



Mate vocal recognition in the Scopoli's shearwater *Calonectris diomedea*: do females and males share the same acoustic code?

Charlotte Curé^{a,b,c,d,*}, Nicolas Mathevon^b, Thierry Aubin^{c,d}

^a Cerema—DTER Est, Acoustics Group, F-67035, Strasbourg Cedex 2, France

^b Equipe Neuro-Ethologie Sensorielle, Neuro-PSI, CNRS UMR 9197, Université de Lyon, Saint-Etienne, France

^c Equipe Communications acoustiques, Neuro-PSI, CNRS UMR 9197, Université Paris-Sud, France

^d Centre National de la Recherche Scientifique, UMR 9197, France

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ABSTRACT

Vocal recognition is an important process allowing partners' reunion in most seabirds. Although the acoustic basis of this recognition has been explored in several species, only a few studies have experimentally tested the acoustic coding-decoding strategy used for mate identification. Here, we investigated mate recognition in the Scopoli's shearwater (*Calonectris diomedea*) by conducting playbacks of calls with modified acoustic features. We showed that females and males in a seabird species with a moderate vocal dimorphism are likely to share the same coding-decoding rule for vocal mate identification. Specifically, a disruption of call temporal structure prevented mate recognition in both sexes, in line with the parameters previously identified as supporting an individual signature. Modifications of spectral cues and envelope structure also impaired recognition, but at a lesser extent: almost half of the tested males and females were still able to recognise their partner. It is likely that this equal ability of female and male Scopoli's shearwaters to vocally recognise their partner could be found in other seabirds.

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1. Introduction

In monogamous seabirds, reliable processes of mutual identification allow partners' reunion, even in dense and overcrowded reproductive colonies where confusion risk between individuals is high (Aubin and Jouventin, 1998, 2002; Charrier et al., 2001). The acoustic channel has been demonstrated as being an important means supporting this mate identification (Bretagnolle, 1996). In order to understand how individual identity can be conveyed by vocalizations, both acoustic analyses and playback experiments are required (Curé et al., 2012). On one hand, acoustic analyses can reveal the vocal parameters signalling the individual identity (coding strategy), i.e. the cues that can potentially be used by animals to identify an individual such as their mate. On the other hand, playback experiments are conducted to determine, among the range of acoustic cues signalling individual identity, the parameters that animals actually use for individual recognition (decoding strategy).

Previous studies have assessed the efficiency of vocal recognition process in several seabird species (Brooke, 1986; Curé et al.,

2009; Lengagne et al., 1999, 2004; Mulard et al., 2008), and investigated the acoustic cues signalling individual signatures (Curé et al., 2009; Lengagne et al., 2000, 2001). It is now known that the coding strategies to signal individual identity can differ across seabird species and depend on both ecological and phylogenetical constraints (Curé et al., 2009, 2010; Dentressangle et al., 2012). Several studies pointed out a sexual dimorphism in vocalisations of some seabird species (Aubin et al., 2007; Brooke, 1978, 1988; Curé et al., 2009; Dentressangle et al., 2012; James and Robertson, 1985; Taoka et al., 1989). However, only a few studies have experimentally tested mate recognition in females and males separately (Dentressangle et al., 2012 for the blue-footed booby *Sula nebouxii*; Curé et al., 2009 for two species of shearwaters). In particular, there is no existing work that has investigated potential differences in the acoustic decoding strategies used respectively by males and females to recognise their mate. Focusing on the Scopoli's shearwater *Calonectris diomedea*, the present study aimed to compare the reliability of mate vocal recognition between sexes by assessing the relative responsiveness of both females and males to modifications of individual vocal signatures.

The Scopoli's shearwater, formerly considered as one of the two Cory's shearwater subspecies (Mediterranean *C. diomedea*, by opposition to the Atlantic *C. d. borealis*), is now rather treated as a separate species (*C. diomedea*, Sangster et al., 2012). It is a pelagic

* Corresponding author at: Cerema—DTER Est, Acoustics Group, F-67035, Strasbourg Cedex 2, France.

E-mail address: charlotte.cure@cerema.fr (C. Curé).

