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Acoustic cues used for species recognition can differ between sexes and sibling species: evidence in shearwaters

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In birds, species identity is one of the most important messages conveyed by vocalizations and is the basis for effective acoustic communication between conspecifics. Acoustic analyses can reveal which acoustic cues signal species identity, that is, the cues that could potentially be used by birds for species recognition, whereas playback experiments aim to determine which cues birds actually use for species recognition. Few studies have compared the acoustic cues used for species-specific recognition between closely related species and between sexes within species. We focused on three shearwater species (*Puffinus yelkouan*, *Puffinus mauretanicus*, *Calonectris d. diomedea*) breeding in the Mediterranean basin. In a previous study we showed that males and females of these three closely related species produce broadband calls strongly modulated in frequency and share a wide range of acoustic features signalling species identity. Here, we investigated whether these birds use similar acoustic cues for species recognition. Playback experiments showed that these cues were more similar between species of the genus *Puffinus* that rely mainly on frequency modulation than between *Puffinus* and *Calonectris* species, the latter using mainly frequency spectrum-related cues. In spite of similarities between the *Puffinus* species, we found substantial differences, *P. mauretanicus* being more sensitive to frequency value modification than *P. yelkouan*. We also found that females of the three species rely on more acoustic parameters to identify species than males. Our results show that the species-specific recognition system can show significant differences between closely related species and between sexes.

How information is coded, including both signalling and recognition of information, has been a central question since the beginning of research on animal acoustic communication (reviewed in Becker 1982; Kroodsma & Byers 1991; Bradbury & Vehrencamp 1998). One of the most important messages conveyed by acoustic communication signals is related to sender identity, for example information about species, sex and individual identity, facilitating recognition at different levels. In most bird species, vocalizations are mainly directed towards conspecifics and thus the coding of species specificity is the basis for effective acoustic communication. Understanding how information, such as species identity, is conveyed by vocalizations involves both acoustic analyses and playback experiments (Becker 1982). Acoustic analyses of the signal can reveal the vocal parameters signalling the species identity, that is, the cues that can potentially be used by animals to identify species. Playback experiments are conducted to determine, among the range of acoustic cues signalling species specificity, the parameters that animals actually use for species recognition.

The evolution of signalling and recognition of information in birds' vocalizations is influenced by various constraints including phylogeny, morphology, habitat structure, background noise, sound function, sympatric conditions with other vocalizing species, and learning (Wiley & Richards 1978, 1982; Kroodsma & Baylis 1982; Ryan & Brenowitz 1985; Podos 2001; Slabbekoorn 2004; Brumm & Slabbekoorn 2005). Vocalizations of songbirds (e.g. oscines) are the result of an interaction between genetics and learning from conspecifics,whereas acoustic signals of other bird species are innate (reviewed in Kroodsma 2004). The evolution of signalling is thus complicated by cultural drift in songbirds. Moreover, in both songbird and nonsongbird species, the use of particular cues rather than others for species recognition may be influenced by heredity and experience, but the relative importance of these two factors is still poorly understood. To understand the contributions of these factors it is important to compare signalling and recognition systems between related species.

Previously, the majority of studies that have examined species signalling systems between closely related species have done so by

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analysing the structure of acoustic signals and identifying putative species-specific signature cues. However, these comparative studies have rarely been followed by playback experiments to determine which cues are actually used in species recognition. In addition, as most previous studies have focused on songbirds in which only the male sings, little is known in regard to females, which are acoustically active in most bird species. A small number of studies have used playbacks to assess sexual differences by broadcasting the male song to males and females and showing that they rely on different cues to extract the species identity information (Dabelsteen & Pedersen 1988; Searcy & Brenowitz 1988; Nowicki et al. 2001). However, playbacks of male songs do not have the same significance for males (territorial signal) as for females (attraction signal), which complicates the interpretation of the differences observed between the sexes. In the present study, we examined and compared the acoustic cues supporting species recognition between closely related species and between the sexes, focusing on three shearwater species (Procellariidae) breeding in the Mediterranean basin: the Yelkouan shearwater (*Puffinus yelkouan*, hereafter YS), the Balearic shearwater (*P. mauretanicus*, BS) and the Cory's shearwater (*Calonectris d. diomedea*, CS). Shearwaters show the following characteristics that make these model species ideal for our study. First, both male and female produce vocalizations. During the incubation period, the territorial call is produced by both sexes in response to conspecific same-sex calls in the context of nest burrow defence, making the investigation of species-specific recognition separately in each sex possible, regardless of constraints imposed by sexual selection. Second, shearwaters use well-stereotyped and innate vocalizations, excluding the variability induced by cultural drift as observed in songbirds, and eliminating the possibility of a change in information signalling that could also affect the choice of cues used for species recognition. Third, the overall acoustic structure of the call is similar among the three shearwater species: calls are made of two to four broadband notes strongly modulated in frequency (Fig. 1). Additionally, acoustic analyses have revealed that calls of the three species are distinguishable on the basis of temporal, energy and frequency features, and share features that could potentially be used by birds for species recognition (Curé et al. 2009, 2010). This suggests that the impact of vocalizations' physical characteristics has been minimal in the selectivity of the acoustic cues used for species recognition. Finally, the species share the same general ecological constraints, such as living in similar habitats (Mediterranean islands), reproducing in colonies, cohabiting with sympatric species.

The two *Puffinus* sibling species (YS and BS) are allopatric and thus geographically isolated from each other (Fig. 2), avoiding the risk of acoustic confusion between species. Moreover, they share similar breeding patterns and show high similarities in the acoustic features of their calls. Therefore, we expected these two sibling species to show rather similar species-specific recognition systems, unless possible differences in their respective experience, regime or microhabitat (different islands of the Mediterranean basin) had influenced their ability to discriminate sounds in different ways.

Both YS and BS are sympatric with CS and consequently face a similar risk of species confusion. In sympatric conditions, interspecific discrimination of sounds minimizes energy costs related to interspecific conflicts (e.g. territorial) and hybridization. In such conditions, several strategies can be used to increase the effectiveness of interspecific sound discrimination (Becker 1982). A first possibility is that species increase the contrast between their vocalizations. A second alternative is that the vocal activity periods do not overlap between species (e.g. difference in timing of breeding). A third solution is that species sharpen their interspecific discrimination ability (e.g. by increasing sensitivity to perceive cues). CS shows marked differences in the acoustic features of the calls and in the timing of breeding compared to *Puffinus* species, which may improve interspecific sound discrimination. It could be that these strategies are sufficient so that species can accurately discriminate conspecifics from heterospecifics, or that, to secure interspecific discrimination, both species have also sharpened their ability to discriminate sounds.

In this study, we first aimed at comparing species-specific acoustic recognition systems among the three closely related shearwater species. We investigated this comparison in two main directions: (1) between sibling, allopatric *Puffinus* species (same genus), whose calls have similar acoustic features and (2) between less closely related, sympatric *Calonectris* and *Puffinus* species (different genus), which have calls with distinct acoustic features and which show overlap in the timing of breeding. Second, for each species we assessed whether sexual differences exist in their species-specific recognition system.

