



# Males' calls carry information about individual identity and morphological characteristics of the caller in burrowing petrels

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1      **Call rate, fundamental frequency and syntax determine**  
2      **male-call attractiveness in blue petrels *Halobaena caerulea***

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## Abstract

In blue petrels (*Halobaena caerulea*), females are supposed to be particularly choosy and mate choice can take a couple of years. In these lifelong monogamous seabirds, choosing a good mate is crucial and has a strong influence on their fitness. Due to their nocturnal habits, the absence of sexual dimorphism and the physical barrier between males calling from their burrow and females flying above the colony, vocal signals seem to be one of the main channels for males to communicate with potential mates. However vocal communication is also costly as it attracts predators. In a previous study, we investigated whether acoustic traits of male calls carry information about morphological characteristics that might be indicators of males' qualities. Here, we test whether these acoustic traits linked to male characteristics are actually attractive to females. To do so, we played-back modified calls of males to females in a colony of blue petrels of the Kerguelen archipelago. We found that flying females were more attracted by high-pitched calls and by calls broadcasted at a high call rate. Previous studies showed a relationship between pitch and bill depth and length. In filter-feeding birds, such as blue petrels, bill morphology influences feeding efficiency. A high call rate is an indicator of sexual motivation and makes the caller easier to locate by potential mates and predators in the hubbub of the colony. We thus hypothesized that producing frequent high-pitched calls may be the result of a trade-off between predation avoidance and conspicuous sexual signalling.

## Keywords

Vocal communication, sexual signal, attractiveness, mate choice, seabird, blue petrel

# 1 Introduction

2       Knowing how animal communication systems work is crucial to understanding social  
3 behaviours. Indeed, social interactions are mediated by signals in one or several modalities, such as  
4 acoustic, olfactory, or visual (Bradbury and Vehrencamp 2011). Among these, vocal signals provide  
5 information mainly to conspecifics, but not exclusively (see Magrath et al. 2015 for a review). Signals  
6 carry different kinds of information, stable information on long-term (e.g. species, sex, social status,  
7 group membership, phenotypic characteristics: Searcy and Nowicki 2005) and temporary information  
8 through acoustic modulations (e.g. motivation: Morton 1977, emotion: Briefer 2018). Vocalizations may  
9 also bear stable individual signatures to allow efficient discrimination among individuals (Beecher 1989,  
10 Tibbets and Dale 2007), particularly in social species. For instance, it has been shown in rodents that  
11 alarm calls contain more individual information in species living in large groups than species living in  
12 small ones (Pollard and Blumstein 2011).

13       Informative content of vocal signals has been particularly well-studied in birds in the framework  
14 of sexual selection likely because the “dual function hypothesis” states that birdsongs serve two main  
15 purposes: attract mates and deter rivals (Kroodsmma and Byers 1991, Catchpole and Slater 2008). Due to  
16 high costs (predation, social aggression, etc) and physiological constraints associated with their  
17 production, vocalizations are considered as honest and reliable signals of male phenotypic qualities,  
18 such as body size and body condition (Gil and Gahr 2002). Individual differences in phenotypic qualities  
19 among males are translated by differences in structure of vocal signals (Rowe and Houde 1996).

20       Several acoustic parameters have been shown to reflect a singer’s characteristics linked to  
21 overall male quality, and there is evidence that females are attracted by specific acoustic parameters  
22 related to male qualities (see Nowicki and Searcy 2004 for a review). A well-known example is the  
23 fundamental frequency (or pitch) which negatively correlates with body size (e.g. Galeotti et al. 1997,  
24 Mager et al. 2007, Favaro et al. 2017, Kriesell et al. 2018). In many species, larger males have a higher  
25 breeding success because body mass is an indicator of physical strength and/or foraging success (Chastel  
26 et al. 1995, Salton et al. 2015) and females rely on fundamental frequency as a sexual signal (review in  
27 Cardoso 2012). Besides frequency parameters, females rely on song output structure, complexity, and

vocal performance (Nowicki and Searcy 2004). For instance, they are attracted by songs constituted of many and/or complex elements (Martín-Vivaldi et al. 2000, Martín-Vivaldi 2004) which may indicate a male in good body condition (Martín-Vivaldi et al. 1998). Females are also attracted by males that perform challenging songs (i.e. with a high rate and/or a large frequency bandwidth), that indicates body size, age, and endurance (Ballentine et al. 2004, Ballentine 2009, Byers et al. 2016).

In many bird species, among the functions that calls and songs fulfil, there is the transmission of individual signature information (Falls 1982, Lambrechts and Dhont 1995). Vocal individual signature is a crucial piece of information as it provides the basis for individual recognition required for almost all aspects of social life (Tibbetts and Dale 2007). Individual recognition is possible when an individual identifies another according to the easily-distinctive characteristics of its signal, for example acoustic parameters of a call (Falls 1982, Dale et al. 2001). Vocal signature has been assessed in many non-songbird species, especially seabirds (e.g. Robisson et al. 1993, Charrier et al. 2001, Aubin and Jouventin 2002, Aubin et al. 2007, Favaro et al. 2017). In many seabirds, adults usually breed in dense colonies (Croxall and Prince 1980, Wittenberg and Hunt 1985), form lifelong monogamous bonds (Warham 1996), and forage far from the colony. Individual recognition would be advantageous when returning to the nest/mate/chick (Warham 1990, Mathevon et al. 2003, Jouventin et al. 1999, Curé et al. 2011), especially for species that have no nest site to meet at (Robisson et al. 1993, Aubin and Jouventin 2002).

Among Procellariidae, burrowing petrels occupy deep burrows and are active, at the colony, at night during the breeding period (Warham 1990). In this context, visual communication seems strongly restricted whereas olfactory and vocal signals may be used for long-range communication. The role of olfaction has been investigated in petrel social interactions. Studies suggest that the chemical signature of nests is used by mates to find their own burrow (Bonadonna et al. 2001, Bonadonna et al. 2004), and that individual body's odour carries individuality signals and some genetic information that may influence mate choice (Bonadonna and Nevitt 2004; Bonadonna and Sanz-Aguilar 2012; Leclaire et al. 2017). Comparatively, acoustic communication has been poorly studied so far. For some burrowing-petrel species, vocal communication is extremely costly because it exposes callers to an increased risk of predation (Mougeot and Bretagnolle 2000). However, during pair formation, bachelor males looking

for a mate intensely vocalize at night from their burrow, while females fly and call over the colony (Bretagnolle 1990, Warham 1996). These costly calls are likely to be reliable sexual signals that attract and/or stimulate suitable mates (Bretagnolle 1990), but we still ignore which one, between male or female, stimulates the other. Petrels also vocalize after being vocally challenged by a conspecific close to the entrance of their burrow. These vocalizations might be aggressive signals to defend the own burrow (occupied year after year) from intruders (Warham 1990, Warham 1996). According to Bretagnolle (1996), burrowing petrels have a small vocal repertoire. For instance, genera *Halobaena* and *Pachyptila* produce a single major call produce in both sexual and agonistic interactions.