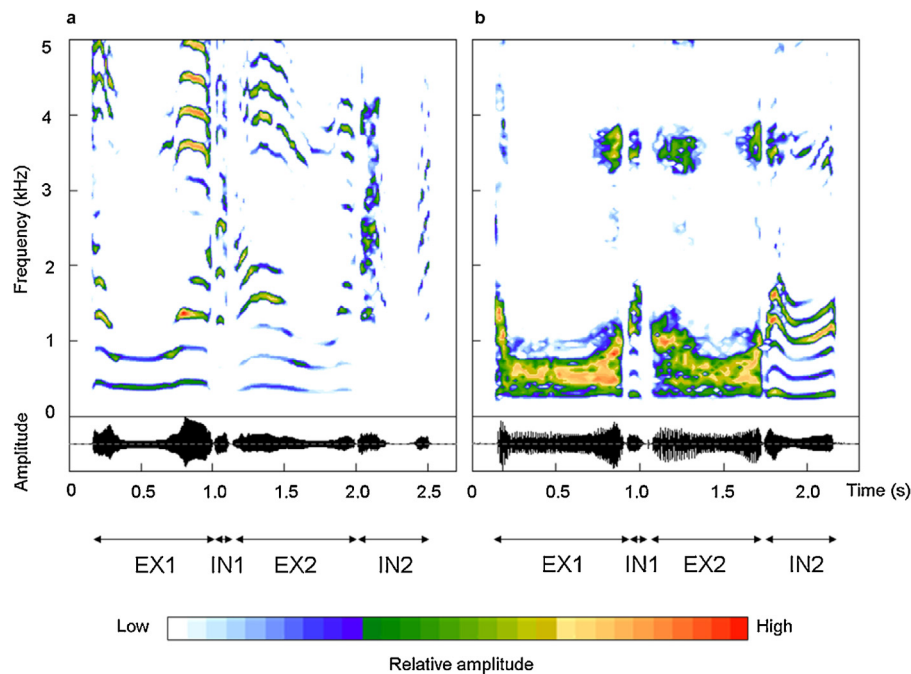


Fig. 1. Spectrograms (Hamming window; FFT length: 1024) and ocollograms of Scopoli's shearwater calls: a) male and b) female calls. In both sexes, the call is composed of two exhalant notes (EX1 and EX2) separated by a short breath (inhalant) note (IN1) and a longer one (IN2).

seabird (family Procellariidae) breeding in the Mediterranean Sea, spending most of its time at sea and coming ashore only to nest (Warham, 1990). This monogamous and highly philopatric species shows an inter-annual fidelity to the mate and to the nest site (Bradley et al., 1990; Bried et al., 2003; Mougin et al., 1999; Mougin, 2000; Ovenden et al., 1991; Rabouam et al., 1998; Thibault, 1994; Weimerskirch et al., 1985). Mate reunion occurs at night (McNeil et al., 1993) in front or within the burrow and is mediated by acoustics with both sexes producing the “major call” (Bretagnolle and Lequette, 1990; Warham, 1996). This call is composed of four broadband notes strongly modulated in frequency: two exhalant notes (EX1 and EX2) separated by a short breath (inhalant) note (IN1) and concluded by a longer inhalant note (IN2) (Fig. 1). Incubating birds usually remain silent in their burrow even when exposed to heterospecific calls and non-mate opposite-sex calls. By contrast, they vocalise in response to conspecifics same-sex calls in contexts of burrow defence and mate guarding, and also in response to their mate calls which ensures pair bond maintenance and mate identification during the breeding season (Curé et al., 2009; 2012).

In a previous acoustic analysis of Scopoli's shearwater's calls, we revealed that male and female calls differed in both the temporal and frequency domains although both sexes shared a similar overall acoustic shape (Curé et al., 2009). Specifically, the male call was higher pitched (higher fundamental frequency and more energy in higher harmonics), and also diverged in its temporal characteristics (e.g. slower amplitude modulation for the female exhalant note; difference in the duration of the call notes between sexes although the duration of the whole call remained similar). The vocal features encoding individuality in males' and females' calls included both temporal and frequency parameters (e.g., note duration, fundamental frequency values and energy spectrum features) (Curé et al., 2009). Therefore, we suspected that a combination of these various acoustic features could potentially support between-partners recognition. Since the note and inter-note durations showed the highest potential of individual coding, our predictions were that temporal features would be particularly important in this context.