METHODS

Study Species

Shearwaters (Procellaridae) are medium-sized pelagic seabirds. They spend most of their time at sea out of land contact and come ashore to their colony only to nest (Warham 1990). They are monogamous, highly philopatric and show interannual fidelity to the mate and the nest (Weimerskirch et al. 1985; Ovenden et al. 1991; Rabouam et al. 1998). Shearwaters usually spend the day at sea feeding and join the colony at night (Del Hoyo et al. 1992; McNeil et al. 1993). At sexual maturity, they search for a nest location and a sexual partner (Warham 1996). Both male and female take turns incubating the egg and later feeding the chick. At the end of the breeding season when the chick is ready to fledge, both adults and chicks leave the colony. The following year, birds return to the colony and pairs normally reunite.

YS and BS both return to the colony in November, whereas CS returns later, in the middle of March, during the laying period of YS and BS. YS and BS leave their colony in the middle of July, when eggs of CS start to hatch (Thibault 1985; Bourgeois 2006).

Study Populations and Period

YS and CS were studied in colonies of the Hyères archipelago where they are sympatric (Port-Cros Island, 43°00′N, 6°23′E, and Porquerolles Island, 43°00′N, 6°12′E). BS was studied in colonies of the Balearic archipelago where it is sympatric with CS (Mallorca Island, 39°35′N, 2°18′E; Fig. 2). The field work was conducted during the 2005, 2006 and 2007 breeding seasons, in the incubation period (March to May for YS and BS, and May to July for CS) when partners take turns every few nights to brood the egg. The experiments were conducted at night, during the period of maximal vocal activity of the colony. As shearwater calls are strongly dimorphic, the sex of birds could be assessed using acoustic analyses. These methods were genetically validated by molecular sexing analyses, which had been carried out in previous studies and provided a noninvasive and 100% reliable method to determine the sex of individuals (Ristow & Wink 1980; Bourgeois et al. 2007; Curé et al. 2010).

All experiments comply with the current laws of the respective countries where they were performed. This study was approved by the following local institutions: the Prefecture of Var in France (for YS and CS) and the Conselleria de Medi Ambient del Govern Balear in Spain (for BS).

Recordings and Signal Acquisition

During incubation, the territorial call is produced by incubating male and female shearwaters during vocal interactions with

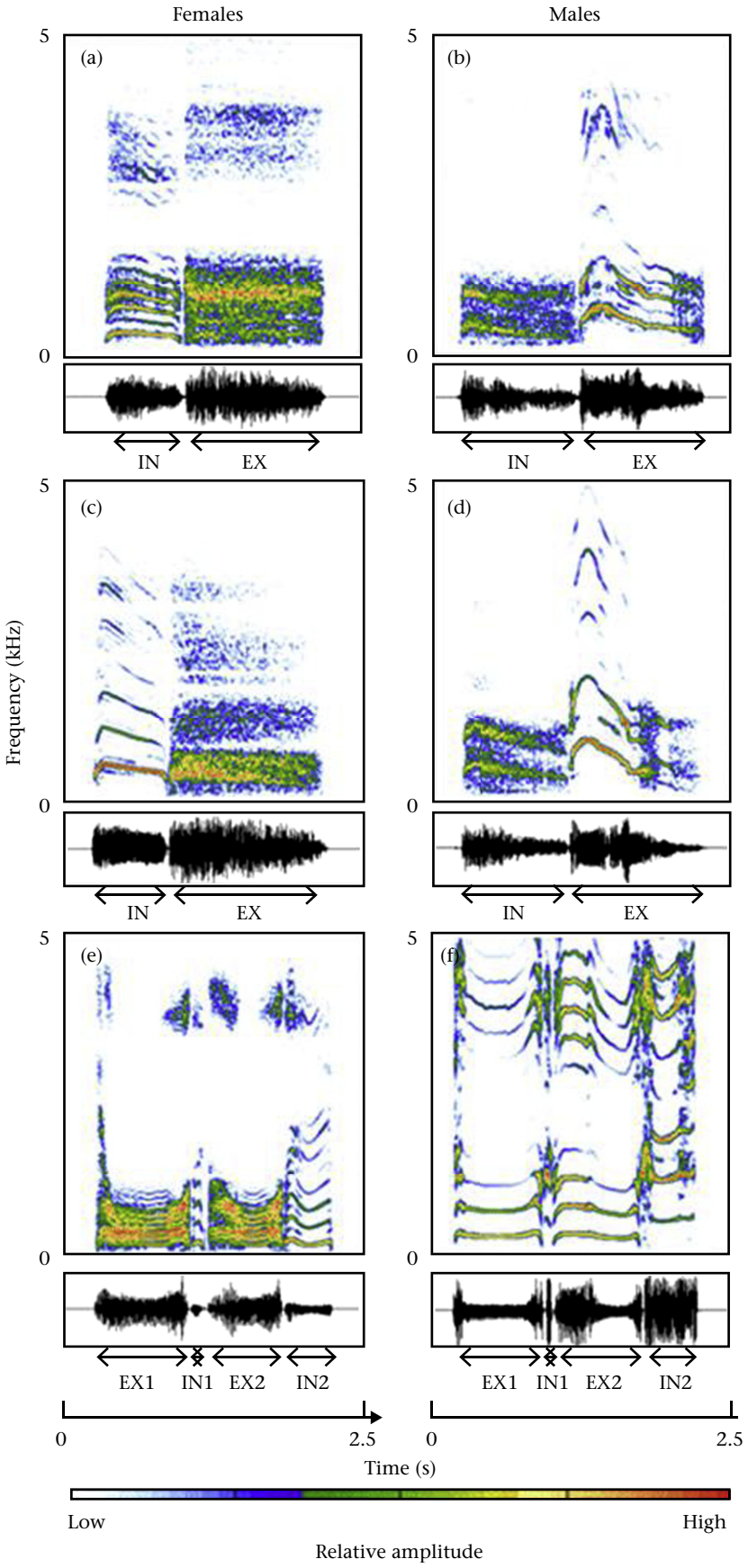

Figure 1. Spectrograms and oscillograms of female and male calls of (a, b) Balearic, (c, d) Yelkouan and (e, f) Cory's shearwaters (Hamming window, FFT length: 1024). Sound is produced during both inhalant (IN) and exhalant (EX) parts of the respiratory cycle. In the two former species, the call comprises two notes (IN and EX) while in the third species, it comprises four notes (IN1, EX1, IN2 and EX2). Spectrograms and oscillograms were prepared using the Seewave package (Sueur et al. 2008) in R software (R Development Core Team). Audio files corresponding to these calls are available as Supplementary Material (Supplementary Audio 1–6).

