (the noise component or downsweep component defined by Zann (1984)).

To describe the frequency modulation of the call, we first isolated the fundamental frequency using the cepstrum method (Aubin, 1994). Three temporal parameters were measured from the fundamental frequency (Fig. 1b): the duration of the ascending frequency modulation of the tonal component (d_{asc}, s), the duration of the stable part of the tonal component (d_{stab}, s), and the duration of the descending frequency modulation of the downsweep component (d_{desc}, s). Four spectral parameters were also measured from the fundamental frequency (Fig. 1b): the start frequency (F_{start}, Hz), the frequency of the beginning of the stable part (F_{stab1}, Hz), the frequency of the end of the stable part (F_{stab2}, Hz), and the end frequency of the call (F_{end}, Hz). These parameters were used to calculate the two following parameters: F_{masc}, the slope of the ascending frequency modulation (Hz s^{-1}) [calculated as ($F_{stab1} - F_{start})/d_{asc}$], and F_{mdesc}, the slope of the descending frequency modulation (Hz s^{-1}) [calculated as ($F_{end} - F_{stab2})/d_{desc}$].

To describe the amplitude change over time, we measured three parameters from the envelope of the signal (Fig. 1c): the mean intensity of the entire call represented by the root-mean-square signal level (RMS$_{aver}$, dB), the highest amplitude in the call (RMS$_{max}$, Pa) and the duration between the beginning of the call and the time at which the highest amplitude in the call occurs (T_{max}, s). We then calculated the parameter RMS$_{max}$/RMS$_{aver}$.

To describe the energy spectrum of the call, measures were performed on the fast Fourier transform (FFT) of the signal. The percentage of energy in each interval of 1000 Hz was assessed. We then quantified six energy intervals corresponding to the percentage of energy of the call between 0 and 1000 Hz (band 1), 1000–2000 Hz (band 2), 2000–3000 Hz (band 3), 3000–4000 Hz (band 4), 4000–5000 Hz (band 5) and 5000–6000 Hz (band 6).

Two parameters were measured from the average power spectrum calculated from the total length of the call with the LPC method (Applying linear predictive coding) (Fig. 1d): the frequency of the first peak amplitude (F_{max}, Hz) and the intensity of this peak (I_{max}, dB), which is normalised by calculating the ratio I_{max}/RMS$_{aver}$.