As previously mentioned, calling in the colony increases the predation risks (Mougeot and Bretagnolle 2000) and should thus provide important benefits to balance these costs. Following the suggestions of the wide literature on other bird species, we can hypothesize that calls play a role in mate choice and/or male competition for mate and burrow. However, informative content of most burrowing-petrel species' calls have been neglected so far. Nevertheless, previous studies have shown that heavy males call with a higher rhythm than light males in blue petrels (Genevois and Bretagnolle 1994) and that large heavy males produce low-pitched calls in snow petrels (Barbraud et al. 2000), suggesting several ways of body size signalling. Here, we investigated the informative content of calls in two burrowing petrels: the blue petrel (*Halobaena caerulea*) and the Antarctic prion (*Pachyptila desolata*) (Procellariidae, Gmelin 1789). These two petrel species, with similar breeding and feeding ecology (Warham 1990, Warham 1996), are highly vocal and suffer from a high predation pressure by the brown skua (Mougeot and Bretagnolle 1998). We tested the hypotheses that acoustic parameters in both temporal and spectral domains of a petrel calls (i) reflect morphological characteristics, and (ii) bear an individual vocal signature.

## Material and Methods

### Studied species

Blue petrels (*H. caerulea*) and Antarctic prions (*P. desolata*) are monogamous medium-sized (about 190 and 160 g, respectively) seabirds belonging to the Procellariidae. They spend most of their life at sea but they breed in dense colonies on coastal grass slopes. This long-lived seabirds do not reach

sexual maturity for five years. A couple of years is needed for establishing stable pair-bonds. They show a high partner fidelity, low extra-pair paternities, and divorces are rare. After pairing, pairs produce a single egg per year. From the incubation (50 days in blue petrels, 45 in Antarctic prions) to the fledging (50 and 53 days, respectively), they exhibit bi-parental cares. Partners regularly alternate fasting period in the burrow and feeding trips at sea (Warham 1990, Warham 1996, Brooke 2004).

Callers are mainly non-breeder males and females looking for a mate but they are tricky to catch, as they occupy inaccessible burrows and fly over the colony, respectively. On the contrary, breeders usually have high mate and burrow fidelity over years (Warham 1996, Brooke 2004). Occupied burrows can be equipped with an artificial access to the incubating chamber, by digging a tunnel and closing it with a stone. From this artificial door, birds become easily accessible. For this reason, we worked only on breeding birds. After some infructuous attempts to obtain females' replies to playback, we constrained our study to only on males' calls. According to the literature, very few breeding females react to the playback of bachelor males' calls (Brooke 1978, Bretagnolle and Lequette 1990, Bretagnolle 1996). A possible explanation is that, in natural conditions, females call only in flight, whereas males call from their burrow. The study was thus restricted on breeding males of the two petrel species: 31 blue petrels (16 in 2017 and 15 in 2018) and 24 Antarctic prions (16 in 2017 and 8 in 2018). Mates take a shift every eight to ten days incubating the eggs (Warham 1990), and occasions when both mates are present in the nest at the same time are quite rare. This enabled us to record the male alone. Petrels well tolerate weak human disturbance (Bergès et al. 2019), allowing us to conduct several recording sessions on the same individuals to assess the individual signature. All the birds were metal ringed and individually identifiable.

## **Study location**

Fieldwork was performed in a small sub-Antarctic island (Ile Verte, 49°51' S, 70°05' E) of the Kerguelen Archipelago, in the southern Indian Ocean, where blue petrels and the Antarctic prions gather in stable colonies during the breeding season. We conducted the study during the 2017 and 2018 birds' incubation period (November 25<sup>th</sup> 2017 to December 12<sup>th</sup> 2017 and November 27<sup>th</sup> 2018 to December 20<sup>th</sup> 2018 for

blue petrels; December 23<sup>rd</sup> 2017 to January 16<sup>th</sup> 2018 and December 25<sup>th</sup> 2018 to January 13<sup>th</sup> 2019 for Antarctic prions).

## **Playback procedure and recording of provoked calls**

During incubation, breeding petrels are silent in the colony, rarely calling spontaneously, seemingly to avoid predation (Mougeot and Bretagnolle 2000). However, it is possible to elicit vocal responses by broadcasting calls of same-gender conspecifics (Taoka et al. 1989, Bretagnolle & Lequette 1990, Curé et al. 2011). Petrel calls consist of a repetition of distinct sections called “phrases”, themselves composed of indivisible elements called syllables (see Catchpole and Slater 2008 for definition, see Fig. 2a and Bretagnolle 1996 for sonograms). Signals to broadcast were graphically synthesized from spontaneous calls of nine bachelor male blue petrels and five bachelor male Antarctic prions recorded in the same colonies in 2013 and 2017 (i.e. series of phrases, themselves constituted of syllables). We used the signal processing software Avisoft–SASLab Pro v 5.2.11 (Specht 2017). Each synthesized call consisted in a two-phrase call of a single blue petrel or Antarctic prion male, separated by a silence of  $200 \pm 60$  ms ( $5.5 \pm 1.6$  s and  $3.43 \pm 0.85$  s, respectively; mean  $\pm$  SD). To avoid pseudoreplication (McGregor et al. 1992), nine blue petrel call series and five Antarctic prion call series were played-back.

At the beginning of the 2017 and 2018 breeding seasons, we checked each burrow of the colony to detect occupied burrows with the presence of an egg. We then choose distant burrows (i.e. separated by a minimum of five meters) for each species. Several recording sessions were performed on each male, with an interval of two to five day between sessions to avoid habituation. In total, we performed a mean of  $3 \pm 1$  recording sessions on 31 blue petrel males and we recorded 172 calls ( $6 \pm 4$  calls per male; mean  $\pm$  SD). We performed  $4 \pm 2$  recording sessions on 24 Antarctic prion males and we recorded 224 calls ( $5 \pm 3$  calls per male; mean  $\pm$  SD). Playbacks were carried out at night during the period of maximal vocal activity of the colony (i.e. between 22:00 and 02:00, unpublished data) in dark nights (Mougeot and Bretagnolle 2000), and in calm weather (i.e. wind speed  $< 4$  km/h and no rain) to limit background noises.

The recording equipment was composed of an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20-20 000 Hz  $\pm$  2.5 dB) connected to a Marantz PMD 660 digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). The microphone was positioned on the ground, at the burrow entrance, and one randomly selected synthesized call was broadcast at a natural sound pressure level ( $\pm$  67 dB, measured on 111 calls from 54 males with a sound level meter) using a TASCAM DR-07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). Calls emitted in reply by the burrow owner were recorded during the playback and two minutes after the end of the playback stimulus. If the focal individual did not reply, the playback was repeated every 30 seconds, up to three times.