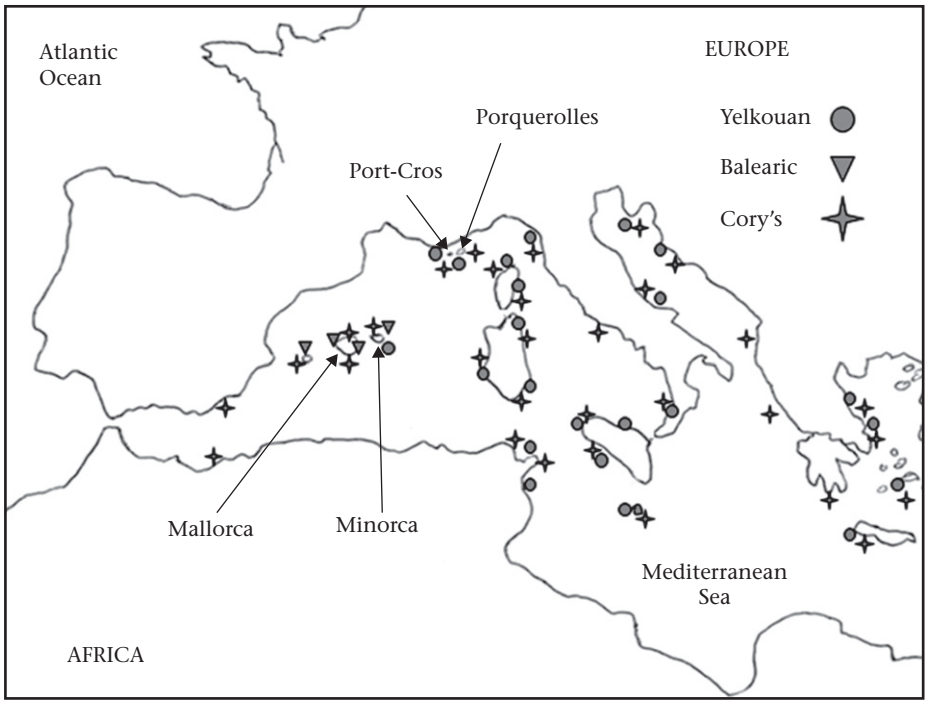

Figure 2. Distribution of the breeding areas of the Balearic, Yelkouan and Cory's shearwaters (updated from Zotier et al. 1992; Thibault et al. 1997; Ruiz et al. 2004; Genovart et al. 2005; Bourgeois & Vidal 2008).

same-sex competitors, and functions as burrow defence (Brooke 1978; Curé et al. 2009). Territorial calls were recorded at the entrance of the burrow (depth of around 1 m) using a MARANTZ PMD 670 recorder (sampling frequency: 44.1 kHz) connected to a Sennheiser MKH70 microphone (frequency response: 30–20 000 Hz ± 1 dB). Calls were resampled at 22.05 kHz before being used for playback experiments.

Playback Experiments

Control signals: conspecific same-sex calls

Previous experiments showed that conspecific same-sex calls played back at the entrance of the burrow elicit a vocal response from the burrow owner (Curé et al. 2009). For each species and for each sex, we thus used a conspecific same-sex call series as a positive control (CTRL). Each call series was composed of a natural sequence of four calls, repeated three times (duration of each series = 30 ± 4 s).

Heterospecific same-sex calls

We tested how birds respond to heterospecific calls. We predicted that birds would not respond or would respond differently to heterospecific calls compared to CTRL calls. We tested YS and BS with sympatric CS calls and, since we studied CS in colonies where it is sympatric with YS, we tested CS with YS calls. As BS and YS do respond to each other's calls (Curé et al. 2010), these two species were also tested with calls of an allopatric closely related species breeding in the Atlantic Ocean, the Manx shearwater, *Puffinus puffinus*, to investigate whether YS and BS respond to other *Puffinus* species.

To avoid pseudoreplication (Hurlbert 1984; Kroodsma 1989; McGregor et al. 1992) we built three different replicates of CTRL signals (i.e. recorded from three different individuals) for each sex and each species. We also used three different call series of Manx shearwaters and three different call series of sympatric species (YS or CS).

Experimental signals

For each of the six bird categories (males and females of each of the three species YS, BS and CS), each of the three different replicates of CTRL signals was used as a reference to build 14 types of experimental signals. We built these stimuli either by modifying the CTRL signals or by synthesis de novo. To test on which acoustic parameters the birds rely for species recognition, we performed modifications and synthesis in the temporal or in the frequency domain (Fig. 3) using Syntana (Aubin 1994), Avisoft SAS LabPro (R. Specht, Berlin, Germany) and Goldwave software, version 5.11 (http://www.goldwave.com/).

(1) To test the importance of the overall acoustic structure of the calls, we synthesized a white noise signal that was band-pass filtered in the same frequency range as the natural calls (50–5000 Hz for YS and BS and 50–10 000 Hz for CS) and we reproduced the natural temporal succession of inhalant and exhalant notes of the CTRL signal. The note durations and the internote and intercall intervals of the white noise signal were thus similar to those found in the corresponding CTRL call series. This signal (NOISE) did not contain frequency or amplitude modulations.

(2) To investigate whether both notes of the call were necessary, we built two signals with either only the inhalant note (signal INH) or only the exhalant note (signal EXH). The temporal pattern of the call was maintained by replacing the removed note with a silent interval of the same duration.

(3) To test the importance of amplitude modulation, we built a signal with a constant amplitude level using the analytic signal calculation, which allows demodulation of an amplitude-modulated signal using a Hilbert transform (Seggie 1987; Mbu-Nyamsi et al. 1994). This signal (NOAM) kept the natural frequency modulation of the call.