2.3. Statistical analysis of acoustic parameters

These measured parameters allowed statistical analysis of the cues potentially supporting individual identity coding. We first performed a non-parametric analysis of variance (Kruskall–Wallis ANOVA, $P = 0.05$). To describe the intra-individual and inter-individual variations of each parameter we used the coefficient of variation (CV) (Sokal and Rohlf, 1995). For each parameter we calculated CV$_i$ (within individual CV)
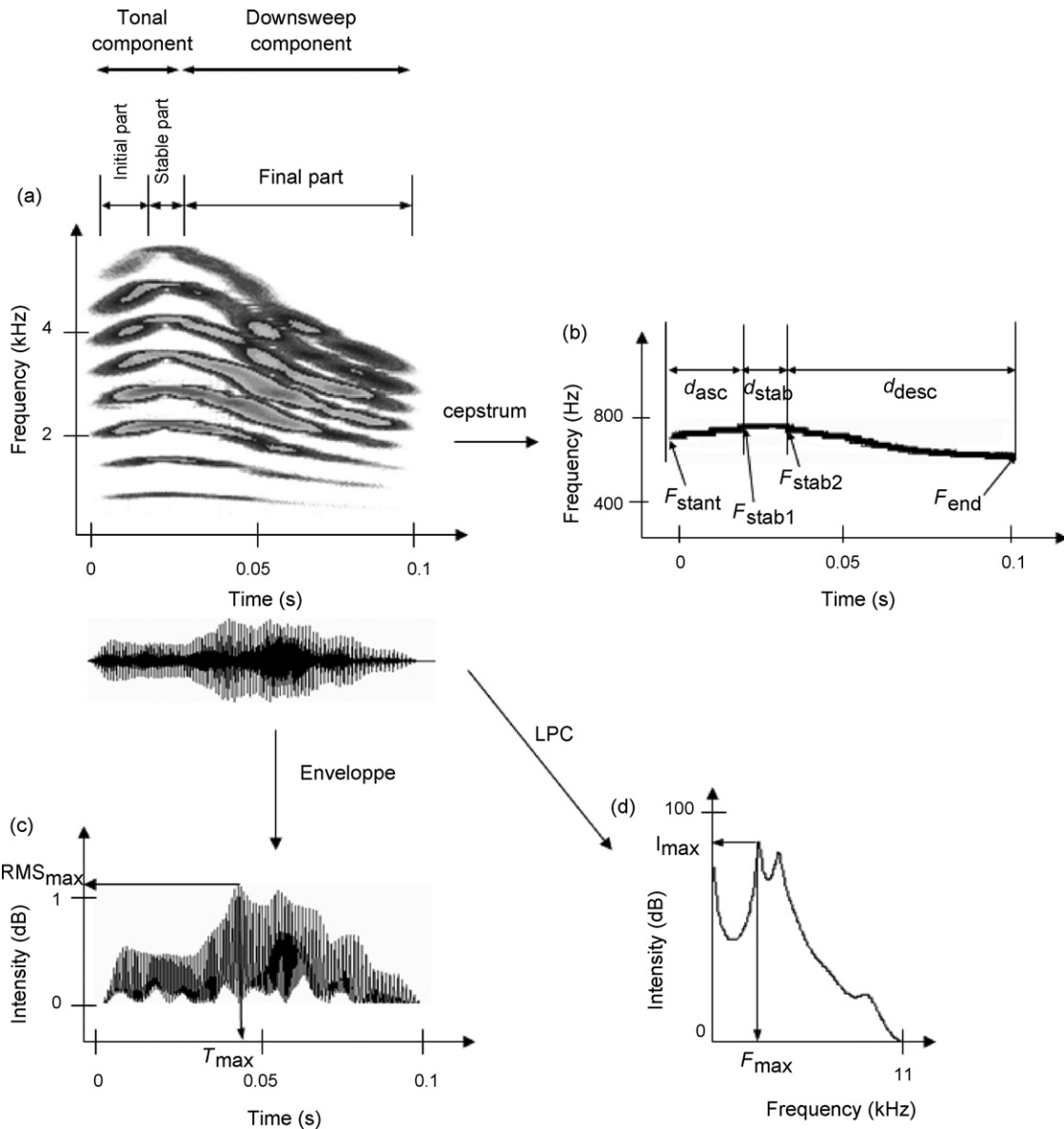
Fig. 1. Acoustic structure of the distance call of a male zebra finch. (a) Spectrogram and oscillogram of the distance call. The distance call is composed of a fundamental frequency and several harmonics. It can be divided into a first segment (the tonal component) composed by an initial rapid ascending frequency modulation of low amplitude followed by a short stable part, and a second segment defined by a long and loud descending frequency modulation (the downsweep component). (b) Fundamental frequency of the call (obtained with the cepstrum method) used to describe the frequency modulation. We measured the duration of the ascending frequency modulation of the tonal component (dasc, s), the duration of the stable part of the tonal component (d_{stab}, s), the duration of the descending frequency modulation of the downsweep component (d_{desc}, s), as well as the start frequency (F_{start}, Hz), the frequency at the beginning of the stable part (F_{stab1}, Hz), the frequency at the end of the stable part (F_{stab2}, Hz), and the end frequency of the call (F_{end}, Hz). (c) Amplitude envelope of the call. The parameters measured were the mean intensity of the entire call (RMS$_{aver}$, dB), the loudest intensity in the call (RMS$_{max}$, Pa) and the duration between the beginning of the call and the time at which the highest amplitude in the call occurs (T_{max}, s). (d) Average power spectrum calculated from the total length of the call with the LPC method (linear predictive coding). The frequency of the first peak amplitude (F_{max}, Hz) and the intensity of this peak (I_{max}, dB) were measured.

and CV_b (between individual CV) according to the formula for small sample size:

$$CV = \left\{ 100 \left(\frac{S.D.}{X_{mean}} \right) \left[1 + \left(\frac{1}{4} \right) n \right] \right\}$$

where S.D. is standard deviation, X_{mean} the mean of the sample and n is the sample size (Robisson et al., 1993). To assess the Potential for Individual Coding (PIC, Robisson et al., 1993) for each parameter, we calculated the ratio CV_b/mean CV_i (mean CV_i being the mean value of the CV_i of all individuals). For

a given parameter, a PIC value greater than one suggests that this parameter may be used for individual recognition since its intra-individual variability is smaller than its inter-individual variability.