### **Morphometric measurements**

Soon after recording, the identity of the bird was checked by capturing the birds and reading the metal ring. The day after, birds were caught again in order to take a blood sample from the brachial vein (0.2 mL in Queen lysis buffer, Seutin et al. 1991) and the following seven morphometric measurements (some shown in Fig. 1, Cramp and Simmons 1977): bill length (CL), from edge of implantation of feathers to the bill tip; bill depth (BD), from angle of gonys to dorsal surface of hook; head length (HL), from supraoccipital to front edge of bill; tarsus length (TL), from middle of mid-tarsal joint to distal end of tarso-metatarsus; wing chord length (WL), maximum flattened chord, from carpal joint to tip of longest primary; mass (MS); wing area (WA).

Head and tarsus measurements (CL, BD, HL, and TL) were taken using a calliper with an accuracy of  $\pm$  0.1 mm. Wing length was measured with a stainless-steel rule with an accuracy of  $\pm$  1.0 mm. To limit measurement biases, a single person (CG) took each measurement three times and calculated the mean. We also took standardized pictures of both sides of the right wing for each tested individual, using a digital camera (Olympus TG-610). Wing area was then measured by a single person (CG) by counting the number of calibrated pixels using ImageJ image analysis software version 1.52a (National Institute of Health, USA). Correlation scores between morphometric measurements and summary are given in Appendices I and II, respectively.

We chose morphometric measurements likely to be indicators of body size and/or to have an effect on call production based on the literature, and/or may be important in the biology of the species.

Head size has been used as an indicator of body size in swallows (Winkler and Allen 1996, Patel et al. 2010) and nestling growth in blue tits (Plummer et al. 2013). Similarly, tarsus and wing lengths are good indicators of body size in passerines (Senar and Pascual 1997, Gosler et al. 1998), although it has not been documented if these indicators are suitable in seabirds. Bill is considered as the end of the vocal tract and its morphology (length and depth) may influence sound production. Bill is also the small petrels' feeding means (Warham 1996), as they filter small crustaceans at the surface of the water. Wing area seems a relevant morphological trait because petrels are a soaring species and travel great distances at sea to feed (Cherel et al. 2002).

Body mass is highly variable in petrels due to their feeding habits. Every ten days or so, mates alternate fasting incubation shifts in the burrow and foraging trips where they restore their energy reserves (Warham 1990). The longer they stay in the burrow incubating, the lighter they get. For instance, in blue petrels, breeders loose about  $45 \pm 6$  g in  $10 \pm 2$  days (mean  $\pm$  SD) during the incubating shift (Chaurand and Weimerskirch 1994a, 1994b). Therefore, we did not include mass in the following statistical analyses.

Birds were genetically sexed following methods for non-ratite birds (Fridolfsson and Ellegren 1999).

## **Acoustic analysis**

Calls recorded were first down sampled at 11.025 kHz to increase the precision of frequency measurements and high-pass filtered (Cutting frequency: 0.10 kHz, FFT filter) to remove the background noise. We described calls at a phrase level by measuring 11 acoustic parameters in the temporal and frequency domains (see Table 1 for abbreviations and description), on oscillograms and spectra of the signal-processing software Avisoft-SASLab Pro v 5.2.11, respectively (Specht 2017). Temporal variables were automatically extracted on the amplitude envelopes using the "Pulse Train Analysis" function, with a resolution of 0.09 ms (hysteresis: +30 dB; start/end threshold: -30 dB). Settings were not manipulated during measurements, except the threshold which was manually adjusted to detect all syllables. Mean fundamental frequencies and variables describing energy spectral distribution were automatically extracted on linear amplitude spectra with a resolution of 22 Hz (FFT

length: 512, Blackman window) (Fig. 2). Automatic extractions are based on clear criteria preliminarily set, insuring objectivity in element demarcation and thus replicable measurements (Fischer et al. 2013). Syllables and phrases were counted on sonograms (Fig. 2). Correlation scores between acoustic-parameter measures and summary are given in Appendices III and IV, respectively.

## Statistical Analysis

We implemented all analysis results under the R software environment version 3.4.4 (R Core Team 2018) with the *ade4* package (Dray and Dufour 2007).

### *Relating acoustic parameters and morphological traits*

Body mass has been shown to be related to vocal performance in birds, i.e. heavy males have a higher calling activity than light males (e.g. Berg et al. 2005, Barnett and Briskie 2011, Yamada and Soma 2016). As previously mentioned, mass is highly variable in petrels and decreased during the fasting periods in the burrow (Chaurand and Weimerskirch 1994a, 1994b), and consequently between successive playback sessions. To avoid potential bias related to the high variation of mass between playback sessions, we considered only the first session of each individual and we omitted mass in our statistical analyses.

We investigated covariance among morphometric measurements and acoustic parameters with a Co-Inertia Analysis (CIA), an ordination method designed to reveal the co-structures among two data tables (Dolédéc and Chessel 1994, Dray et al. 2003). A summary table of acoustic and morphometric data are given in Appendices I and II, respectively. We first summarized the morphometric measurement table with the two first axes of a normed Principal Component Analysis ( $PCA_1$ ), which explained together 55.6 % for blue petrel (32.2 and 23.3 % for  $PC_{11}$  and  $PC_{12}$ , respectively) and 60.6% of total inertia for Antarctic prion (34.6 and 26.0 % for  $PC_{11}$  and  $PC_{12}$ , respectively). We ordinated the acoustic parameters table with a Between-Class Analysis ( $PCA_2$ ), a PCA which accounts for the clustering of object (here phrases) by a grouping factor (here individuals), similarly as in a redundancy analysis (Dolédéc and Chessel 1987). We retained the two first axes of the  $PCA_2$  in both species (28.2% and 24.7% of variance explained by  $PC_{21}$  and  $PC_{22}$ , respectively, in blue petrel; 34.6% and 24.9% in Antarctic prion). We built the CIA as an ordination of  $PCA_1$  and  $PCA_2$ . Overall similarity between the

two ordination tables was assessed by the RV coefficient, a correlation coefficient between two sets of variables recorded from the same sample (0: no similarity, 1: equal tables).

### ***Individual signature***

We assessed whether males can be discriminated based on their calls using a Between-Class Analysis (BCA, Dolédec and Chessel 1987). Then, we compared the intra and inter-individual variations for each acoustic parameter to highlight the most discriminant parameters. As a single recording session is not sufficient to highlight a vocal signature (Průchová et al. 2017), we considered only males that have been recorded at least three times to run the BCA. In total, we had 127 blue petrel calls from 21 males ( $6 \pm 4$  calls per male), and 224 Antarctic prion calls from 16 males ( $5 \pm 3$  calls per male).