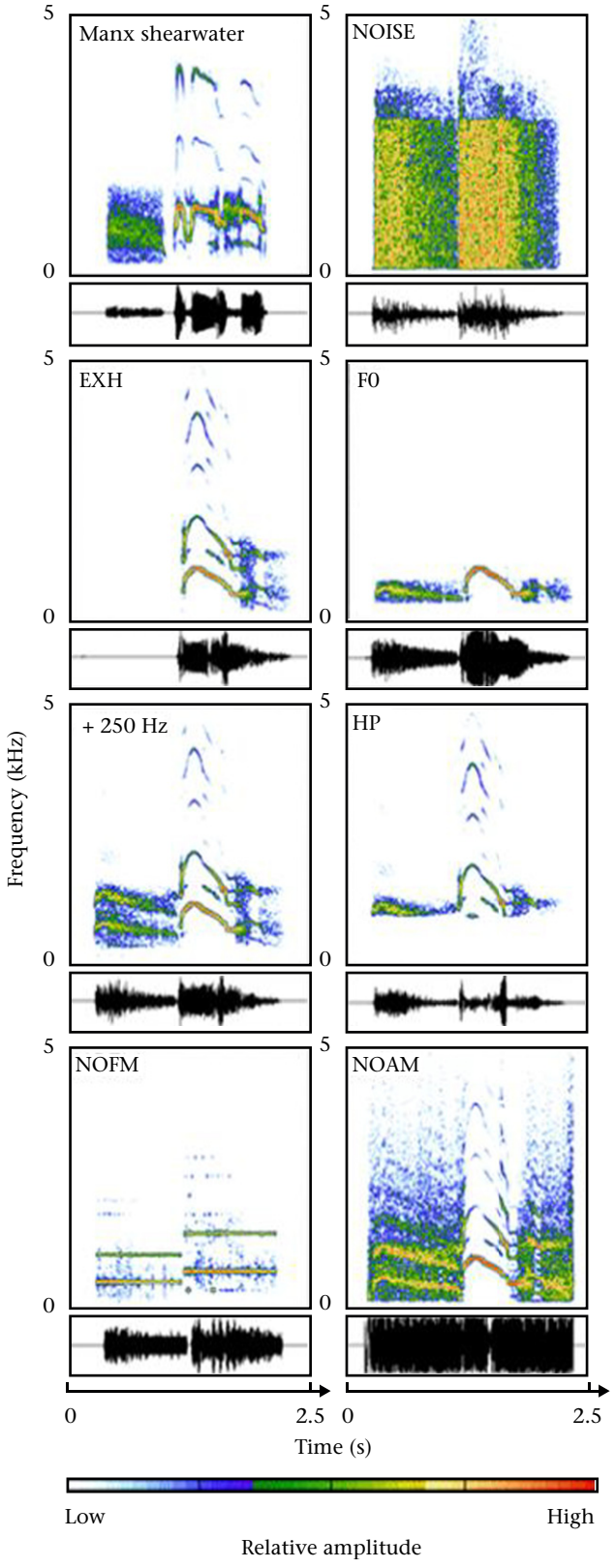

Figure 3. Spectrograms and oscillograms of some acoustic signals played back to male Yelkouan shearwaters: call of a male Manx shearwater and experimental signals built by modifications of a male Yelkouan call (NOISE, EXH, F0, +250 Hz, HP, NOFM and NOAM). NOISE: white noise signal band-pass filtered in the same frequency range as the control signal; EXH: control signal with only exhalant part of the call, F0: control signal without harmonics above the fundamental frequency; (+) 250 Hz: control signal with linear shift up by +250 Hz; HP: control signal with only the higher part of the call spectrum; NOFM: control signal without frequency modulation, with only amplitude modulation; NOAM: control signal without amplitude modulation, with only frequency modulation.

(4) To test the importance of the main temporal pattern of the call, we built a signal with a lengthened internote duration by multiplying the internote intervals by a factor of 20 (signal INTNOTx20). This call rhythm falls outside the typical range of the studied species (Curé et al. 2009, 2010).

(5) To assess the relevance of frequency modulation, we synthesized a new signal keeping the natural amplitude envelope but without any frequency modulation (NOFM). The natural distribution of energy among the harmonic spectrum was respected. To ensure that the synthesis method itself did not change the information encoded in the signal, we built a synthetic copy of the CTRL signal (CTRL-SYN). We predicted that the synthetic control (CTRL-SYN) would induce behavioural responses similar to those generated by the natural control CTRL.

(6) To assess the importance of frequency value discrimination, we linearly shifted the natural calls up or down. We performed each linear shift by picking a data record through a square window, applying short-term overlapping (50%) fast Fourier transform (FFT), followed by a linear shift (+ or −) of each spectrum and by a short-term inverse FFT (Randall & Tech 1987). The window size was 2048 points ($\Delta F = 9.8$ Hz) and the values of the shifts were ±500 and ±250 Hz (signals '+250 Hz', '−250 Hz', '+500 Hz' and '−500 Hz'). These values were chosen because the fundamental frequency of shearwaters' calls is around 500 Hz, depending on the species (see Curé et al. 2010). We tested two categories of frequency shifts, one within the range of the species (−250 Hz and +250 Hz) and the other outside this range (−500 and +500 Hz). The aim was to investigate whether birds are tuned to precise frequency values for species identification.

(7) To test whether harmonic series above the fundamental are necessary, we removed all harmonics by a low-pass digital filter and kept only the fundamental frequency (signal F0). This was done by applying optimal filtering with an FFT (Press et al. 1988). The window size was 2048 points ($\Delta F = 9.8$ Hz).

(8) To test whether the whole spectrum of the calls is required for species recognition, we built low- and high-pass filtered signals ('LP' and 'HP') by digital filtering (FFT window size: 2048). We used a cutoff frequency that divided the spectral energy equally between the two signals. As spectra were highly different between individuals' call series, the cutoff frequency was different for each of them.

Playback procedure

Signals were played back with a MARANTZ PMD 690 connected to a custom-built 4 ohm loudspeaker (frequency response: 100–9000 Hz ± 3 dB; diameter: 15 cm) placed at the entrance to the burrow. To avoid variability in recording quality from propagation-induced sound modifications, only nests located at a depth of around 1 m from the entrance of the burrow were chosen for the study. Calls were broadcast at a natural sound pressure level, estimated to be on average 90 dB SPL re. 2.10^{-5} Pa for CS and 80 dB SPL re. 2.10^{-5} Pa for YS and BS, measured at 1 m from individuals with a 2235 Bruel and Kjaer sound level meter (microphone type 4176, linear setting). An experimental playback session consisted of broadcasting five call series chosen at random from the 16 different stimuli for CS (one heterospecific call series of the sympatric species + one CTRL call series + 14 experimental signals modified from the corresponding CTRL call series) or from the 17 different ones for YS and BS (idem + Manx shearwater call series). For each call series played back, we assessed the behavioural response (see below) of the tested bird. Each stimulus type

was played back to a mean ± SD of 16 ± 2 individuals (= one stimulus type times three different replicates times five or six tested individuals). All signals were broadcast in a balanced manner between the tested birds. Therefore, among the five signals played back during an experimental playback session, the signal CTRL was not necessarily included.

For each sex of each species, the mean ± SD number of individuals tested was 53 ± 6. Eight individuals out of 321 tested birds were tested twice. For those individuals a period of at least 1 week separated the two playback sessions and the five experimental signals played back were from two different replicates of CTRL call series between the two sessions.

Behavioural assessment

In natural conditions, incubating birds remain silent inside their burrow except when they are confronted by same-sex competitors, a situation that happens several times per night (C. Curé, personal observation). Usually, the competitor comes close to the entrance of the burrow and calls. The incubating bird responds vocally while remaining incubating inside its burrow. After several vocal exchanges the competitor usually leaves. We adapted our playback protocol by limiting the duration of the sound stimulus to minimize the disturbance of the birds (maximum of 30 s of playback, with a 5 min period of silence separating the call series).

We quantified the behavioural responses of the birds exposed to playbacks by assessing the presence/absence (binary response yes/no) of the vocal responses and the latency to respond. Latency was defined as the time elapsed between the beginning of the first call series played back and the first call produced in response by the tested bird. In the context of species recognition, longer response latency to a given signal is interpreted as a difficulty for the receiver in identifying the species (reviewed in Becker 1982). We systematically recorded vocal responses within a 60 s period (30 s maximum of playback + 30 s of observation). We measured latencies on the waveform of the recordings using the Avisoft SAS LabPro software (Specht 2004, http://www.avisoft.com/). If the bird did not respond to a stimulus, we inserted 5 min of silence immediately after the stimulus had finished playing, before broadcasting the next stimulus. If there was a vocal response to a stimulus, we waited until the tested bird stopped calling and remained silent to insert the 5 min of silence.

Statistical Analyses

Effect of playback stimulus on response

To test whether a particular playback stimulus had an influence on the response and whether this influence differed between species and sexes, we used generalized linear mixed models (GLMMs; Baayen 2008) in which we included species, sex, treatment and all their interactions up to the third order as fixed effects. In addition, we included playback session (first or second for individuals tested twice) and the sequence in which treatments were delivered per subject (order of the five stimuli within a playback session) as fixed effects to control for their potential influence. As random effects we included the ID of the particular control stimulus out of which the test treatment stimulus was constructed and the ID of the tested individual. As response variables we used whether the subject responded (yes/no; fitted with binomial error structure and logit link function) and the latency to respond (fitted with Gaussian error and identity link function). For the latter we excluded experiments in which subjects did not respond to the stimulus (see Appendix for details). Hence, results of the analysis of response latencies are conditional on the subjects responding at all.