Besides this univariate analysis, we used a multivariate approach to test if calls could be reliably classified according to the identity of their emitter. This multivariate analysis was done on the variables that were identified as potentially relevant by the ANOVA (i.e., with P values < 0.05). We transformed these variables into a set of non-correlated components using a prin-

cipal component analysis (Beecher, 1989). We then a performed a discriminant analysis on the new data set.

All statistical tests were performed using Statistica software version 6.1.

2.4. Playback procedure

For playback tests, each tested female ($n = 6$) was moved from the aviary and placed in an experimental cage (240 cm × 50 cm × 50 cm, equipped with roosts) one night prior to the start of stimulus presentation. The experimental cage was in a soundproof chamber with a 12L/12D photoperiod. Another cage was placed near the experimental cage in the chamber. According to the demonstrated effect of social context on the response of zebra finches to playback tests (Vignal et al., 2004), this companion cage contained one male–female pair and represented a simulated social context for the tested bird. As this audience was composed of different individuals during each trial, we can assume that the response of the tested birds were independent. All experiments occurred between 8 a.m. and 10 a.m. The playback equipment consisted of a Marantz PMD690/W1B recorder and an amplifier (Yamaha AX-396) connected to two high fidelity speakers (Triangle Comete 202) placed at either end of the cage. During each test, only one randomly chosen speaker emitted the playback stimuli (sound level: 70 dB(A) SPL at 1 m; each experimental signal was rescaled to match the root mean square amplitude of the control signal in order to get the same output level). The tested bird was presented with eight series of stimuli: one series of synthetic copies of natural distance calls of its mate (positive control), one series of synthetic copies of natural distance calls of a familiar male (negative control), and six experimental series of modified mate distance calls (in each series: calls played at natural rates, i.e., 2 calls s^{-1}; series broadcast at random; series duration: 10 s; interval between series: 30 s).

As the birds (recorded males, audience birds, and tested females) had been bred in the same aviary, all acoustic stimuli can be considered as perceptually equivalent for all of the birds.

2.5. Playback experiments

2.5.1. Experimental signals

A synthetic copy of one distance call (selected at random) of each recorded bird ($n = 6$ males, same individuals as those used for analysis) was created using the graphic synthesizer module of Avisoft-SAS Lab-Pro software (version 4.16, 2002). The copies were built to match as accurately as possible the acoustic characteristics of the original signals. As most of the energy in male distance calls is encompassed by seven harmonics in our population of zebra finches, all copies were synthesized with seven harmonics. These synthetic control copies were used to address the following questions.

2.5.2. Do female zebra finches respond selectively to their mate voice?

To test the ability of female zebra finches to discriminate their mate among others, we played back to the females a series

of 20 synthetic copies of male calls from their own mate and a series of 20 synthetic copies of calls from a familiar male. To rule out effects of particular individuals and limit the risk of pseudoreplication during playback experiments (McGregor, 1992), each female was tested with calls from different familiar males.

2.5.3. What are the acoustic cues used by the female for mate recognition?

In order to decipher how females identify a caller using the acoustic structure of its call, we used modified mate calls whose original characteristics were mixed with calls features of a familiar male.

Modifications of the temporal structure: we replaced temporal elements of the mate call with those of a familiar male. The first experimental signal was built using the tonal component of the mate call associated with the downsweep component of the call of a familiar male (signals TM, Fig. 2a); the second experimental signal was built using the tonal component of a familiar male call associated with the downsweep component of the mate call (signals TF, Fig. 2a). Because the most individualized part of the male call is the downsweep component (see Section 3), we tested whether this part alone (signals DS, Fig. 2a) is sufficient to evoke selective response from the female. All the following signal modifications concern this final downsweep component alone. For each modification, we chose to replace the initial mate call parameter by the same parameter measured in the call of a familiar male.