Based upon these previous results, here we performed playback experiments using mate calls and modified signals derived

from the mate calls, and we compared the reliability of mate vocal recognition in female and male Scopoli's shearwaters. We modified acoustic cues of the calls in the temporal, amplitude and frequency domains, and tested to what extent these modifications disrupt mate recognition in both sexes.

2. Material and methods

2.1. Ethics statement

This study was authorised by the Regione Siciliana, Assessorato Agricoltura e Foreste, Prot. 65887 dated 23/07/07.

2.2. Subjects

We conducted the present study on colonies of Scopoli's shearwaters located on Linosa (43°52'N, 12°52'E), a volcanic island off Sicily. There, birds breed inside burrows made by crevices in the lava formation, and are mostly concentrated on the northern side of the island (Müller et al., 2014). We conducted the fieldwork in June, during the incubation period. We selected burrows that were at least 2 m distant to the closest other nest and we marked them. Because pair mates take turns to brood the egg every few days and are seldom simultaneously present at the nest, we were able to record and test males and females separately. Since incubation relays typically occurred at night, recordings and playback experiments were performed at dark between 9pm and 4am, when birds were incubating in their burrows. As illustrated by Fig. 1, Scopoli's shearwater calls are dimorphic, providing a non-invasive and 100% reliable method to assess the sex of individuals by the mean of acoustic analyses (Bretagnolle and Thibault, 1995; Curé et al., 2009; Ristow and Wink, 1980).

2.3. Recordings and signal acquisition

We recorded the calls of 27 birds (14 females and 13 males) at the entrance of their burrows using a MARANTZ PMD 670 recorder (sampling frequency: 44.1 kHz) connected to a Sennheiser MKH70

microphone (frequency response: 30–20000 Hz $\pm$ 1 dB). To avoid any variability in recording quality due to propagation-induced sound modifications, only nests located at a depth of around 1 m from the entrance of the burrow were selected for the study. Calls were re-sampled at 22.050 kHz to increase the accuracy of frequency measurements and low-frequency background noise was removed with a high-pass FFT filter (150 Hz cut-off frequency).

Spectrograms and oscillograms (Figs. 1 and 2) were made using the Seewave package (Sueur et al., 2008) in R software (R Development Core Team, 2007). Audio files corresponding to calls on Figs. 1 and 2 are available as Supplementary Material (Appendix A).

2.4. Playback experiments

To determine the parameters used by birds to identify their mate, we conducted playback experiments on 14 males and 13 females. Each tested bird was challenged with six different signals: a natural recorded sequence of mate calls (“MATE” signal), a natural recorded sequence of non-mate opposite-sex calls (“NON MATE” signal), and four experimental signals corresponding to modifications of the same MATE signal. Modifications of the MATE signal were performed in the time, amplitude and frequency domains. For each experimental signal, all parameters remained within the typical range of the studied sex and species (Curé et al., 2009), ensuring that sex- and species- specific parameters were not affected by the modifications. Therefore, if a tested bird responded differently to one of the four experimental signals compared to the MATE signal, we assumed that the bird misrecognised its partner, but not the species.

First, to test the importance of the frequency modulation and note duration, we elongated the MATE signal by +30% (“STRETCH” signal) or shortened the MATE signal by –30% (“COMPRESS” signal) using Goldwave software (Craig, 2004). The duration of the notes and silence intervals between the notes were elongated or shortened although their relative durations were kept. The spectral content of the notes (i.e. the distribution of energy between the harmonics) was also preserved. Second, to test the importance of the amplitude modulation, we used Syntana software (Aubin, 1994) to replace the amplitude envelope of the mate call by the natural envelope of another same-sex bird call (“ENV” signal). We extracted the envelope by using the analytic signal calculation which allows demodulation of an amplitude modulated signal using a Hilbert transform (Seggie 1987; Mbu-Nyamsi et al., 1994). The frequency modulation, the spectral distribution and the time parameters of the original signal were kept. Finally, to test the importance of the spectral energy features, we modified the energy distribution among harmonics using Goldwave software (Craig, 2004). We switched the amplitude level of the harmonic having the maximum amplitude and one of the lowest amplitude harmonics (“SPEC” signal). This modification changed the spectral energy distribution and the amplitude modulation of the mate calls but kept the frequency modulation and the time parameters.