We calculated the Potential of Individuality Coding (PIC) of each call acoustic parameter. PIC is defined as the ratio between intra-individual variation ( $CV_w$ ) and inter-individual variation ( $CV_b$ ) of a given acoustic parameter. For each parameter and each individual, we calculated the coefficient of intra-individual variation  $CV_w$  corrected for small samples (Scherrer 1984):  $CV_w = 100 \left( \frac{std}{\bar{X}} \right) \left( 1 + \frac{1}{4n} \right)$  with  $\bar{X}$  the mean of the parameter measured, and  $n$  is the number of measures. We calculated the inter-individual variation coefficient as  $CV_b = 100 \left( \frac{std}{\bar{X}} \right)$  where  $std$  and  $\bar{X}$  are the standard deviation and the mean calculated with all measures of a given parameters, respectively, from all individuals. PIC values have been calculated as  $PIC = \frac{CV_w}{CV_b}$ . If  $PIC > 1$ , intra-individual variability is smaller than inter-individual variability for a given parameter, suggesting that this parameter may potentially carry individual information. PIC values are considered high (i.e. likely to carry individual information), when they are superior to 2 (Robisson et al. 1993, Lengagne et al. 1997).

## **Results**

### **Relation between acoustic parameters and morphological traits**

In blue petrels, the RV coefficient of the CIA between morphometric measurements and acoustic parameters is 0.34. The first two axes of the CIA explained 51.0% and 22.8% of total variance, respectively. The first CIA axis shows the duration and the syllable number of the phrase are mainly related to head and bill length (HL, CL). More precisely, males with a small head (HL) and a short bill

(CL) produce short calls with few syllables. The second CIA axis shows rhythm and syllable rate are related to both wing measurements (WL, WA). More precisely, males with short, large wings produce slow (i.e. low phrase rate) calls with long syllables (i.e. high rhythm) and short interphrase silences. Frequency parameters are weakly related to the chosen morphometric measurements (Fig. 3).

In Antarctic prions, the RV coefficient of the CIA between morphometric measurements and acoustic parameters is 0.40. The first two axes of the CIA explained 52.9% and 25.6% of total variance, respectively. The first CIA axis shows head-bill length (HL) and wing area (WA) are related to energy quartiles. More precisely, males with a short head (HL) and slim wings (WA) produce high-pitched calls. The second CIA axis shows temporal parameters (duration, interphrase silences and phrase rate) are mainly related to wing length (WL) and bill length (CL). In other words, males with long wings and a short bill produce short, fast (i.e. high phrase rate, and short interphrase silences) calls (Fig. 4).

Tables of CIA scores for both species are given in Appendix V.

## **Individual signature**

We focused here on the individual information carried in males' calls. We did not investigate the sexual signature or species signature, both already described in the literature (Bretagnolle 1996, Bretagnolle and Genevois 1997).

The total inertia explained by the differences between males in blue petrels and Antarctic prions was 74% and 65%, respectively, showing that the chosen acoustic parameters allow a significant vocal discrimination of individuals ( $p < 10^{-5}$  in both species). Composite plots of BCA analyses are given in Appendix VI.

The PIC values of each of the 11 acoustic parameters used to describe blue petrel and Antarctic prion calls are presented in Fig. 4. All values in both species are higher than one, suggesting that all acoustic parameters considered here may bear the vocal signature (Robisson et al. 1993). Eight out of 11 parameters are higher than two, suggesting they potentially code more than others for individual information (Robisson et al. 1993). In both species, acoustic parameters with highest PIC values are upper energy quartiles in spectral domain, duration, and phrase rate in time domain (Table 2). BCA and PIC methods gave similar results.

## Discussion

We aimed to investigate the informative content of calls in two species of burrowing petrels, the blue petrel and the Antarctic prion. Results show acoustic parameters carry information about the caller individuality and morphological traits, for males of both species.

### Relationship between acoustic parameters and morphological traits

In both species, results obtained by CIA show a clear relationship between acoustic parameters of males' calls and some morphological traits which may constraint call productions (bill morphology, body size indicators), and/or may be relevant considering the feeding ecology (bill morphology, wing morphology) of these species.

Specifically, frequency parameters (i.e. fundamental frequency and energy quartiles) are related to bill morphology, especially head-bill length, in both species even though the relationship is weak in blue petrels. Males with a short head and bill produce low-pitched calls in blue petrels whereas they produce high-pitched calls in Antarctic prions. Relationship between bill morphology and frequency is unclear in birds and both opposite patterns have been observed in many species (e.g. Palacios and Tubaro 2000, Laiolo and Rolando 2003, Christensen et al. 2006). Other studies have found no relationships between frequencies and bill morphology (e.g. Garcia and Tubaro 2018).

Head-bill length is also a body size indicators, suggesting frequencies are related to body size. This frequency-body size relationship has been illustrated in many species at the light of the source-filter theory (e.g. Taylor & Reby 2010). This theory states that vocal signals result from a two-stage production: the source signal is generated by membrane vibrations in the vocal organ (larynx in mammals or syrinx in birds), and subsequently filtered by the vocal tract and the mouth/nostrils (Fant 1960). Consequently, the anatomy of the "source", particularly the length and mass of vibrating membranes, shapes the fundamental frequency. Muscular interactions changes the airflow in the "source" and thus influence temporal parameters such as rhythm, duration and amplitude. The "filter" influences the formants, i.e. the resonant frequencies (Titze 1994, Taylor and Reby 2010). Although this theory is valid in mammals, the relationships between frequencies and body size remains unclear in

birds (Galeotti et al. 1997, Mager et al. 2007, Favaro et al. 2017, Kriesell et al. 2018 but see Patel et al. 2010).

Our results show some temporal parameters are related to body size in both species, suggesting big males produce more challenging songs than small males. More precisely, in blue petrels, males with a long head, wings and tarsus produce long, fast calls with many syllables. In Antarctic prions, males with long wings produce short, fast calls. In many species, females are more attracted by males performing physically challenging songs/calls (e.g. high rate, long duration), likely because they reflect male characteristics linked to qualities such as endurance (Ballentine et al. 2004), survival (Byers et al. 2016), age, and size (Ballentine 2009).

Results show a strong relationship between acoustic parameters and wing morphology, especially wing length in both species, and wing area even though this relationship is weaker in blue petrels. We thus suggest that for soaring seabirds, which travel great distances at sea to feed, wing morphology is a relevant parameter to be considered (Cherel et al. 2002). We can hypothesize that cues that may inform females on this male characteristic might be important as wing morphology is correlated with foraging behaviour (Hertel and Ballance 1999) and reproductive costs (Mauck and Grubb 1995). In other Procellariidae, a reduction of parents' flying abilities (e.g. clipping feather tips, removing flight feathers, adding extra weight) affects the incubation routine and results in a decrease of their body condition and/or a deterioration of chick condition (Saether et al. 1993, Weimerskirch et al. 1995, Navarro and Gonz  les-Sol  s 2007). In many species, females are more attracted by males performing physically challenging songs/calls (e.g. high rate, long duration), likely because they reflect male characteristics linked to qualities such as endurance (Ballentine et al. 2004), survival (Byers et al. 2016), age, and size (Ballentine 2009).