To test the effect of treatment we first compared the full model including treatment and all its interactions with species and sex with a null model not comprising treatment and its interactions (but all other terms) by using a likelihood ratio test (Dobson 2002). To test individual main effects or interactions we used likelihood ratio tests if there was a response (yes/no) or Markov Chain Monte Carlo (MCMC, Baayen 2008) analysis for latencies. We tested the significance of individual effects or interactions only once the full model revealed significance, and we report P values for main effects only when they were not involved in interactions (and we derived these P values from models with the nonsignificant interactions removed). For two-way interactions we proceeded correspondingly (i.e. tested their significance only once the three-way interaction was nonsignificant and removed from the model).

Acoustic features used for species recognition

To identify on which acoustic parameters birds rely for species recognition, we split the data file by species and sex and conducted pairwise comparisons between the positive control stimulus (CTRL) and all other stimuli. These tests can be considered post hoc comparisons conducted only after significant interactions between species or sexes were found, aimed at detecting the key acoustic cues used for species recognition. For latencies, these tests were also carried out using GLMMs in which we included the same control variables and random effects as for the GLMMs used for the full data set. For the binary response (yes/no), reliable GLMMs could not be conducted because in the control treatments all individuals invariably responded leading to very large standard errors of the estimated coefficients. Hence, for this response we conducted pairwise comparisons using a test for related samples with missing values (rsvmv-test; Mundry 1999) with the positions of the missing values kept fixed and 10 000 permutations of the responses within subjects.

We fitted mixed models in R version 2.11.1 (R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) using the function lmer of the package lme4 (Bates & Maechler 2011). MCMC analysis was conducted using the function pvals.fnc of the package languageR (Baayen 2010). For models with Gaussian error functions, we visually inspected residuals plotted against fitted values to ensure that the assumption of normally distributed and homogeneous residuals was fulfilled. To achieve this we log transformed the response latencies. The rswmv-test was run using a self-written R-function.

RESULTS

Effect of Acoustic Stimulus, Sex and Species

Overall, the treatment had marked effects on the response ($P < 0.001$; see Table A1 in Appendix, rows 'treatment'), and for latencies these effects clearly differed between species and sexes ($P < 0.001$; Table A1, rows 'interaction'). Details of statistical analyses are provided in the Appendix. There were no obvious effects of order of playback (for none of 18 different subsets of data: $P < 0.05$; for two of them: $P < 0.1$; average $P = 0.53$) nor of playback session for birds tested twice (none of six: $P < 0.05$; one: $P < 0.1$; average $P = 0.47$; no error level correction applied). Altogether, these results showed that birds responded significantly differently to different stimuli played back and that the responses to the stimuli varied according to species and sex.

In the following, we present pairwise comparisons between different stimuli, conducted separately for different species and both sexes to identify what caused the significant interactions. These comparisons aim at identifying the acoustic cues used by birds for call-based species identification and at investigating whether these cues differ between species and sexes.

Acoustic Cues used for Species-Specific Recognition

The results of the species-specific recognition system analyses are reported in Fig. 4 and Table 1.

Conspecific and heterospecific same-sex calls

Pairwise comparisons revealed that all species and both sexes responded significantly more frequently and with lower latencies to calls of their own species than to heterospecific calls (permutation test for related samples with missing values; Fig. 4a; GLMM: Table 1). This result confirms the species specificity of the shearwaters' calls.

Experimental signals

Overall acoustic structure. The signal NOISE hardly ever elicited a response (Fig. 4a), and when it did, the response latency was generally higher than for CTRL (GLMM: Table 1). These results show that the call rhythm alone does not contribute sufficient information for species recognition (Fig. 4a) but that the overall acoustic structure is necessary.

Call notes. For YS and BS females only, and for both CS sexes, the exhalant note appeared to be a crucial parameter for species recognition since the removal of this exhalant note (signal INH) elicited a significant decrease in the number of responding birds compared to the CTRL (permutation test for related samples with missing values; Fig. 4b). In contrast, for all bird categories, the inhalant part of the call was not required for species recognition since birds responded significantly differently to EXH and CTRL (Fig. 4b, Table 1).

Amplitude modulation. Among the six bird categories, only CS males responded significantly less when amplitude modulation was removed compared to the CTRL (only 60% of birds responded to NOAM) showing that these birds rely on amplitude modulation to recognize species (Fig. 4c). Neither YS nor BS showed this sexual asymmetry since males and females of both species did not show any difference in their responses to NOAM versus CTRL.

Temporal pattern. Among all the tested birds, only YS females responded vocally significantly less to INTNOTx20 and with longer latencies than to CTRL. This result shows that the silence duration between the notes of the call is an important feature for species recognition in YS females.

Frequency modulation. The analysis of the parameters used to recognize the species (Fig. 4) shows that both YS and BS rely on frequency modulation since birds responded significantly less frequently to the signal NOFM from which the frequency modulation was removed than to the CTRL signal, whereas CS do not seem to take this cue into account (permutation test for related samples with missing values; Fig. 4c). The synthetic copy of the control (CTRL-SYN) induced no significant difference in the vocal response of birds compared to the natural control, CTRL, signal (for both sexes of the three species; Fig. 4a, Table 1), ensuring that the effect of the playback of the NOFM signal on vocal responses was due to the suppression of the frequency modulation but not to the synthesis method used to build the NOFM signal.

Frequency value discrimination. Males responded less to signals shifted up in frequency and females less to signals shifted down in frequency. Thus, when frequencies were shifted to higher values (+500 Hz), only male BS and male CS showed significantly weaker vocal response than to CTRL (Fig. 4d), and male YS responded less quickly to the signal +500 Hz than to CTRL (Table 1). Even though no significant difference was observed in the number of responding females to positive-shift signals, female BS responded to the +500 Hz signal with a significantly longer latency than to CTRL (female BS: mean $\pm$ SD = 9.1 $\pm$ 3.9 s, $N = 16$ for CTRL and 26.7 $\pm$ 20.8 s, $N = 12$ for +500 Hz; GLMM: $P < 0.05$). Frequency shifts to lower values (−500 Hz) elicited a significant decrease in the vocal response of females only (for CS: $P = 0.05$: permutation test for related samples with missing values; Fig. 4d). Compared to CTRL, the vocal response to the −500 Hz signal appeared more significantly altered in BS females than in YS females (42% of responding female BS versus 73% for female YS).

Neither a negative nor a positive shift of 250 Hz elicited significant alterations of the vocal responses of CS, YS and female BS, whereas male BS showed a significantly weaker response to the +250 Hz signal than to CTRL (Fig. 4d, Table 1).

Harmonic series above the fundamental. The harmonic series above the fundamental frequency appeared to be an important feature for species-specific recognition in the six bird categories since birds responded significantly less to signals in which only the fundamental frequency was kept (signal F0; Fig. 4c).

Whole spectrum of the call. All birds responded significantly less frequently to HP than to CTRL (Fig. 4b), and some of the responding birds (female BS, male YS and male CS) responded with a longer latency than to CTRL (GLMM: Table 1) demonstrating that the lower part of the spectrum comprises important cues. The higher part of the spectrum seemed to be important only for females in which the number of responding individuals was significantly lower to LP than to CTRL (Fig. 4b).

Altogether, these results show that in all three species, males and females use a different combination of cues for species identification.