Modification of the fundamental frequency: the fundamental frequency of the mate call was shifted to reach the mean values of fundamental frequency of the familiar male call (signals FF, Fig. 2b). The natural amplitude envelope, the energy
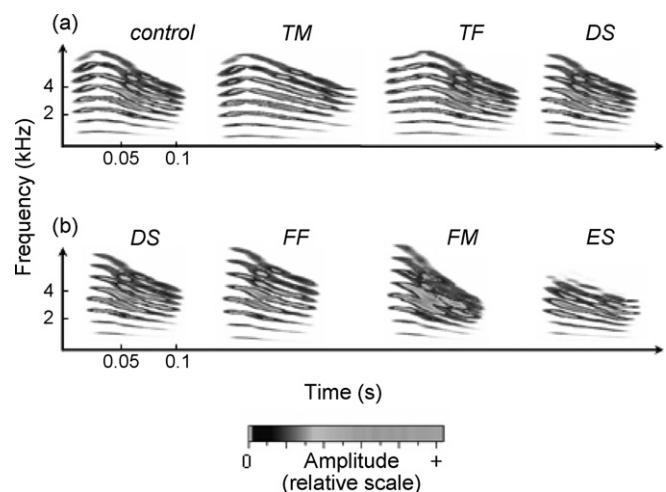

Fig. 2. Spectrograms of a male distance call and experimental modified calls. (a) Control male call (mate call) and calls presenting modifications of their temporal structure. TM: the tonal component of the mate call is associated with the final downsweep component of the call of a familiar male. TF: the tonal component of a familiar male call is associated with the final downsweep component of the call of the mate. DS: the final downsweep component of the mate call is tested alone. (b) The final downsweep component (DS) of the mate call and its modifications in the frequency and the time domains. FF: shift of the fundamental frequency. FM: modification of the frequency modulation. ES: modification of the energy spectrum.

spectrum and temporal structures of the mate call remained unchanged.

Modification of the frequency modulation: the slope of frequency modulation of the fundamental frequency of the mate call was modified to reach the slope of frequency modulation of the fundamental frequency of a familiar male call (signals FM), Fig. 2b). The natural amplitude envelope, the energy spectrum and the natural mean fundamental frequency remained unchanged.

Modification of the energy spectrum: the natural energy spectrum of the final downsweep component of the mate call was replaced with the energy spectrum of a familiar male call (signals ES, Fig. 2b). The natural amplitude and frequency structures remained unchanged.

2.6. Criteria of response

During the playback test, the vocal and locomotor activity of the tested bird was monitored with a video recorder (SONY DCR-TRV24E). We measured the latency of the vocal response (LR in seconds) and the number of distance calls emitted during the broadcasting of the stimuli (NC). Prior to the beginning of playback broadcasting, we made sure that the bird spontaneous activity was low (no vocalizations emitted during the minute that preceeded the experiment).

2.7. Statistical analysis of playback experiments

When a female showed a shorter latency (LR) and/or a greater number of calls (NC) in response to mate calls than to familiar male calls, its response was considered as mate recognition behaviour. To assess the effectiveness of mate call recognition by female zebra finches, the number of females showing a mate recognition behaviour was compared to the number of females showing no mate-directed behaviour using binomial test.

To assess the behavioural response to experimental (modified) signals and mate calls, we defined two ratios of reference:

(1) the reference latency ratio = (LR in response to familiar calls)/(LR in response to mate calls) and (2) the reference calling ratio = (NC in response to mate calls + 1)/(NC in response to familiar calls + 1). A mate recognition behaviour was expressed as follows: reference latency ratio + reference calling ratio ≥2. For each tested modification and for each bird, we defined the two following ratios: (1) the latency ratio = (LR in response to modified calls)/(LR in response to mate calls) and (2) the calling ratio = (NC in response to modified calls + 1)/(NC in response to familiar calls + 1). These ratios were compared to the reference ratios. If latency ratio > reference latency ratio, the stimulus received 0 point, if latency ratio < reference latency ratio, the stimulus received 2 points, and if latency ratio < reference latency ratio but is bigger than one, the stimulus received 1 point. In case of no response to a stimulus, no point was assigned to this stimulus. If calling ratio > reference calling ratio, the stimulus received 2 point, if calling ratio < reference calling ratio, the stimulus received 0 point, and if calling ratio < reference calling ratio but is bigger than one, the stimulus received 1 point. In case of no response to a stimulus, no point was obtained by this stimulus. A stimulus was considered to induce a mate recognition behaviour if its total score was ≥2. To compare the number of recognition responses obtained by modified calls with the number of recognition responses obtained by control mate calls, we used Wilcoxon paired-samples tests with a Bonferroni correction for multiple tests.