Blue petrels and Antarctic prions form lifelong monogamous bonds. Pair bonding takes up to two years and partners equally share parental care during the incubation period (Chaurand and Weimerskirch 1994a, Warham 1990, Warham 1996). Sexual maturity is reached tardily (around seven years), they show low fecundity (one single egg per year without a replacement clutch), and extra-pair paternity is extremely rare (Jouventin and Mougin 1981, Warham 1996). Consequently, choosing the “wrong” mate affects fitness more than in species that change mates at each breeding. Females should

rely on attractive and reliable cues to evaluate the quality of a potential partner (Darwin 1871, Smith 1991). As in many bird species, males' calls are likely to be sexual signals that attract and/or stimulate a potential mate (Bretagnolle 1990). Especially as they are highly vocal, despite the predation cost, and as living in burrows prevents visual communication on long-range. We hypothesize, thus, that the information contained in male calls about the caller body size may have a significant role in sexual selection. In blue petrels, bigger males at the beginning of the breeding season have a higher breeding success (Chastel et al. 1995). Moreover, calls contain information about wing morphology, which may be linked to reproductive success in these soaring birds (Saether et al. 1993, Weimerskirch et al. 1995, Navarro and Gonz  les-Sol  s 2007).

### **Individual signature**

Our results suggest that individuality in calls of males of both species is coded by several parameters in spectral (energy quartiles) and temporal domain (phrase rate and duration). Individual identity coded by frequency parameters has been shown in numerous species (e.g. Robisson et al. 1993, Jouventin et al. 1999, Charrier et al. 2001, Charrier et al. 2004, Favaro et al. 2017). Among these parameters, the fundamental frequency often codes for individual signature in many birds, likely because it is linked to anatomical structure of the vocal tract (Fletcher and Tarnopolsky 1999). Nevertheless, our results show that fundamental frequency has the lowest PIC value and that its correlation with morphological traits is weak. This is consistent with previous studies on blue petrels (Genevois and Bretagnolle 1994), although a negative correlation between mass and fundamental frequency has been highlighted in the snow petrel (Guillotin and Jouventin 1980).

In many seabirds, vocal identity is crucial in social interactions, such as mate reunion or kin recognition (e.g. Spheniscidae: Robisson et al. 1993, Jouventin et al. 1999, Aubin and Jouventin 2002, Procellariidae: Barbraud et al. 2000, Cur   et al. 2011, Stercorariidae: Charrier et al. 2001, Laridae Mathevon et al. 2003). However, in burrowing petrels, finding relatives and nest sites seems not based on vocal signals. As they return from their foraging trip at sea, petrels rely on olfactory signals to find their burrow (Bonadonna et al. 2001, Bonadonna et al. 2004) and take the place of their mate incubating in the burrow, without emitting any call (FB and CG personal observation). Therefore, vocal signature

does not seem to be involved in mate reunion. Vocal signatures do not systematically imply recognition (Townsend et al. 2010). So far, there is no clear evidence that burrowing petrels vocally recognize conspecifics as shown in other seabird families (e.g. Spheniscidae: Robisson et al. 1993, Jouventin et al. 1999, Aubin and Jouventin 2002, Procellariidae: Barbraud et al. 2000, Curé et al. 2011, Stercorariidae: Charrier et al. 2001, Laridae: Mathevon et al. 2003). Nonetheless, vocal signature could be used in neighbour/stranger discrimination processes. Indeed, blue petrel and Antarctic prion males call from their burrow in crowded colonies (respectively up to 0.7 and 1.4 burrows/m<sup>2</sup> according to Croxall and Prince 1980). The significant costs of calling behaviour (Mougeot and Bretagnolle 2000) suggests that males should call only when necessary, for instance in the presence of a stranger male not belonging to the neighbouring community, to avoid higher predation risks and useless energy expenditures. This “dear-enemy phenomenon” (Fisher 1954) has been documented in many territorial songbirds where males are less aggressive with neighbours than with strangers when defending their breeding territory (Temeles 1994). One hypothesis is that territory owners adjust their aggressive behaviour according to the familiarity and/or threat degrees and thus minimizes fighting costs (Temeles 1994).

Knowing which information is passed through vocal signals is crucial to understanding many social behaviours, such as female mate choice or male-male competition. Here, we investigated the informative content of males’ calls in blue petrels and Antarctic prions, two under-studied species that use vocal signals in their social interactions. Results highlight similarities on informative content of males’ calls between the two study species, such as the relationship between body size - element rates, and individual-identity coding strategy. However, results also highlight dissimilarities. Although these species are phylogenetically and ecologically close (Warham 1990, Warham 1996), they exhibit calls that differ by their structure, with two different strategies of body-size vocal signalling. In Antarctic prions, frequencies bear information on the caller body size whereas this information is only coded by temporal parameters in blue petrels. These results are consistent with previous studies on blue petrels (Genevois and Bretagnolle 1994) and snow petrels (Barbraud et al. 2000), suggesting the existence of different coding strategies in Procellariidae. Syntactic differences between blue petrel and Antarctic prions calls (Bretagnolle 1996) or differences of the intensity of predation pressure (Mougeot et al. 1998) might be possible explanations for these different coding strategies.

Globally, our results showing that several call parameters correlate with male body size, suggest that they might be potential indicators of male quality for females. However, so far, there is no evidence showing that females are more attracted to males with particular morphological traits. Several call parameters also bear an individual signature. Nevertheless, individual recognition has not been explored in these species. Our study is the first step to understand the importance of vocal signals in burrowing petrels' social lives. The direction for future studies will be to assess how the informative content of males' calls influence conspecific behaviours, for instance, by using playback experiments to test the existence of individual vocal recognition and whether call characteristics could be good predictors of female preference.

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## References

- Aubin, T. and Jouventin, P. 2002. How to vocally identify kin in a crowd: the penguin model. - Adv. Study Behav. 31: 243–277.
- Aubin, T., Mathevon, N., Staszewski, V. and Boulinier, T. 2007. Acoustic communication in the kittiwake *Rissa tridactyla*: potential cues for sexual and individual signatures in long calls. - Polar Biol. 30: 1027–1033.
- Ballentine, B. 2009. The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*. - Anim. Behav. 77: 973–978.

406 Ballentine, B., Hyman, J. and Nowicki, S. 2004. Vocal performance influences female response to  
 407 male bird song: an experimental test. - Behav. Ecol. 15: 163–168.

408 Barbraud, C., Mariani, A. and Jouventin, P. 2000. Variation in call properties of the snow petrel,  
 409 *Pagodroma nivea*, in relation to sex and body size. - Aust. J. Zool. 48: 421–430.

410 Barnett, C. A. and Briskie, J. V. 2011. Strategic regulation of body mass and singing behaviour in  
 411 New Zealand robins. - Ethology 117: 28–36.

412 Beecher, M. 1989. Signalling system for individual recognition: an information theory approach. -  
 413 Anim. Behav. 38: 248–261.

