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# Males use time whereas females prefer harmony: individual call recognition in the dimorphic blue-footed booby

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In breeding birds, acoustic signalling is often an important cue for reunion between sexual partners. However, in spite of its potential interest, mate recognition has rarely been examined by comparing the two sexes. We studied the blue-footed booby, *Sula nebouxii*, a socially monogamous seabird, with a dramatic call sexual dimorphism suggesting two different strategies for identity coding: the female call is an amplitude-modulated sound with a harmonic series slowly modulated in frequency, while the male call is a noisy whistle strongly modulated in frequency. To compare acoustic strategies between the sexes, we (1) recorded calls of both males and females, (2) searched for an individual signature and characterized it, and (3) tested, using a playback experiment, whether the calls of males and females were equally efficient for mate recognition. Results showed that an individual signature was present in the calls of both sexes. However, the acoustic parameters involved differed: female individual identification was principally achieved by a spectral analysis of the call whereas males' identity relied mostly on temporal cues. More than 70% of both females and males tested in playback experiments successfully recognized their mate. This suggests that the coding strategies are equally efficient in terms of individual recognition between mates. From a broader point of view, our results underline the importance of assessing both males and females within the same investigative framework.

Most animal behaviour studies consider males and females differently, by attributing them conventional roles (Karlsson Green & Madjidian 2011). As a consequence, scientific questions and approaches are usually sex-biased, with questions and experimental paradigms differing between the sexes. Although a differential approach between males and females may be appropriate in some cases (e.g. when considering sexual selection questions or behaviours that are only expressed in one sex), this bias is also found in studies in which there is no a priori reason to expect male and female behaviours to differ. This is problematic since true differences between male and female behaviours are of primary interest from an evolutionary point of view. However, demonstrating behavioural differences between the sexes generally requires that male and female be treated equally, with identical and reciprocal experimental approaches for both sexes. Unfortunately, this approach is still rarely taken (Karlsson Green & Madjidian 2011).

One field in which studies of female and male behaviours are biased by a common view of sex roles is animal communication, in which the role of the 'receiver' is often attributed to females (Tibbetts & Dale 2007; Karlsson Green & Madjidian 2011). This is probably because of the abundance of animal species showing a pronounced sexual dimorphism in the type of communication signals used (e.g. species in which only males sing) or in the roles played in social interactions (e.g. courtship and expulsion of rivals).

In birds, as male songs are generally used for mate attraction, females are often tested with male vocalizations to investigate their mate choice process. Besides their partner attraction role, acoustic signals in monogamous bird species are important for partner reunions and pair bond maintenance (Aubin & Jouventin 2002; Elie et al. 2010). Seabirds usually form long-lasting pair bonds and reciprocal mate recognition is mandatory for successful reproduction, especially in species that gather in dense colonies with a high risk of confusion between individuals. In this behavioural context, there is no reason to consider that males and females should differ in their ability to discriminate between their mate and a stranger individual (e.g. Seddon & Tobias 2010; Berg et al. 2011). However, individual recognition of mates has rarely been examined by comparing the sexes using the same experimental paradigm.

Until now, most studies that have considered both sexes have not provided a comparison between males' and females' calls (e.g.

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Aubin & Jouventin 2002), or only presented qualitative sexual differences, with insufficient sample size to allow statistical comparison (Mulard et al. 2008; Cure et al. 2011). To our knowledge, only one study, on the Mediterranean Cory's shearwater, *Calonectris diomedea diomedea*, has demonstrated reciprocal mate vocal recognition (Cure et al. 2009). Sexually dimorphic calls have been reported in this species (Bretagnolle & Lequette 1990) as well as in various colonial seabirds (e.g. *Puffinus gravis*: Brooke 1988; *Pachyptila belcheri*: Bretagnolle et al. 1998; *Rissa tridactyla*: Aubin et al. 2007; Mulard et al. 2008; *Puffinus yelkouan*: Cure et al. 2009), in which differences between males' and females' vocalizations can sometimes be extreme (e.g. *Sula* spp.: Nelson 1978). As the potential of coding information about individual identity depends on acoustic signal structure (Aubin & Jouventin 2002), testing mate vocal recognition in a species with a dramatic vocal dimorphism between sexes represents a situation in which sex differences in vocal discrimination should have the greatest chance to appear.

In boobies (*Sula* spp.) the greeting calls used during courtship and partners' reunions are high-pitched whistles in males and loud trumpet-like honks in females (Nelson 1978). This strong sexual dimorphism has been used in the field to sex individuals of Nazca, *Sula granti*, masked, *Sula dactylatra*, blue-footed, *Sula nebouxii*, and Peruvian, *Sula variegata*, boobies and has been reported for the brown booby, *Sula leucogaster* (Nelson 1978; Anderson 1993; Velando & Alonso-Alvarez 2003; Zavalaga et al. 2009). Given that acoustic signal structure differs strongly between female and male, the coding strategy of individual identity may vary accordingly and so may the efficiency of both sexes to recognize their partner.