3. Results

3.1. Description of male calls and potential for individual identity coding

The fundamental frequency of the distance call of the male zebra finch has a mean start frequency of 730 Hz (Table 1), its short stable part (mean duration .018 s) presents a mean frequency between 827 and 1031 Hz, and its mean end frequency

Table 1
Analysis of the individuality of the acoustic parameters of the male distance call

Variable	Mean	Standard Deviation	Mean CV_i	CV_b	PIC CV_b/mean CV_i	Kruskal–Wallis *P* value
d_{stab} (s)	0.018	0.006	36.5	33.61	0.92	*P* > .05
T_{max} (s)	0.05465	0.02028	26.77	37.28	1.39	*
F_{start} (Hz)	730	25.1	2.77	3.47	1.25	*
F_{stab1} (Hz)	827	17	1.67	2.07	1.24	*
F_{stab2} (Hz)	1031	313.3	3.44	30.53	**8.87**	*
F_{end} (Hz)	509	54	7.19	10.66	1.48	*
F_{masc} (Hz s^{-1})	3800	845.5	22.46	22.44	1.00	*P* > .05
F_{mdesc} (Hz s^{-1})	5607	1883	12.46	33.74	**2.71**	*
RMS$_{max}$/RMS$_{aver}$	0.0056	0.0024	28.47	43.05	1.51	*
I_{max}/RMS$_{aver}$	0.741	0.0453	3.59	6.14	1.71	*
F_{max} (Hz)	2809	309.5	7.77	11.07	1.42	*
Band 1 (%)	0.29	0.29	61.51	100.45	1.63	*
Band 2 (%)	2.7	2.4	48.67	89.29	1.83	*
Band 3 (%)	37	21	41.71	57.01	1.37	*
Band 4 (%)	52	59	46	113.98	**2.48**	*
Band 5 (%)	17	38	58.92	224.55	**3.81**	*
Band 6 (%)	5.5	14	70.08	255.70	**3.65**	*

To describe the intra-individual and inter-individual variations of each parameter we used the coefficient of variation (CV) (Sokal and Rohlf, 1995). For each parameter we calculated CV_i (within individual CV) and CV_b (between individual CV). * Corresponds to *P* < .05. Bold PIC values correspond to PIC > 2.

is of 509 Hz. Thus, the call is frequency modulated, with a mean ascending frequency modulation of the initial segment of 3800 Hz s^{-1} and a descending final segment with a mean frequency modulation of 5607 Hz s^{-1}. Most of the call energy is concentrated between 2000 and 4000 Hz (bands 3 and 4) and the first peak of amplitude have a mean frequency of 2809 Hz. The call is amplitude modulated: the ratio RMS_{max}/RMS_{aver} is different from 1. The highest peak of amplitude occurs during the final downsweep part.

As summarised in Table 1, all the measured parameters except d_{stab} and F_{masc} are significantly modified by the identity of the caller (Kruskal–Wallis ANOVA, $P < .05$). For all these parameters, the coefficients of variation within individuals are smaller than those among individuals: all the parameters except d_{stab} and F_{masc} are potential cues for individual identity coding. The PIC values of two frequency parameters are greater than 2: the frequency of the end of the stable part (F_{stab2}) and the slope of the descending frequency modulation (F_{mdesc}) are thus highly individualized. Three spectral parameters (bands 4, 5 and 6) present a PIC greater than 2: the energy spectrum of the call is thus well individualized.

The results of the multivariate approach also reveal an individual signature in the distance call of male zebra finches. Using the principal components calculated with the acoustic parameters showing significant between-individuals variation, we performed a discriminant analysis that separate 100% of the calls of the six males.