DISCUSSION

The aims of this study were (1) to compare the species-specific acoustic recognition systems among three shearwater species and (2) to investigate whether the species-specific recognition system is based on different acoustic cues in males and females within each of the species. Although the three species have a similar overall acoustic structure of the call (broadband notes modulated in frequency) and the same potentialities for coding the species identity (Curé et al. 2009, 2010), our results show that the two most closely related species (*Puffinus* spp.) rely mostly on temporal call features (frequency modulation) whereas the other, less-related, species (*C. d. diomedea*) uses the spectrum cues above all. Comparing sexes, it appears that females of the three species pay attention to a larger number of acoustic parameters than males.

Vocal Identification of Species

Playback experiments showed that the three shearwater species responded vocally to territorial calls of their own species but almost none responded to heterospecific calls. Shearwaters are thus able to discriminate between conspecific and heterospecific calls, emphasizing that territorial vocalizations allow species identification (reviewed in Becker 1982; Catchpole & Slater 1995).

The two *Puffinus* species YS and BS did not respond to the calls of an allopatric closely related species breeding in the Atlantic Ocean, the Manx shearwater. This absence of response can be explained by the fact that Manx shearwaters are never in contact with YS or BS breeding sites and thus may not represent competitors. Moreover, CS, BS and YS almost never responded to calls of

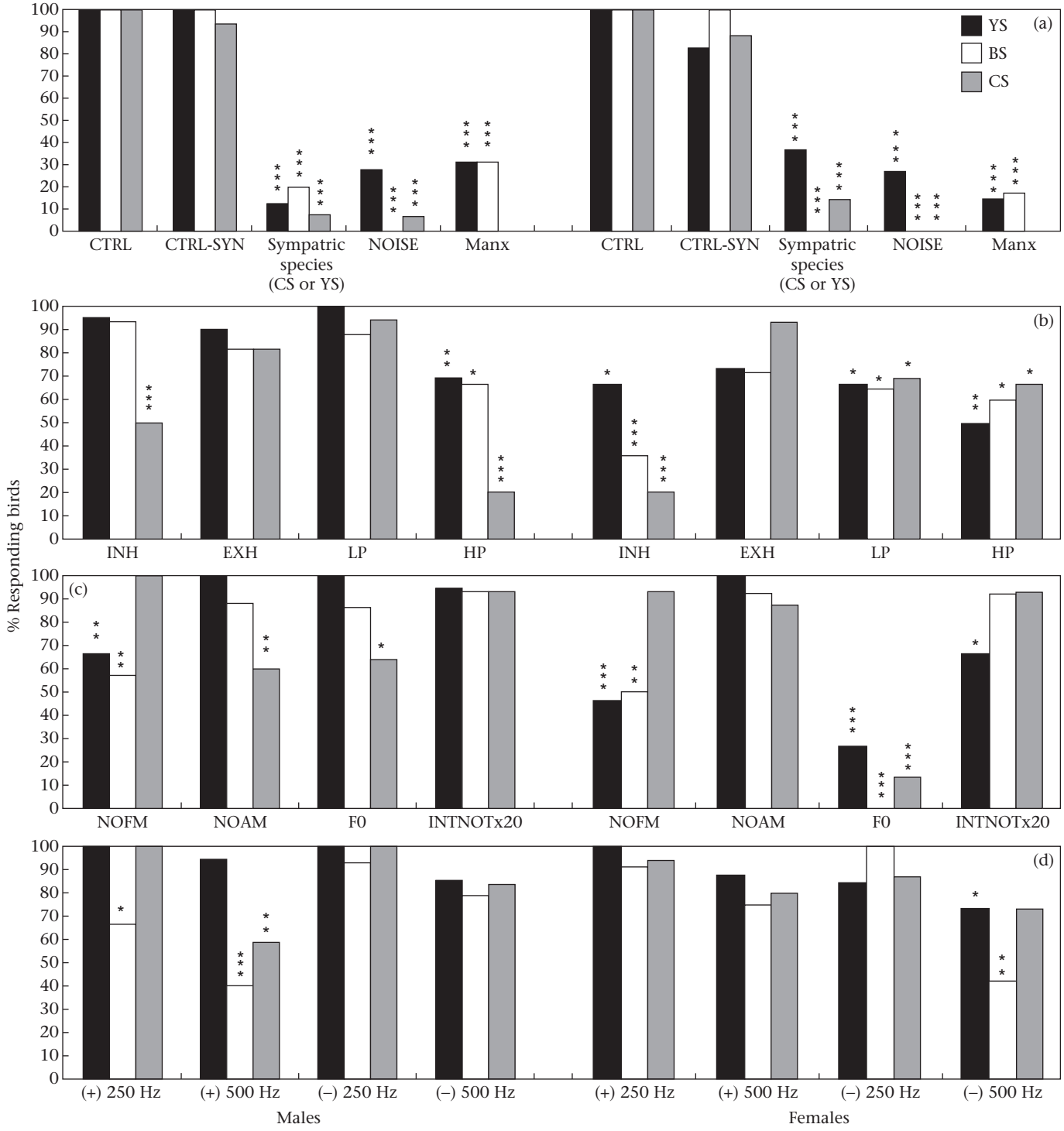

Figure 4. Vocal responses (in % of responding birds) of males and females of the three shearwater species (BS, YS and CS) to the playback of the following acoustic stimuli: (a) CTRL, CTRL-SYN, sympatric species, NOISE, Manx; (b) INH, EXH, LP, HP; (c) NOFM, NOAM, F0, INTNOTx20, (d) (+) 250 Hz, (+) 500 Hz, (−) 250 Hz, (−) 500 Hz. The asterisks denote the significance levels of pairwise comparisons between CTRL and each experimental acoustic signal (permutation test for related samples with missing values). †$P = 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. We broadcast all signals to the three species, except the Manx shearwater call series signal, which we broadcast only to YS and BS. For each signal we tested on average 17 ± 3 female YS, 19 ± 6 male YS, 13 ± 1 female BS, 16 ± 3 male BS, 17 ± 5 female CS and 16 ± 2 male CS. For details of NOISE, EXH, F0, HP, NOFM and NOAM see Fig. 3; CTRL: control signal corresponding to natural conspecific same-sex calls; CTRL-SYN: synthetic copy of the control signal; Sympatric species: natural calls of the sympatric species (CS for YS and BS, and YS for CS). Manx: natural calls of the Manx shearwater; INH: control signal with only the inhalant part of the call; LP: control signal with only the lower part of the call spectrum; INTNOTx20: signal with a lengthened internote duration multiplied by a factor of 20; (+) 250 Hz, (+) 500 Hz, (−) 250 Hz, (−) 500 Hz: control signals with respective linear shifts up by +250 Hz and +500 Hz, or down by −250 Hz and −500 Hz.