Each tested bird was exposed to the 6 signals on the same night. Each of these signals was repeated three times at 2 s intervals (total duration of the playback for each signal: mean $\pm$ SD = 30 $\pm$ 4 s; with a total of 12–15 calls), and a minimum of 5 min silence duration was applied between two successive different signals (i.e. the time elapsed between the end of the tested bird’s vocal response to a broadcast signal and the start of the next signal) to avoid a possible bias due to cumulative excitation. To prevent any order effect, the order of presentation of the six signals was randomized between birds.

To avoid pseudoreplication (Hurlbert, 1984; Kroodsmas, 1989; McGregor et al., 1992), we used for each sex, five different replicates (i.e. recorded from five different individuals) of NON MATE signals,

which were then selected at random for playback experiments. These NON MATE calls were recorded from familiar birds located in the same area of the colony (not further than 50 m from the tested bird); however we did not broadcast calls from immediate neighbours since shearwaters may display lower levels of responsiveness towards this category of individuals (Mackin, 2005).

When a bird did not vocally respond to a signal, we waited for 5 min after the end of the broadcast signal before broadcasting the next one. When a vocal response occurred, the broadcast of the signal was interrupted to avoid overexcitement.

Based on our previous results (Curé et al., 2009), we expected that birds would vocally respond to mate calls (MATE signal, as positive control) but not to non-mate opposite sex calls (NON MATE signal, as negative control).

Signals were played back with a MARANTZ PMD 690 connected to a custom-built 30 W autonomous amplifier and a 4 ohm Audax loudspeaker (frequency response: 100–9 000 Hz $\pm$ 3 dB; diameter: 15 cm) placed at the entrance of the burrow. Calls were broadcast at a natural sound pressure level at 93.1 $\pm$ 1.2 dB_{SPL} (re. 2.10^{−5} Pa, n = 10 birds) measured at 1 m from individuals with a 2235 Brüel and Kjaer sound level meter (microphone type 4176, linear scale, slow setting).

2.5. Assessment of the behavioural response

During each playback, we systematically recorded the vocal response of the tested bird during a 60 s period (30 s max of playback + 30 s of post-playback). To quantify the birds’ behavioural reaction, we first assessed the occurrence of a vocal response (binary response, yes/no) within the 60 s period. In case of a vocal response, we further measured the time elapsed between the start of the broadcast signal and the first call emitted by the tested bird (latency time to respond). In this context of mate recognition, an absence of vocal response or a high latency time to respond was interpreted as an inability or a difficulty for the receiver in identifying the mate (Curé et al., 2009). We measured latencies on the waveform of the recordings using Avisoft SAS Lab Pro software (Specht, 2004).

2.6. Statistical analyses

2.6.1. Effect of the signal type, sex and playback order on the vocal response

First, to test whether the signal type and sex had an effect on the vocal response, we used Generalized Estimating Equation (GEE) models (Hardin and Hilbe, 2003) specifying a blocking unit (i.e., the bird identity, as each tested bird was exposed to six signals—repeated measures) in which we included the explanatory variables (=factor covariates) *signal* (six levels: MATE, NON MATE, COMPRESS, STRETCH, SPEC, ENV), *sex* (two levels: male, female) and the interaction term *signal* $\times$ *sex* as fixed effects. In addition, we included the explanatory variable *playback order* (six levels: from 1 to 6) as fixed effect to test for its potential influence on the vocal response. As the Sandwich variance estimator can be biased for small sample size ($N < 30$), a Jackknife variance estimator was applied. As response variables, we used the “occurrence of vocal response” (two levels of response = yes/no; fitted with binomial error structure and logit link function), and the “latency time to respond” (fitted with Gaussian error and identity link function). For the GEE model conducted on the response latency time, we excluded experiments in which subjects did not respond to the signal and so the factor covariate “*signal*” had only five levels (i.e., all playback signals except the NON MATE signal since no birds responded to this stimulus).