414 Berg, M. L., Beintema, N. H., Welbergen, J. A. and Komdeur, J. 2005. Singing as a handicap: the  
 415 effects of food availability and weather on song output in the Australian reed warbler  
 416 *Acrocephalus australis*. - J. Avian Biol. 36: 102–109.

417 Bergès, M., Choquet, R. and Bonadonna, F. 2019. Impact of long-term behavioural studies in the wild:  
 418 the blue petrel, *Halobaena caerulea*, case at Kerguelen. - Anim. Behav. 151: 53–65.

419 Bonadonna, F., and Nevitt, G. A. 2004. Partner-specific odour recognition in an Antarctic seabird. -  
 420 Science 306: 835.

421 Bonadonna, F., and Sanz-Aguilar, A. 2012. Kin recognition and inbreeding avoidance in wild birds:  
 422 the first evidence for individual kin-related odour recognition. - Animal Behav. 84: 509–513.

423 Bonadonna, F., Spaggiari, J. and Weimerskirch, H. 2001. Could osmotaxis explain the ability of blue  
 424 petrels to return to their burrows at night? - J. Exp. Biol. 204: 1485–1489.

425 Bonadonna, F., Villafane, M., Bajzak, C. and Jouventin, P. 2004. Recognition of burrow's olfactory  
 426 signature in blue petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark.  
 427 - Anim. Behav. 67: 893–898.

428 Bradbury, J. W. and Vehrencamp, S. L. 1998. Principles of animal communication.

429 Bretagnolle, V. 1990. Behavioural affinities of the blue petrel *Halobaena caerulea*. - Ibis (Lond.  
 430 1859). 132: 102–105.

431 Bretagnolle, V. 1996. Acoustic communication in a group of nonpasserine birds, the petrels. - In:  
 432 Kroodsma, D. E. and Miller, E. H. (eds), Ecology and Evolution of Acoustic Communication in  
 433 Birds. Cornell Un. pp. 160–177.

434 Bretagnolle, V. and Lequette, B. 1990. Structural Variation in the Call of the Cory's Shearwater  
 435 (*Calonectris diomedea*, Aves, Procellariidae). - Ethology 85: 313–323.  
 436 Bretagnolle, V. and Genevois, F. 1997. Geographic variation in the call of the blue petrel: effects of  
 437 sex and geographical scale. - Condor 99: 985–989.  
 438 Bretagnolle, V., Genevois, F. and Mougeot, F. 1998. Intra- and intersexual functions in the call of a  
 439 non-passerine bird. - Behaviour 135: 1161–1184.  
 440 Briefer, E. F. 2018. Vocal contagion of emotions in non-human animals. - Proc. R. Soc. B Biol. Sci.  
 441 285: 20172783.  
 442 Brooke, M. L. 1978. Sexual differences in the voice and individual vocal recognition in the Manx  
 443 shearwater (*Puffinus puffinus*). - Anim. Behav. 26: 622–629.  
 444 Brooke, M. 2004. Albatrosses and petrels across the world.  
 445 Byers, B. E., Akresh, M. E. and King, D. I. 2016. Song and male quality in prairie warblers. -  
 446 Ethology 122: 660–670.  
 447 Candolin, U. and Voigt, H. R. 2001. Correlation between male size and territory quality: consequence  
 448 of male competition or predation susceptibility? - Oikos 95: 225–230.  
 449 Cardoso, G. C. 2012. Paradoxical calls: the opposite signaling role of sound frequency across bird  
 450 species. - Behav. Ecol. 23: 237–241.  
 451 Catchpole, C. K. and Slater, P. J. B. 2008. Bird song: biological themes and variations.  
 452 Charrier, I., Jouventin, P., Mathevon, N. and Aubin, T. 2001. Individual identity coding depends on  
 453 call type in the south polar skua *Catharacta maccormicki*. - Polar Biol. 24: 378–382.  
 454 Charrier, I., Bloomfield, L. L. and Sturdy, C. B. 2004. Note types and coding in parid vocalizations. I:  
 455 The chick-a-dee call of the black-capped chickadee (*Parus atricapillus*). - Can. J. Zool. 82:  
 456 769–779.  
 457 Chastel, O., Weimerskirch, H. and Jouventin, P. 1995. Body condition and seabird reproductive  
 458 performance: a study of three petrel species. - Ecology 76: 2240–2246.  
 459 Chaurand, T. and Weimerskirch, H. 1994a. Incubation routine, body mass regulation and egg neglect  
 460 in the blue petrel *Halobaena caerulea*. - Ibis (Lond. 1859). 136: 285–290.  
 461 Chaurand, T. and Weimerskirch, H. 1994b. The regular alternation of short and long foraging trips in

462 the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a  
 463 pelagic seabird. - J. Anim. Ecol. 63: 275.

464 Cherel, Y., Bocher, P., Trouvé, C. and Weimerskirch, H. 2002. Diet and feeding ecology of blue  
 465 petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. - Mar. Ecol. Prog. Ser.  
 466 228: 283–299.

467 Christensen, R., Kleindorfer, S. and Robertson, J. 2006. Song is a reliable signal of bill morphology in  
 468 Darwin's small tree finch *Camarhynchus parvulus*, and vocal performance predicts male pairing  
 469 success. - J. Avian Biol. 37: 617–624.

470 Cramp, S. and Simmons, K. E. L. 1977. The birds of the Western Palearctic. Vol. 1. Ostrich to ducks. -  
 471 In: Handbook of the Birds of Europe. Oxford University Press, pp. 722.

472 Croxall, J. P. and Prince, P. A. 1980. Food, feeding ecology and ecological segregation. -  
 473 Environment: 103–131.

474 Curé, C., Aubin, T. and Mathevon, N. 2011. Sex discrimination and mate recognition by voice in the  
 475 yelkouan shearwater *Puffinus yelkouan*. - Bioacoustics 20: 235–250.

476 Dale, Lank and Reeve 2001. Signaling individual identity versus quality: a model and case studies  
 477 with ruffs, queleas, and house finches. - Am. Nat. 158: 75.

478 Darwin, C. 1871. The descent of man, and selection in relation to sex (Murray, Ed.).

479 Dolédec, S. and Chessel, D. 1994. Co-inertia analysis: an alternative method for studying species-  
 480 environment relationships. - Freshw. Biol. 31: 277–294.

481 Dolédec, S., and D. C. 1987. Rythmes saisonniers et composantes stationnelles en milieu aquatique I-  
 482 Description d'un plan d'observations complet par projection de variables. - Acta Oecologica.  
 483 Oecologia Gen. 8: 403–426.

484 Dray, S. and Dufour, A.-B. 2015. The ade4 package: implementing the duality diagram for ecologists.  
 485 - J. Stat. Softw 22: 1-20.

486 Dray, S., Chessel, D. and Thioulouse, J. 2003. Co-inertia analysis and the linking of ecological data  
 487 tables. - Ecology 84: 3078–3089.