Blue-footed boobies are long lived (around 20 years old) marine birds and colonial breeders with biparental care (Nelson 1978). They are monogamous during the breeding period and use feet colour for mate selection and maternal investment as evidenced by various experimental manipulations (Torres & Velando 2003; Velando et al. 2006; Dentressangle et al. 2008). These studies highlight the importance of visual cues in this species, in which integument coloration (Velando et al. 2006; Morales et al. 2009) seems to be an efficient communication channel, which enables mates to be informed continuously about the quality and health status of their partner. Nevertheless, as feet colour can change in less than 48 h if no food is provided (Velando et al. 2006), such a highly dynamic signal may not be a reliable mate recognition cue. Blue-footed boobies show a strong sexual dimorphism in size, with females generally 32% heavier than males (Torres & Drummond 1997), as well as in vocalizations as in other booby species, with males producing long drawn-out beseeching whistles and females nasal honks (Nelson 1978). Greeting calls are part of the courtship in this species accompanying the typical sky-pointing display and are also used in mate interactions during nest shifts (saluting) and in aggressive interactions (yes-headshaking) with other birds (Nelson 1978).

In this study, we analysed the structure of signals produced by male and female blue-footed boobies and we compared the ability of both sexes to recognize their partner's call in a reciprocal playback paradigm. To our knowledge, this is the first study investigating how highly sexually dimorphic signals within a species encode for individual identity and whether or not both signals achieve similar efficiency in terms of mate recognition. The pronounced audible difference between male and female calls suggests that the two sexes may use a different acoustic code for individual identity, leading to potential differences in mate recognition abilities. Additionally, given the importance of visual cues for mate selection in this species, it is important to determine whether or not the acoustic channel is used for mate recognition.

## METHODS

### Field Study

Recordings and playback experiments were carried out during March–April 2006 in the breeding colony of blue-footed boobies located at Isla Isabel, off the Pacific coast of Mexico (25°52′N, 105°54′W). We selected 20 pairs (at least 15 m apart) with one or two chicks from 7 to 25 days old distributed along the coast of the island on a 400 m transect. All nests were individually marked with numbered flags and chicks were banded with numbered plastic colour bands to confirm nest identity. For each focal pair, we recorded a series of calls of adult males and females using a Sennheiser ME64 microphone fixed on a 4 m long pole and connected to a Marantz PMD 670 recorder (sampling frequency = 44 100 Hz; frequency response: 50–15 000 Hz ± 2.5 dB frequency range). The experiment complied with the current laws of Mexico; permissions were granted by SEMARNAT (SGPA/DGVS/01583/06) and the Parque Nacional Isla Isabel.

### Sound Analysis

To test for the presence of a vocal signature in calls, we measured and analysed 11 features in females' calls and 10 in males' calls (Fig. 1a, b). Call features were measured in both temporal and frequency domains using a customized routine analysis built with the Seewave R package (Sueur et al. 2008; see Fig. 1 for details of measured variables). The fundamental frequency was tracked through a short-term cepstral transform (Fig. 1c, d, Oppenheim & Schafer 2004). From the measurements of the start frequency (Fundstart), the maximal frequency (Fundmax), the end frequency (Fundfin), the duration between the temporal positions of Fundmax and Fundstart and the duration between the temporal positions of Fundfin and Fundmax, we calculated two slopes representing the modulation of the fundamental frequency (Slope FM1 and Slope FM2). The mean of the fundamental frequency (Fund mean) and its SD (Fund SD) were also calculated. The sound duration (Duration, Fig. 1e, f) was measured from the amplitude envelope (amplitude threshold for signal detection = 10%). By smoothing the envelope (sliding window = 40 points) and using an amplitude threshold for signal detection of 20%, we measured the mean time period of the main amplitude modulation of female calls (AM envelope). Because of the absence of a pronounced and regular amplitude modulation in male calls, this parameter was not measured for males. The call frequency spectrum (Fig. 1g, h, window length = 1024, overlap = 99%) was characterized by its mean frequency (Freq mean) and its SD (Freq SD), two parameters reporting the distribution of energy (frequency at the first quartile, Q25, and frequency at the third quartile, Q75), and the spectral entropy (sh) calculated as $S = -\text{sum}(y \log y)/\log(N)$ with $y$ = relative amplitude of the $i$ frequency with $\text{sum}(y) = 1$ and $N$ = number of frequencies (the spectral entropy of a noisy signal will tend towards 1 whereas the spectral entropy of a pure tone signal will tend towards 0, Sueur et al. 2008).

Our sample for sound analysis was composed of a total of 721 and 603 calls from 17 females and 16 males, respectively (21–80 calls/individual). To avoid different weightings in the analysis as extracted variables have different units (e.g. fundamental frequency in Hz, sound duration in s), they were transformed into z scores (centred and normalized).

### Statistical Analysis

We used a multivariate approach to test whether calls produced by each individual could be reliably classified. As male and female