3.2. Playback experiments

3.2.1. Female zebra finches respond selectively to mate voice

Females responded with shorter latency (individuals f1, f2, f3, f5 and f6, Table 2) and/or with more calls (individuals f1, f3, f4, f5 and f6, Table 2) to mate calls than to familiar male calls, thus showing a mate recognition behaviour (mean latency to mate calls = 1.56 ± 2.4 s, mean latency to familiar calls = 5.69 ± 6.08 s; mean number of calls in response to mate calls = 3.7 ± 2, mean number of calls in response to familiar calls = 2.2 ± 2; two-tailed binomial test $P = 0.03$). The responses of all of the six tested females verified that reference latency ratio + reference-calling ratio ≥ 2.

3.2.2. Female recognition seems to be sensitive to frequency features alterations of mate call

Due to the small number of tested individuals, the results show only tendencies and are not supported by statistical validity (after Bonferroni corrections). Nevertheless, it appears that some of the modifications are likely to impair mate vocal recognition more deeply than others (Table 2).

The most reliable signals are those presenting temporal alterations. Four females among the six tested individuals showed a mate recognition behaviour in response to composite signals built using the association of the tonal component of the mate call and the final downsweep component of the call of a familiar male (signal TM) and three females recognized composite signals built using the association of the tonal component of a

Table 2
Responses of females to mate calls, familiar calls and modified mate calls

Tested females	LR mate calls	LR familiar calls	Reference latency ratio	NC mate calls	NC familiar calls	Reference calling ratio	Total score of mate	Total score of TM	Total score of TF	Total score of DS	Total score of FF	Total score of MF	Total score of ES
f1	0.356	1.579	4.43	5	2	2	2	3	1	2	0	0	0
f2	0.33	1.579	4.78	2	6	0.43	2	0	4	0	0	2	0
f3	1.705	16.59	9.73	1	0	2	2	0	3	3	0	1	1
f4	0.449	0.376	0.84	6	2	2.33	2	4	1	2	0	0	3
f5	0.172	6.446	37.48	5	1	3	2	2	2	2	2	2	2
f6	6.326	7.562	1.19	3	2	1.33	6	3	0	0	4	0	0
Number of females performing mate recognition							4	2	4	2	2	2
P value (Wilcoxon test)							0.89	0.79	0.29	0.22	0.07	0.11

LR: latency of the vocal response (in seconds), NC: number of distance calls emitted during the broadcasting of the stimulus.

familiar male call and the final downsweep component of the mate call (signal TF). The final downsweep component alone (signal DS) elicited recognition response by four females among the six tested individuals.

Conversely, shifts of the fundamental frequency of the final downsweep component of the mate call (signal FF) elicited recognition response by only two females among the six tested individuals. Likewise, mate vocal recognition seems especially impaired when the frequency modulation or the energy spectrum of the mate call was replaced, respectively by the frequency modulation or the energy spectrum of a familiar male call (signal FM). Indeed, only two females among the six tested individuals showed recognition responses in both situations.

4. Discussion

4.1. Acoustic features encoding individual signature in male distance calls

The analysis of the distance calls of male zebra finches highlights that some acoustic parameters are likely to be used as cues for individual identity coding. Particularly, frequency parameters of the fundamental frequency of the call – like the frequency of the end of the stable part (F_{stab2}) and the slope of the descending frequency modulation (F_{mdesc}) – as well as spectral parameters – like the band energy between 3000 and 6000 Hz – are highly individualized. Consequently, information about individual identity is likely to be encoded in both spectral domain and temporal pattern: the energy spectrum of the call as well as the temporal pattern of frequency modulation of the final downsweep part are good candidates for individual identity coding. Frequency modulation is known to support acoustic coding of information in several bird species (Jouventin et al., 1999; Lengagne et al., 2000; Mathevon and Aubin, 2001; Charrier et al., 2001) but also in mammals (Charrier et al., 2002).

According to our analysis, some parameters are unlikely to encode individual identity. Temporal parameters like the duration of the stable part (d_{stab}) or the slope of the ascending part of the call (F_{masc}) are variable features both within individuals and among individuals. Such acoustic cues cannot encode any information about the identity of the caller.

Consequently, we hypothesize that the acoustic parameters used by females to identify their mate may be characteristic of the well individualized final downsweep part of the call like (i) its frequency modulation, (ii) the absolute values of its fundamental frequency and (iii) its energy spectrum.