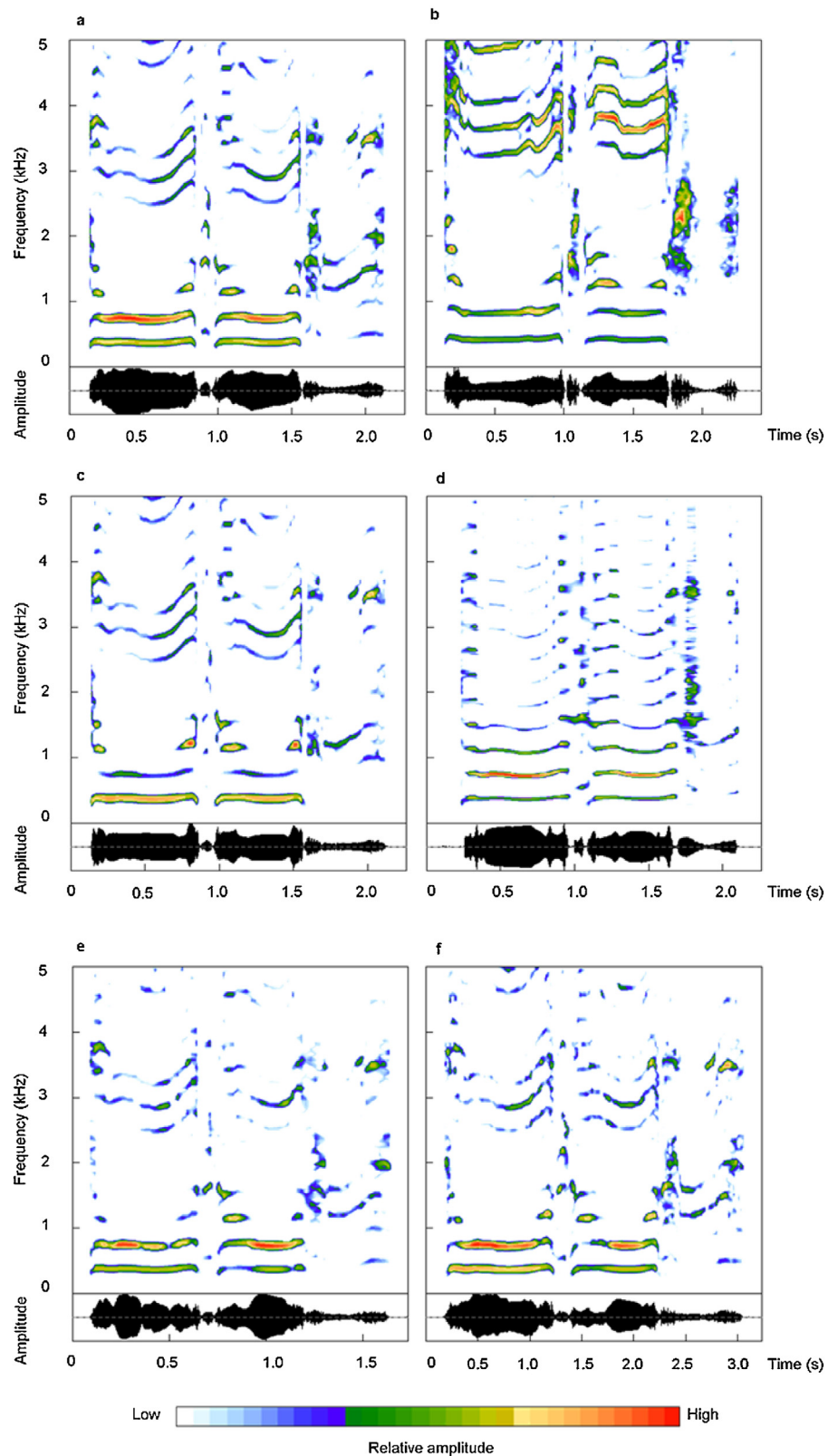


Fig. 2. Spectrograms and oscillograms of calls used to test a female: a) MATE call, b) NON-MATE call, c) "SPEC" call showing a modification of the repartition of energy between the harmonics of the MATE call, d) experimental signal "ENV" with natural envelope of the MATE call replaced by the natural envelope of another male call, e) and f) "COMPRESS" and "STRETCH" calls showing the modifications of frequency and amplitude modulations induced by the respectively -30% or +30% length change of the MATE call.

For these GEE models, we conducted an ANOVA (Wald test) for which results indicate the contribution of each factor covariate to the model fit.