Table 1
Results of the GLMM on response latencies

Species	Effect	Response latencies					
		Females			Males		
		Estimate	SE	P_{MCMC}	Estimate	SE	P_{MCMC}
Yelkouan	Intercept	2.056	0.216		1.979	0.157	
	Ctrl_Syn	0.010	0.163	0.996	−0.003	0.131	0.972
	EXH	−0.175	0.179	0.349	0.341	0.118	**0.003**
	F0	0.690	0.276	**0.024**	0.269	0.126	0.054
	HP	−0.112	0.195	0.510	0.368	0.143	**0.015**
	INH	0.031	0.185	0.936	−0.078	0.119	0.663
	IntNotx20	0.689	0.186	**<0.001**	−0.117	0.117	0.369
	LP	0.034	0.168	0.759	−0.188	0.127	0.267
	Manx	0.742	0.375	0.081	0.759	0.203	**0.003**
	(−) 250 Hz	−0.083	0.159	0.497	0.058	0.130	0.652
	(−) 500 Hz	0.192	0.181	0.294	0.129	0.137	0.459
	NOAM	0.246	0.162	0.098	0.034	0.122	0.680
	NOFM	−0.006	0.212	0.713	0.481	0.139	**0.002**
	NOISE	0.435	0.269	0.234	1.254	0.200	**<0.001**
	(+) 250 Hz	−0.103	0.162	0.390	0.118	0.126	0.403
	(+) 500 Hz	0.127	0.168	0.420	0.425	0.124	**0.001**
	Symp. spec.	0.941	0.214	**<0.001**	1.352	0.254	**<0.001**
	session	−0.034	0.176	0.794	0.002	0.128	0.899
	order	0.032	0.028	0.211	0.001	0.020	0.793
Balearic	Intercept	2.211	0.146		2.229	0.138	
	Ctrl_Syn	0.268	0.180	0.173	−0.079	0.161	0.499
	EXH	0.261	0.189	0.174	0.345	0.166	0.057
	F0				0.282	0.167	0.253
	HP	0.723	0.198	**0.001**	0.320	0.191	0.211
	INH	0.219	0.242	0.382	−0.082	0.167	0.532
	IntNotx20	−0.015	0.181	0.891	0.321	0.165	0.138
	LP	0.795	0.199	**<0.001**	−0.051	0.173	0.445
	Manx	0.288	0.356	0.480	0.888	0.285	**0.013**
	(−) 250 Hz	−0.014	0.185	0.938	−0.084	0.194	0.555
	(−) 500 Hz	−0.044	0.242	0.845	0.459	0.210	0.078
	NOAM	−0.003	0.180	0.859	−0.059	0.176	0.602
	NOFM	0.240	0.226	0.339	0.263	0.221	0.549
	NOISE						
	(+) 250 Hz	0.354	0.189	0.075	0.610	0.199	**0.009**
	(+) 500 Hz	0.530	0.197	**0.010**	0.301	0.263	0.478
	Sympatric species				0.876	0.312	**0.008**
	order	−0.027	0.031	0.374	−0.027	0.038	0.634
Cory's	Intercept	2.734	0.081		2.530	0.102	
	Ctrl_Syn	0.106	0.105	0.641	0.260	0.128	0.231
	EXH	0.089	0.107	0.769	0.054	0.127	0.556
	F0	0.347	0.250	0.573	0.559	0.145	**0.008**
	HP	0.005	0.121	0.953	0.723	0.227	**0.008**
	INH	0.180	0.204	0.489	0.318	0.149	0.069
	IntNotx20	0.185	0.105	0.112	0.384	0.127	0.059
	LP	−0.006	0.117	0.829	0.252	0.118	0.184
	(−) 250 Hz	0.041	0.107	0.894	0.034	0.116	0.757
	(−) 500 Hz	0.144	0.118	0.762	0.364	0.124	0.110
	NOAM	−0.014	0.106	0.698	0.487	0.143	**0.018**
	NOFM	0.038	0.105	0.906	0.293	0.125	0.184
	NOISE				1.332	0.377	**0.009**
	(+) 250 Hz	−0.059	0.103	0.626	0.224	0.119	0.220
	(+) 500 Hz	0.027	0.115	0.695	0.303	0.143	0.246
	Sympatric species	0.782	0.248	**0.010**	0.822	0.380	0.149
	order	0.020	0.017	0.272	0.003	0.019	0.940

Table shows estimates, SEs and *P* values (based on Monte Carlo Marcov Chain analysis), separately for each species * sex combination. Significant *P* values are shown in bold.

their sympatric species. One possibility explaining this lack of vocal response would be a difference in some ecological traits between the three species. Indeed, preferences in the physical characteristics of the nest, timing pattern of the breeding cycle, and intrasex communication rules between mates of a pair show substantial differences between *Calonectris* and *Puffinus* species, which would suggest that species may not represent mutual competitors to one another (Bourgeois 2006; Bourgeois & Vidal 2007; Curé et al. 2009).

Comparison of Species-Specific Acoustic Recognition Systems

Calonectris *versus* Puffinus *species*

As a general result, the three shearwater species used a combination of various relevant acoustic features to identify species. For instance, the exhalant part of the call or the lower part of the call spectrum contained sufficient information to allow species identification. This information coding strategy based on many parameters may be a means to secure species-specific information transfer from the signaller to the receiver (Aubin & Jouventin 2002). A striking result is that, as predicted, the acoustic cues used for species recognition are more similar between *Puffinus* species than *Calonectris*. *Puffinus* and *Calonectris* species have a call structure that is highly frequency modulated and shows visible harmonics series and both species could potentially use these features to identify species (Curé et al. 2009). Yet, our playback experiments show that *Puffinus species* rely mostly on frequency modulation for species recognition whereas *Calonectris* mainly use spectrum cues but not the frequency modulation. Altogether, these findings suggest a divergence in the species-specific acoustic recognition system between *Puffinus* and *Calonectris* species. Although this divergence may result from genetic drift, it could be an adaptation to different constraints. For instance, a possible explanation could be that by experiencing particular conditions such as interspecific interactions, birds of each species have learned to favour the use of particular acoustic cues. As *Puffinus* and *Calonectris* are sympatric and their respective breeding periods overlap, they face interspecific interactions. Both species have distinct acoustic features in their calls, helping minimize the risk of interspecific confusion. In addition, selection may have also sharpened the ability of interspecific discrimination, resulting in divergences in the recognition systems between species. Alternatively, the differences observed in the recognition systems between bird categories (between sexes or species) could have been partly driven by differences in interindividual variability in their calls. Indeed, the more the acoustic parameters are stereotyped among individuals of a given bird category, the better these parameters can signal the species specificity and be good candidates for species recognition.

Sibling Puffinus *Species*

In a previous study, we showed that BS and YS do respond to each other's calls (Curé et al. 2010). Thus, for both species, heterospecific calls of the sister species would have a territorial meaning that may represent a threat in different ways: (1) the intruder may damage the nest site and harm the eggs, (2) the intruder may usurp the burrow, and (3) the intruder may usurp the partner and try to mate either genetically (clutch of new eggs) or socially. This response to the calls of the sister species may be caused by a high similarity of acoustic parameters between BS and YS calls. In fact, acoustic analyses have revealed that BS and YS calls differ mainly in frequency values, YS calls being approximately 100 Hz higher pitched than BS calls (Curé et al. 2010).