4.2. Acoustic parameters used by female zebra finches for mate call recognition

Since only six females were tested and given the mixed results we obtained, it is difficult to sketch a precise picture of how females proceed to identify a caller. However, it remains possible to draw a general tendency. First, mate vocal recognition seems to remain possible even if a part of the call is absent or modified. Second, whereas mate recognition can be performed using the downsweep part alone, modifications of its frequency

modulation, its energy spectrum, or the absolute values of its fundamental frequency are likely to impair the recognition process. Given these results and the data from call analysis, females could use both the energy spectrum and the slope of frequency modulation of the downsweep part to identify the call of their mate. The vocal signature is certainly multiparametric, presenting a redundancy between tonal and downsweep parts that allows females to compensate the absence of segments by using the remaining information. Given the high temporal and frequency discrimination abilities of zebra finches (e.g., Weisman et al., 1998; Lee et al., 2006; Lohr et al., 2006; Friedrich et al., 2007), this vocal recognition system is likely to be efficient in spite of the noisy environment of the colony.

4.3. A vocal signature participating in pair-bond maintenance

As proposed by some authors, the maintenance of long-lasting pair bonds could avoid the necessity for active, elaborate display before breeding and thus could allow reducing activity and energy expenditure in an unpredictable environment (Davies, 1982). This could provide an evolutionary explanation for monogamy in species of arid areas like the zebra finch. Monogamy could thus provide a ready-to-use reproductive system, which could rapidly start breeding after uncertain rainfall periods (Cynx, 2001). In such opportunistic species, there is thus a need for a bird to efficiently recognize its mate during and outside the breeding season. Particularly, nomadic species like the zebra finch need to perform mate recognition without site fidelity. Some previous studies report that whereas tactile contact between mates is necessary in the process of pair-formation, established pair bonds can be maintained by auditory contact alone between mates (Silcox and Evans, 1982). Our results show that female zebra finches perform mate recognition using male calls. Nevertheless, it does not exclude that other sensory channels can be used for mate recognition, e.g., visual cues have been demonstrated to play a role in zebra finches pair-bond maintenance (Butterfield, 1970).

References

Aubin, T., 1994. Syntana: a software for the synthesis and analysis of animal sounds. Bioacoustics 6, 80–81.

Aubin, T., 2004. Penguins and their noisy world. In "Advances in Bioacoustics". Ann. Acad. Brasil. Ciênc. 76, 279–283.

Aubin, T., Jouventin, P., 2002. How to vocally identify kin in a crowd? The penguin model. Adv. Stud. Behav. 31, 243–277.

Aubin, T., Mathevon, N., Staszewski, V., Boulinier, T., 2007. Acoustic communication in the kittiwake *Rissa tridactyla*: potential cues for sexual and individual signatures in long calls. Polar Biol. 30, 1027–2033.

Beecher, M.D., 1989. Signaling systems for individual recognition: an information theory approach. Anim. Behav. 38, 248–261.

Beer, C.G., 1970. Individual recognition of voice in the social behavior of birds. Adv. Stud. Behav. 3, 27–74.

Bloomfield, L.L., Charrier, I., Sturdy, C., 2004. Note types and coding in parid vocalizations. II. The chick-a-dee call of the mountain chickadee (*Poecile gambeli*). Can. J. Zool. 82, 780–793.

Butterfield, P.A., 1970. The pair-bond in the Zebra finch. In: Social Behaviour in Birds and Mammals: Essays on the Social Ethology of Animals and Man. Academic Press, London.

Charrier, I., Mathevon, N., Jouventin, P., Aubin, T., 2001. Acoustic communication in a black-headed gull colony: how chicks identify their parent? Ethology 107, 961–974.

Charrier, I., Mathevon, N., Jouventin, P., 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. J. Exp. Biol. 205, 603–612.

Charrier, I., Bloomfield, L.L., Sturdy, C.B., 2004. Note types and coding in parid vocalizations. I. The chick-a-dee call of the black-capped chickadee (*Poecile atricapillus*). Can. J. Zool. 82, 769–779.

Clayton, N.S., 1990. Mate choice and pair formation in Timor and Australian Mainland zebra finches. Anim. Behav. 39, 474–480.