2.6.2. Identification of the acoustic cues used for mate recognition

Second, to identify on which acoustic parameters birds rely for mate recognition, we split the data file by sex and conducted pair-

wise comparisons between the positive control signal (MATE) and all other signals. These tests can be considered post hoc comparisons conducted only after significant interactions between *signal* and *sex* were found (i.e. significant contribution of the factor *signal* $\times$ *sex* from results of Wald test ANOVA of the GEE explained in Section 2.6.1).

To assess whether birds can vocally discriminate their mate from other opposite-sex birds, we compared the number of responding birds to mate calls (MATE signal) versus non-mate calls (NON MATE signal). To investigate whether modifications of the mate calls disrupt the mate recognition, we compared the occurrence of vocal responses (yes/no) and the response latencies to each of the four experimental signals (COMPRESS, STRETCH, ENV and SPEC signals) versus the MATE signal.

For latencies, the pairwise comparisons were carried out using GEE models in which we included the explanatory variables *signal* (six levels: MATE, NON MATE, COMPRESS, STRETCH, SPEC, ENV) and *playback order* (from 1 to 6) as fixed effect. Results of the Wald test ANOVA indicated the contribution of each factor to the GEE model fit. Results of the GEE models indicated for each factor covariate the significance of the difference between pairs of the factor levels (e.g. difference between MATE and COMPRESS). If the factor covariate *playback order* was not significant in explaining the response variable, it was removed from the model and the GEE was rerun to obtain the best fit GEE model. Pair comparisons were conducted by setting the reference level of the factor *signal* as “MATE signal” to which each other signals was compared.

For the occurrence of vocal response (yes/no), reliable GEEs could not be conducted for pairwise comparisons because all individuals invariably responded to the MATE signal (reference factor level) leading to very large standard errors of the estimated coefficients. Hence, for this response variable, we performed pair wise post-hoc comparisons between the positive control (MATE signal) and all other signals by using a Sign test for related samples. As multiple comparisons were made with the same positive control signal (MATE), the significance level was Bonferroni-adjusted.

Lastly, to test specifically for a possible sexual dimorphism in the vocal response to mate calls, the latency time to respond to the MATE signal was compared between sexes using a Mann Whitney U test for independent samples (P-value level set at $P \leq 0.05$).

All statistical tests were performed using STATISTICA version 6.0 and R software version 3.0.2 (R Development Core Team, 2007; Venables and Ripley, 2002). GEEs were conducted using the geepack (Carey et al., 2012) in R software.

3. Results

3.1. Signal type and not playback order influenced the behavioural response to playback

Results of the Wald test ANOVA conducted on the GEE applied on the full dataset (i.e. including male and female data) showed that the interaction term *signal* $\times$ *sex* contributed significantly in explaining the variance of both the occurrence of vocal response and the response latencies (occurrence of response: χ^2 (5, $N=27$) = 34.07, $P < 0.0001$; latency to response: χ^2 (4, $N=27$) = 60.4, $P < 0.0001$). Following these results, we could conduct post-hoc GEEs separately on each sex.

To test the overall effect of the factors *signal* and *playback order* on the occurrence of vocal response, we analysed the results of the Wald test ANOVA conducted on the GEE models applied on each sex. For each response variable, i.e. the occurrence of vocal response and the response latencies, *signal* was the only significant factor in explaining the response variable (see Supplementary Table 1; occurrence of response: males: χ^2 (5, $N=14$) = 263.768,

$P < 0.0001$; females: χ^2 (5, $N=13$) = 4442.2, $P < 0.0001$; latency to respond: males: χ^2 (4, $N=14$) = 33.2, $P < 0.0001$; females: χ^2 (4, $N=13$) = 7.63 10^{15} , $P < 0.0001$).

Altogether, these results showed that the factor *signal* had marked effects on both the occurrence of vocal response and the latency time to respond whereas the order of presentation of signals did not have any influence.

3.2. Tested birds recognised their mate voice

Birds from both sexes responded to their mate's calls but never to non-mate's calls (Fig. 3). Moreover, males responded as quickly as females to the MATE signal (Mann Whitney U test: latency times = 11.4 ± 5.5 s for males vs. 8.5 ± 5.4 s for females, $z = 1.747$, $P = 0.08$, $N = 14$ males and $N = 13$ females).