488 Falls, J. B. 1982. Individual recognition by sounds in birds. - In: Kroodsma, D. E. and Miller, E. H.  
 489 (eds), Acoustic Communication in Birds. Academic Press, pp. 237–278.

490 Fant, G. 1960. Acoustic theory of speech production.

491 Favaro, L., Gamba, M., Gili, C. and Pessani, D. 2017. Acoustic correlates of body size and individual  
492 identity in banded penguins. - PLoS One 12: e0170001.

493 Fisher, J. 1954. Evolution and bird sociality. - *Evol. as a Process*: 71–83.

494 Fletcher, N. H. and Tarnopolsky, A. 1999. Acoustics of the avian vocal tract. - *J. Acoust. Soc. Am.*  
495 105: 35–49.

496 Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of non-  
497 ratite birds. - *J. Avian Biol.* 30: 116–121.

498 Funghi, C., Leitão, A. V., Ferreira, A. C., Mota, P. G. and Cardoso, G. C. 2015. Social dominance in a  
499 gregarious bird is related to body size but not to standard personality assays. - *Ethology* 121: 84–  
500 93.

501 Galeotti, P., Saino, N., Sacchi, R. and Møller, A. P. 1997. Song correlates with social context,  
502 testosterone and body condition in male barn swallows. - *Anim. Behav.* 53: 687–700.

503 García, N. C. and Tubaro, P. L. 2018. Dissecting the roles of body size and beak morphology in song  
504 evolution in the “blue” cardinalids (Passeriformes: Cardinalidae). - *Auk* 135: 262–275.

505 Genevois, F. and Bretagnolle, V. 1994. Male blue petrels reveal their body mass when calling. - *Ethol.*  
506 *Ecol. Evol.* 6: 377–383.

507 Gil, D. and Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. - *Trends*  
508 *Ecol. Evol.* 17: 133–141.

509 Gosler, A. G., Greenwood, J. J. D., Baker, J. K. and Davidson, N. C. 1998. The field determination of  
510 body size and condition in passerines: a report to the British Ringing Committee. - *Bird Study*  
511 45: 92–103.

512 Guillotin, M. and Jouventin, P. 1980. Le pétrel des neiges à Pointe Géologie. - *Gerfaut* 70: 51–72.

513 Hertel, F. and Ballance, L. T. 1999. Wing ecomorphology of seabirds from Johnston Atoll. - *Condor*  
514 101: 549–556.

515 Jouventin, P. and Mougin, J.-L. 1981. Les strategies adaptatives des oiseaux de mer. - *Rev. Ecol.*  
516 (Terre vie) 35: 217–249.

517 Jouventin, P., Aubin, T. and Lengagne, T. 1999. Finding a parent in a king penguin colony: the

518 acoustic system of individual recognition. - Anim. Behav. 57: 1175–1183.

519 Kriesell, H. J., Aubin, T., Planas-Bielsa, V., Benoiste, M., Bonadonna, F., Gachot-Neveu, H., Le

520 Maho, Y., Schull, Q., Vallas, B., Zahn, S. and Le Bohec, C. 2018. Sex identification in king

521 penguins *Aptenodytes patagonicus* through morphological and acoustic cues. - Ibis (Lond. 1859).

522 160: 755–768.

523 Kroodsma, D. E. and Byers, B. E. 1991. The function(s) of bird song. - Am. Zool. 31: 318–328.

524 Laiolo, P. and Rolando, A. 2003. Comparative analysis of the rattle calls in *Corvus* and *Nucifraga*: the

525 effect of body size, bill size and phylogeny. - Condor 105: 139-144.

526 Lambrechts, M. M. and Dhondt, A. A. 1995. Individual voice discrimination in birds. - In: Powers, D.

527 M. (ed), Current Ornithology. Springer US, pp. 115–139.

528 Leclaire, S., Strandh, M., Mardon, J., Westerdahl, H. and Bonadonna, F. 2017. Odour-based

529 discrimination of MHC-similarity in birds. - Proc. R. Soc. B 284: 2016-2466.

530 Lengagne, T., Lauga, J. and Jouventin, P. 1997. A method of independent time and frequency

531 decomposition of bioacoustic signals: inter-individual recognition in four species of penguins. -

532 Comptes Rendus l'Académie des Sci. - Ser. III - Sci. la Vie 320: 885–891.

533 Mager, J. N., Walcott, C. and Piper, W. H. 2007. Male common loons, *Gavia immer*, communicate

534 body mass and condition through dominant frequencies of territorial yodels. - Anim. Behav. 73:

535 683–690.

536 Magrath, R. D., Haff, T. M., Fallow, P. M. and Radford, A. N. 2015. Eavesdropping on heterospecific

537 alarm calls: From mechanisms to consequences. - Biol. Rev. 90: 560–586.

538 Martín-Vivaldi, M., Palomino, J. J. and Soler, M. 1998. Song structure in the hoopoe (*Upupa epops*) -

539 strophe length reflects male condition. - J. fur Ornithol. 139: 287–296.

540 Martín-Vivaldi, M., Palomino, J. J. and Soler, M. 2000. Attraction of hoopoe *Upupa epops* females

541 and males by means of song playback in the field: influence of strophe length. - J. Avian Biol.

542 31: 351–359.

543 Martín-Vivaldi, M., Palomino, J. J. and Soler, M. 2004. Strophe length in spontaneous songs predicts

544 male response to playback in the hoopoe *Upupa epops*. - Ethology 110: 351–362.

545 Mathevon, N., Charrier, I. and Jouventin, P. 2003. Potential for individual recognition in acoustic

546 signals: A comparative study of two gulls with different nesting patterns. - *Comptes Rendus -*  
547 *Biol.* 326: 329–337.

548 Mauck, R. A. and Grubb, T. C. 1995. Petrel parents shunt all experimentally increased reproductive  
549 costs to their offspring. - *Anim. Behav.* 49: 999–1008.

550 McGregor, P. K. 1992. Quantifying responses to playback: one, many, or composite multivariate  
551 measures? - In: *Playback and Studies of Animal Communication*. Springer US, pp. 79–96.

552 Morton, E. S. 1977. On the occurrence and significance of Motivation-Structural Rules in some bird  
553 and mammal sounds. - *Am. Nat.* 111: 855–869.

554 Mougeot, F. and Bretagnolle, V. 2000. Predation as a cost of sexual communication in nocturnal  
555 seabirds: an experimental approach using acoustic signals. - *Anim. Behav.* 60: 647–656.

556 Mougeot, F., Genevois, F. and Bretagnolle, V. 1998. Predation on burrowing petrels by the brown  
557 skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen. - *J. Zool.* 244: 429–438.

558 Navarro, J. and González-Solís, J. 2007. Experimental increase of flying costs in a pelagic seabird:  
559 effects on foraging strategies, nutritional state and chick condition. - *Oecologia* 151: 150–160.