Cynx, J., 2001. Effects of humidity on reproductive behavior in male and female zebra finches (*Taeniopygia guttata*). J. Comp. Psychol. 115, 196–200.

Davies, S.J.J.F., 1982. Behavioural adaptations of birds to environments where evaporation is high and water is in short supply. Comp. Biochem. Physiol. A 71, 557–566.

Friedrich, A., Zentall, T., Weisman, R., 2007. Absolute pitch: Frequency-range discriminations in pigeons (*Columbia livia*)—comparisons with zebra finches (*Taeniopygia guttata*) and Humans (*Homo sapiens*). J. Comp. Psychol. 121, 95–105.

Jouventin, P., Aubin, T., Lengagne, T., 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. Anim. Behav. 57, 1175–1183.

Lee, T.T.Y., Charrier, I., Bloomfield, L., Weisman, R., Sturdy, C.B., 2006. Frequency-range discriminations and absolute pitch in black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*Poecile gambeli*), and zebra finches (*Taeniopygia guttata*). J. Comp. Psychol. 120, 217–228.

Lengagne, T., Aubin, T., Jouventin, P., Lauga, J., 2000. Perceptual salience of individual distinctive features in the calls of adult king penguins. J. Acoust. Soc. Am. 107, 1–9.

Lengagne, T., Lauga, J., Aubin, T., 2001. Intra-syllabic acoustic signatures used by the king penguin in parent-chick recognition: an experimental approach. J. Exp. Biol. 204, 663–672.

Lohr, B., Dooling, R.J., Bartone, S., 2006. The discrimination of temporal fine structure in call-like harmonic sounds by birds. J. Comp. Psychol. 120, 239–251.

Marzluff, J.M., 1988. Vocal recognition of mates by breeding Pinyon Jays, *Gymnorhinus cyanocephalus*. Anim. Behav. 36, 296–298.

Mathevon, N., 1996. Individuality of contact calls in the Greater Flamingo *Phoenicterus ruber* and the problem of background noise in a colony. IBIS 139, 513–517.

Mathevon, N., Aubin, T., 2001. Species-specific recognition in the Blackcap *Sylvia atricapilla* shows high tolerance to signal modifications. Behaviour 138, 511–524.

McGregor, P.K., 1992. Quantifying responses to playback: one, many, or composite multivariate measures? In: Playback Studies of Animal Communication. Plenum, New York.

Miller, D.B., 1979. The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*). Anim. Behav. 27, 376–380.

Okanoya, K., Dooling, R.J., 1991. Detection of species-specific calls in noise by zebra finches *Poephila guttata* and budgerigars *Melopsittacus undulatus*: time or frequency domain? Bioacoustics 3, 163–172.

Robertson, B.C., 1996. Vocal mate recognition in a monogamous, flock-forming bird, the silvereye, *Zosterops lateralis*. Anim. Behav. 51, 303–311.

Robisson, P., Aubin, T., Brémond, J.C., 1993. Individuality in the voice of emperor penguin *Aptenodytes forsteri*: adaptation to a noisy environment. Ethology 94, 279–290.

Silcox, A.P., Evans, S.M., 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch, *Taeniopygia guttata*. Anim. Behav. 30, 1237–1243.

Simpson, H.B., Vicario, D.S., 1990. Brain pathways for learned and unlearned vocalizations differ in zebra finches. J. Neurosci. 10, 1541–1556.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. Freeman & Company, New York.

Vicario, D.S., Naqvi, N.H., Raksin, J.N., 2001. Sex differences in discrimination of vocal communication signals in a songbird. Anim. Behav. 61, 805–817.

Vignal, C., Mathevon, N., Mottin, S., 2004. Audience drives male songbird response to mate's voice. Nature 430, 448–451.

Weisman, R., Njegovan, M., Sturdy, C., Phillmore, L., Coyle, J., Mewhort, D., 1998. Frequency-range discriminations: Special and general abilities in zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). J. Comp. Psychol. 112, 244–258.

Zann, R., 1984. Structural variation in the zebra finch distance call. Zeit. für Tierpsychol. 66, 328–345.

Zann, R., 1996. The Zebra Finch: A Synthesis of Field and Laboratory Studies. Oxford University Press, Oxford.