3.3. Modifications of the mate call's acoustic structure impaired vocal recognition in both sexes

The COMPRESS signal elicited a vocal response in only 3 out of the 14 tested males and 1 out of the 13 tested females (Fig. 3a; Supplementary Table 2). Similar results were found with the STRETCH signal: only 1 male and 1 female vocally responded to this stimulus (Fig. 3a; Supplementary Table 2). Therefore, the modifications of amplitude and frequency modulations characterizing these signals largely impaired mate vocal recognition in both sexes. For the few responding birds, the latency time to respond to the COMPRESS signal was significantly longer compared to the MATE signal (Fig. 3b; Supplementary Table 3). The latency time to respond to the STRETCH signal was significantly longer only for the responding female (Fig. 3b; Supplementary Table 3).

The SPEC signal induced a vocal response in only 5 out of the 14 tested males and in 5 of the 13 tested females (Fig. 3a). This result indicated that the spectral content is an important feature for mate identification in both sexes. Moreover, both responding males and females showed a longer latency time to respond to the SPEC signal compared to the MATE signal, although results were significant only for females (Fig. 3b; Supplementary Table 3).

When the natural envelope of the mate calls was removed and replaced by the envelope of another bird (ENV signal), more than half of the tested males and females did not vocally reply to the playback (Fig. 3a), indicating that amplitude modulation is an important feature for mate identification in both sexes. Moreover, most of the responding birds displayed longer latencies to respond than those obtained with the MATE signal, although the difference was significant only for females (Fig. 3b; Supplementary Table 3).

4. Discussion

The present study confirmed that both female and male Scopoli's shearwaters reliably recognise their partner on the basis of the voice. Moreover, we showed that both sexes seem to be equally sensible to a disruption of the acoustic cues supporting individual signatures and are therefore likely to rely on the same acoustic features to vocally identify their partner.

Whereas all tested birds immediately vocalised in reply to their mate's call, none responded to the playback of a non-mate call. This underlined the perfect reliability of mate recognition in this shearwater species, and provided a solid ground for the interpretation of behavioural responses observed with modified experimental signals.

It thus appeared that temporal modifications conducted by compressing or stretching the calls highly impaired mate recognition in both sexes since the proportion of non-responding males and females to such modified mate signals reached almost 100%. As