560 Nowicki, S. and Searcy, W. A. 2004. Song function and the evolution of female preferences: why  
561 birds sing, why brains matter. - *Ann. N. Y. Acad. Sci.* 1016: 704–723.

562 Palacios, M. G. and Tubaro, P. L. 2000. Does beak size affect acoustic frequencies in woodcreepers? -  
563 *Condor* 102: 553–560.

564 Patel, R., Mulder, R. A. and Cardoso, G. C. 2010. What makes vocalisation frequency an unreliable  
565 signal of body size in birds? A study on black swans. - *Ethology* 116: 554–563.

566 Plummer, K. E., Bearhop, S., Leech, D. I., Chamberlain, D. E. and Blount, J. D. 2013. Winter food  
567 provisioning reduces future breeding performance in a wild bird. - *Sci. Rep.* in press.

568 Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. -  
569 *Nature* 409: 185–188.

570 Pollard, K. A. and Blumstein, D. T. 2011. Social group size predicts the evolution of individuality. -  
571 *Curr. Biol.* 21: 413–417.

572 Průchová, A., Jaška, P. and Linhart, P. 2017. Cues to individual identity in songs of songbirds: testing  
573 general song characteristics in chiffchaffs *Phylloscopus collybita*. - *J. Ornithol.* 158: 911–924.

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

576 Rowe, L. and Houlde, D. 1996. The lek paradox and the capture of genetic variance. - Proc. Biol. Sci.  
 577 263: 1415–1421.

578 Sæther, B. E., Andersen, R. and Pedersen, H. C. 1993. Regulation of parental effort in a long-lived  
 579 seabird an experimental manipulation of the cost of reproduction in the Antarctic petrel,  
 580 *Thalassoica antarctica*. - Behav. Ecol. Sociobiol. 33: 147–150.

581 Salton, M., Saraux, C., Dann, P. and Chiaradia, A. 2015. Carry-over body mass effect from winter to  
 582 breeding in a resident seabird, the little penguin. - R. Soc. Open Sci. 2: 140390–140390.

583 Scherrer, B. 1984. Biostatistique. - Gaetan Morin Editeur.

584 Searcy, W. A. and Nowicki, S. 2005. The evolution of animal communication: reliability and  
 585 deception in signaling systems.

586 Senar, J. C. and Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body  
 587 size. - Ardea 85: 269–274.

588 Seutin, G., White, B. N. and Boag, P. T. 1991. Preservation of avian blood and tissue samples for  
 589 DNA analyses. - Can. J. Zool. 69: 82–90.

590 Smith, J. M. 1991. Theories of sexual selection. - Trends Ecol. Evol. 6: 146–151.

591 Taylor, A. M. and Reby, D. 2010. The contribution of source-filter theory to mammal vocal  
 592 communication research. - J. Zool. 280: 221–236.

593 Temeles, E. J. 1994. The role of neighbours in territorial systems: when are they “dear enemies”? -  
 594 Anim. Behav. 47: 339–350.

595 Tibbetts, E. A. and Dale, J. 2007. Individual recognition: it is good to be different. - Trends Ecol.  
 596 Evol. 22: 529–537.

597 Titze, I. R., & Martin, D. W. (1998). Principles of voice production.

598 Townsend, S. W., Hollén, L. I. and Manser, M. B. 2010. Meerkat close calls encode group-specific  
 599 signatures, but receivers fail to discriminate. - Anim. Behav. 80: 133–138.

600 Warham, J. 1990. The petrels: their ecology and breeding systems (A Press, Ed.).

601 Warham, J. 1996. The behaviour, population biology and physiology of the petrels. - In: Elsevier, in

602           press.

603   Weimerskirch, H., Chastel, O. and Ackermann, L. 1995. Adjustment of parental effort to manipulated

604           foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. - Behav. Ecol.

605           Sociobiol. 36: 11–16.

606   Winkler, D. W. and Allen, P. E. 1996. The seasonal decline in tree swallow clutch size: physiological

607           constraint or strategic adjustment? - Ecology 77: 922–932.

608   Wittenberger, J. F. and Hunt, G. L. 1985. The adaptive significance of coloniality in birds. - In: Avian

609           Biology. Academic P. xx, pp. 1–78.

610   Yamada, K. and Soma, M. 2016. Diet and birdsong: short-term nutritional enrichment improves songs

611           of adult Bengalese finch males. - J. Avian Biol. 47: 865–870.

612

613 **Table 1.** Abbreviations and descriptions for the acoustic parameters measured on each phrase of blue petrel and  
614 Antarctic prion provoked calls.

Acoustic parameters		Description
NbPh	Number of phrases in a call	
NbSy	Number of syllables in a phrase	
<b>Temporal analysis</b>		
Duration	Phrase duration (s)	
Interphrase	Duration of silence between two phrases (s)	
Rhythm	Phrase rhythm (i.e. ratio between syllable and silence duration for each phrase)	
SyllRate	Syllable rate (i.e. number of syllables per second for each phrase)	
PhRate	Phrase rate (i.e. number of phrases per second for each call)	
<b>Frequency analysis</b>		
q25	Upper quartile (frequency in Hz at the upper limit of the 25% of phrase energy)	
q50	Medium quartile (frequency in Hz at the upper limit of the 50% of phrase energy)	
q75	Lower quartile (frequency in Hz at the upper limit of the 75% of phrase energy)	
F0	Mean fundamental frequency of the phrase (Hz)	

615

616 **Table 2.** Potential of Individual Coding (PIC) for the acoustic parameters measured on blue petrel (top) and  
617 Antarctic prion (bottom) calls. Abbreviations of acoustic parameters as in Table 1. PIC values above 2.0 are in  
618 bold.

Acoustic features	PIC	
	Blue petrel	Antarctic prion
NbPh	<b>2.24</b>	<b>2.52</b>
NbSy	<b>2.05</b>	<b>2.24</b>
Duration	<b>2.44</b>	<b>2.27</b>
Interphrase	<b>2.17</b>	<b>2.10</b>
Rhythm	1.63	1.65
SyllRate	1.79	<b>2.07</b>
PhRate	<b>2.32</b>	<b>3.97</b>
q25	<b>2.01</b>	1.95
q50	<b>2.33</b>	<b>2.76</b>
q75	<b>3.15</b>	<b>3.22</b>
F0	1.56	1.28

619

## Figure captions

**Figure 1.** Tarsus and head measurements from Cramp and Simmons (1977), taken on blue petrels and Antarctic prions: head length (HL), bill depth (BD), bill length (CL) and tarsus length (TL).

**Figure 2.** (a) Sonogram (top) and oscillogram (bottom) of a male blue petrel call constituted of 2 phrases. (b) Linear amplitude spectrum of a call phrase. Red lines indicate energy quartiles and blue line indicates the mean frequency of the phrase.

**Figure 3.** In blue petrels, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.

**Figure 4.** In Antarctic prions, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.