Nevertheless, although BS responded to YS calls, they responded quicker to calls of their own species than to YS calls, demonstrating that BS is able to discriminate between conspecific and YS calls (Curé et al. 2010). Conversely, YS responded as quickly to YS calls as to BS calls. At present, we are not able to tell whether the similar vocal responses of YS to both species' calls could be attributed to an inability of birds to discriminate between these calls. In the present study, although differences between YS and BS species-specific recognition systems were less clear-cut than those existing between CS and each of the two sibling species, they did appear. The striking result was that BS was more sensitive to frequency

shifts than YS. We showed that BS, and particularly males, responded significantly less to experimental signals with positive frequency shifts which could mimic YS calls than to the control signal (CTRL). Conversely, YS did not seem to take frequency values into account. These findings show that, although they show high similarities in call acoustic features and share the same acoustic cues for species signalling, YS and BS have substantial differences in their species-specific recognition systems. One possible explanation of such differences between sibling species could be that, experiencing different conditions, such as differences in costs/benefits of species recognition errors, BS but not YS has sharpened its ability to discriminate between interspecific sounds by increasing the sensitivity to frequency value modifications. Alternatively, the differences observed in the species-specific recognition systems between these two geographically separated sibling species could be the result of genetic drift. Indeed, shearwaters breed on remote oceanic islands providing natural geographical isolation and are highly philopatric (Rabouam et al. 1998), two factors that promote genetic drift. In this case, the differences existing in the recognition systems between sibling species could be responsible for the different territorial responses between YS and BS facing their sister species' calls

The two sister *Puffinus* species are allopatric except on one small island of the Balearic archipelago (Menorca) normally inhabited only by BS, where it has been recently discovered that hybridization between BS and YS has occurred (Genovart et al. 2005). This suggests that the species-specific recognition systems of YS and BS are too similar to avoid heterospecific confusion with the sister species.

Comparison Between the Sexes

In the three studied shearwater species, both females and males responded to the playback of same-sex territorial calls, allowing the assessment and comparison of species-specific recognition systems between the sexes. We showed that, for all species, females and males used a different combination of acoustic features to recognize the species. For instance, the removal of the higher part of the spectrum significantly decreased the vocal response only in females showing that females but not males rely on the higher part of the spectrum to recognize the species. The species-specific recognition system of females, involving more acoustic features than that of males, appears more secure in regard to heterospecific confusion. A first explanation could be that, although territorial intrasex interactions of males and females appear remarkably similar, they show slight qualitative differences between the sexes. A second potential explanation could be related to a sexual difference in the level of vocal activity. Indeed, in shearwaters and other petrels, calls coming from burrows or underground during the incubation period predominantly come from males (Bretagnolle 1996). Males call more often than females, generating a higher redundancy of the signal, which could facilitate information transfer during intrasex interactions in males compared to females. In contrast, females would have less chance to hear calls from other females and should rely on other acoustic cues than signal redundancy to secure information transfer. A third alternative could be sexual differences in the relative importance of acoustic cues and other kinds of cues such as olfactory ones to identify species. Olfaction is well developed in petrel species (Bang 1966; Bang & Wenzel 1985) and it has been experimentally demonstrated that olfactory cues can be used for mate and nest recognition (Bonadonna & Nevitt 2004; Bonadonna et al. 2004). It could be that females show less ability for using olfactory cues than males and consequently need more acoustic cues to secure a species identification system.

To conclude, we showed that, despite having similar acoustic cues in their vocalizations for species identity signalling and living under generally similar ecological constraints, closely related species can have different combinations of acoustic cues supporting a species-specific recognition system. These results emphasize that in animal acoustic communication, several strategies, that is, using different combinations of acoustic parameters, can resolve the same problem, in this case, species recognition by voice. Moreover, within species, although both sexes take turns for the same breeding tasks, shearwater females use more acoustic cues than males for species recognition. Our present knowledge of species-specific sound parameters in animals is derived almost entirely from the reactions of males to conspecific vocalizations. A sex-biased approach in which questions and experimental paradigms differ between the sexes is common in animal behaviour studies (Karlsson Green & Madjidian 2011). Thus, little is known about acoustic features used by females for species recognition. The present results show evidence of a sexual dimorphism in the species-specific cues used for species recognition. This finding highlights the importance of studying both the male and the female if we aim to get an accurate and complete picture of animal acoustic communication systems.

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Supplementary Material

Supplementary audio files associated with this article are available, in the online version, at doi:10.1016/j.anbehav.2012.04.039.

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Appendix

Data sets used for testing

Fitting models with the interactions between species, sex and treatment required a fully crossed design with regard to these factors (i.e. each combination of levels of these factors being represented in the data) with at least two replicates per combination of their levels. Hence, we had to discard the data for the Manx shearwater stimulus from all initial analyses or discard the data from tested CS birds (because the Manx stimulus was not played back to CS). We also had to discard the data regarding the playback of stimuli F0, NOISE and sympatric species from the initial analysis of the response latency because for these stimuli some species–sex combinations did not respond and thus no latencies were available. To test the influence of these stimuli we ran additional models on subsets of the data that were fully crossed with regard to these factors. For the model testing the response latencies (fitted with Gaussian error and identity link function) we also excluded playbacks in which subjects did not respond to the stimulus. Hence, results of the analysis of response latencies are conditional on the subject responding at all.

Likelihood ratio tests

As shown in Appendix Table A1, the treatment had marked effects on the response (rows 'treatment'). For response latencies, these effects differed between species and sexes (rows 'interaction'). For the binary response (yes/no), the three-way interaction between species, sex and treatment was nonsignificant (data set without stimulus Manx: $P = 0.086$; data set without tested CS: $P = 0.18$; Table A1). In these cases, however, all two-way interactions between

treatment, on the one hand, and species or sex, on the other, revealed significance (GLMM, data set without stimulus Manx: sex * stimulus: $\chi^2_{15} = 83.4$, $P < 0.001$; species * stimulus: $\chi^2_{30} = 98.6$, $P < 0.001$; data set without tested CS: sex * stimulus: $\chi^2_{16} = 61.6$, $P < 0.001$; species * stimulus: $\chi^2_{16} = 42.3$, $P < 0.001$; tests were conducted after the three-way interaction was removed from the model). The interaction between sex and species revealed significance for the data set without responses to stimulus Manx ($\chi^2_2 = 6.6$, $P = 0.036$) but not for the data set without responses of tested CS ($\chi^2_1 = 0.59$, $P = 0.44$). These last results mean that for the data set without CS (comparison only between YS and BS), the global pattern of vocal responses was similar among males and females of YS and BS, whereas for the data without stimulus Manx (comparison between CS, YS and BS, excluding YS and BS responses to Manx) it appeared significantly different between the six categories of birds (males and females of each of the three species YS, BS and CS).

Table A1
Likelihood ratio tests

Response	Excluded stimuli and data; *N*	Test	χ^2	*df*	*P*
Latency	Stimuli Manx, F0, NOISE and Sympatric species; 1047	Treatment	184.6	72	<0.001
		Interaction	74.6	24	<0.001
Latency	Stimuli F0, NOISE and Sympatric species; responses of tested CS; 704	Treatment	159.2	52	<0.001
		Interaction	45.4	13	<0.001
Yes/No	Stimulus Manx; 1556	Treatment	740.5	90	<0.001
		Interaction	41.1	30	0.086
Yes/No	Responses of tested CS; 1086	Treatment	465.6	64	<0.001
		Interaction	20.9	16	0.182

Table shows the results of likelihood ratio tests comparing the deviance of full models including treatment (stimulus) and its interactions with species and sex with null models comprising neither treatment nor any of its interactions (but species and sex and their interaction as well as the control variables session and treatment sequence and the random effects, as the null model; test = 'treatment'), and tests of the three-way interaction between treatment, species and sex (test = 'interaction'). Excluding certain stimuli and data served to avoid empty cells in the design (see Methods for details).