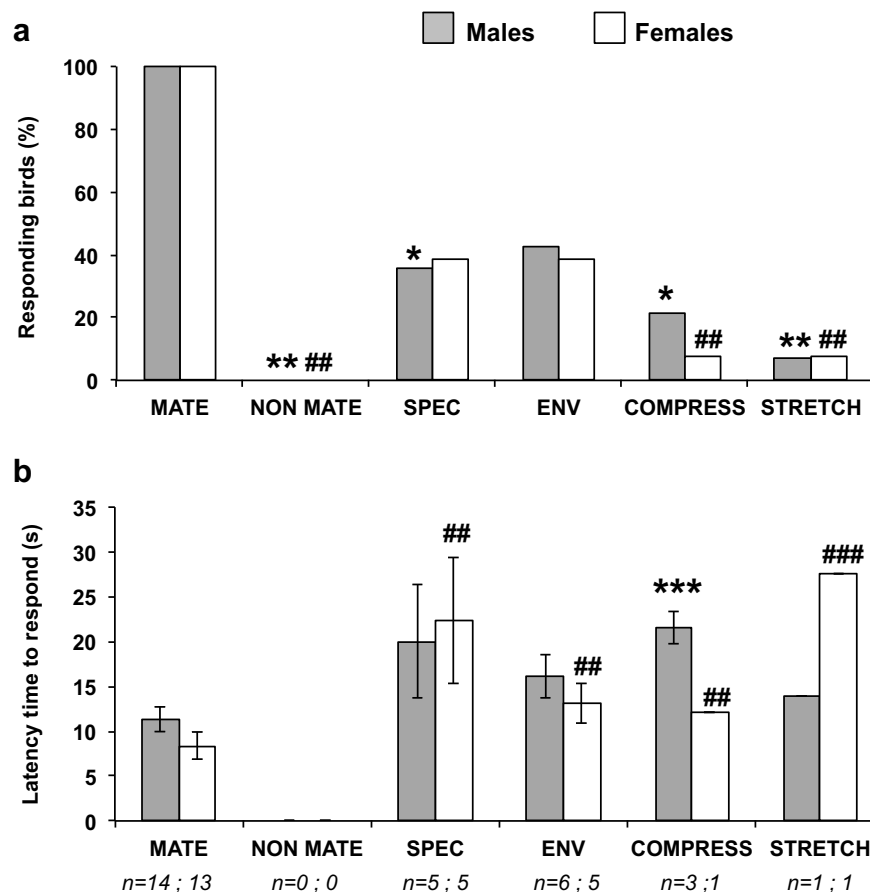


Fig. 3. Vocal responses of male and female Scopoli's shearwaters to the played-back signals: a) proportion of responding birds ($N=14$ males and 13 females); b) mean $\pm$ SEM latency time to respond (in s). The number of responding birds is indicated at the bottom of the graph as $N = \text{number of responding males; number of responding females}$. The asterisks (for males) and hashtags (for females) denote the significance levels of pairwise comparisons between mate calls (MATE signal) and each of the five other acoustic signals. For the occurrence of response (a), a sign test for related samples was applied (p-values are Bonferroni adjusted) and significant levels are indicated as follows: * or # $P < 0.01$, ** or ## $P < 0.001$, *** or ### $P < 0.0001$ (see Supplementary Table 2). For the response latencies (b), GEE models were conducted with significant levels (Jackknife variance estimator suitable for small sample size) indicated as follows: * or # $P < 0.05$, ** or ## $P < 0.01$, *** or ### $P < 0.001$ (see Supplementary Table 3).

these changes in the signal structure altered both the amplitude and frequency modulations as well as the note and inter-note silence durations without modifying the spectrum cues, it meant that an intact spectral content was not sufficient to allow mate recognition. This result is in line with sound analysis showing that notes' duration is the most individualized variable of Scopoli's shearwater calls (Curé et al., 2009). Notes' duration, once modified, may drive such a drastic change in the vocal signature so that recognition becomes nearly impossible.

Besides, modifications of the envelope structure or of the spectral content of the notes without altering the temporal cues also disrupted mate recognition in both sexes, even if it was at a lesser extent. Experimental signals with modified envelope or spectrum were identified as mate calls by less than a half of the tested females and males. In addition, these responding individuals showed longer latency times than when they reacted to their control mate calls, suggesting that they needed more time to recognise the modified mate calls as belonging to their mate.

Although the set of acoustic cues to identify the partner appeared to be remarkably similar between females and males, slight differences were found. Indeed, among the few birds that responded to experimental signals with stretched calls, modified envelope or modified spectrum, only the females responded significantly with longer latencies compared to the MATE signal. This indicates that the mate recognition system of females might be slightly more reliable than males in regard to potential mate confusion. However, given the low number of responding birds to those

signals, these differences between sexes are likely to be due to inter individual variability rather than actual differences between males and females.

We showed in a previous study that both female and male Scopoli's shearwater calls support a well-defined individual signature, with individuals of both sexes calling in a very stereotypical way (Curé et al., 2009). Here, modifications of mate vocal signatures equally impaired the recognition process in both sexes. This means that the coding-decoding process of vocal individual identity should be largely shared by both sexes in this species.

An efficient mutual recognition between partners seems essential for the breeding success in this monogamous shearwater species (Warham, 1990). This is also the case for numerous other seabirds nesting in colonies (Bried et al., 2003). We thus assume that in all seabird species, we should find an equal ability of females and males to recognise their partner although not necessarily with both sexes sharing the same acoustic coding-decoding process. In species with stronger vocal sexual dimorphism, females and males might rely on different acoustic cues, though reaching similar performance in mate recognition (e.g. in the blue-footed booby, Dentressangle et al., 2012). Also, it could be that for some species, males and/or females use other alternative or additional communication strategies than acoustics to recognise their mate, such as olfaction. Olfaction is indeed well developed in many seabird species (Bang, 1966; Bang and Wenzel, 1985) and can be involved in mate recognition as it has been experimentally demonstrated

in the Antarctic prion (*Pachyptila desolata*; Bonadonna and Nevitt, 2004).

From a broader point of view, studies about animal communication usually address potential sex differences, with questions and approaches differing between males and females (Green and Madjidjian, 2011), or conversely do not take into account sex as a possible important factor (Mackin, 2005). We think that experimental paradigms treating equally and comparing each sex should be more often considered as they may bring fundamental information regarding differential or shared abilities between females and males.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2016.04.013>.

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