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► **To cite this version:**

Charlène Gémard, Thierry Aubin, Francesco Bonadonna. Males' calls carry information about individual identity and morphological characteristics of the caller in burrowing petrels. *Journal of Avian Biology*, 2019, 50 (12), pp.e02270. <10.1111/jav.02270>. <hal-02371209>

HAL Id: hal-02371209

<https://hal.science/hal-02371209v1>

Submitted on 17 Nov 2020

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HAL Authorization

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

3 Charlène Gémard^{1,2}, Thierry Aubin², Eliette L. Reboud¹, Francesco Bonadonna¹

4 ¹CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

5 ²Equipe Communications Acoustiques, UMR 9197, Neuro-PSI-CNRS, Université Paris-Sud, Bat.446, 91405

6 Orsay, France.

7 **Acknowledgments**

8 This work was financially and logistically supported by the French polar institute Paul Emile Victor (IPEV,
9 program no. 354 ETHOTAAF). We are very grateful to Jessica Graham who improved the English of this
10 manuscript, and to Guilhem Battistella and Jean-Yves Barnagaud for their precious help on the field.

11

12 **Abstract**

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

29 **Keywords**

30 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 (Kroodsma 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

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

33 In many bird species, among the functions that calls and songs fulfil, there is the transmission
34 of individual signature information (Falls 1982, Lambrechts and Dhont 1995). Vocal individual
35 signature is a crucial piece of information as it provides the basis for individual recognition required for
36 almost all aspects of social life (Tibbetts and Dale 2007). Individual recognition is possible when an
37 individual identifies another according to the easily-distinctive characteristics of its signal, for example
38 acoustic parameters of a call (Falls 1982, Dale et al. 2001). Vocal signature has been assessed in many
39 non-songbird species, especially seabirds (e.g. Robisson et al. 1993, Charrier et al. 2001, Aubin and
40 Jouventin 2002, Aubin et al. 2007, Favaro et al. 2017). In many seabirds, adults usually breed in dense
41 colonies (Croxall and Prince 1980, Wittenberg and Hunt 1985), form lifelong monogamous bonds
42 (Warham 1996), and forage far from the colony. Individual recognition would be advantageous when
43 returning to the nest/mate/chick (Warham 1990, Mathevon et al. 2003, Jouventin et al. 1999, Curé et al.
44 2011), especially for species that have no nest site to meet at (Robisson et al. 1993, Aubin and Jouventin
45 2002).

46 Among Procellariidae, burrowing petrels occupy deep burrows and are active, at the colony, at
47 night during the breeding period (Warham 1990). In this context, visual communication seems strongly
48 restricted whereas olfactory and vocal signals may be used for long-range communication. The role of
49 olfaction has been investigated in petrel social interactions. Studies suggest that the chemical signature
50 of nests is used by mates to find their own burrow (Bonadonna et al. 2001, Bonadonna et al. 2004), and
51 that individual body's odour carries individuality signals and some genetic information that may
52 influence mate choice (Bonadonna and Nevitt 2004; Bonadonna and Sanz-Aguilar 2012; Leclaire et al
53 2017). Comparatively, acoustic communication has been poorly studied so far. For some burrowing-
54 petrel species, vocal communication is extremely costly because it exposes callers to an increased risk
55 of predation (Mougeot and Bretagnolle 2000). However, during pair formation, bachelor males looking

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

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

78 **Material and Methods**

79 **Studied species**

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

83 sexual maturity for five years. A couple of years is needed for establishing stable pair-bonds. They show
84 a high partner fidelity, low extra-pair paternities, and divorces are rare. After pairing, pairs produce a
85 single egg per year. From the incubation (50 days in blue petrels, 45 in Antarctic prions) to the fledging
86 (50 and 53 days, respectively), they exhibit bi-parental cares. Partners regularly alternate fasting period
87 in the burrow and feeding trips at sea (Warham 1990, Warham 1996, Brooke 2004).

88 Callers are mainly non-breeder males and females looking for a mate but they are tricky to catch,
89 as they occupy inaccessible burrows and fly over the colony, respectively. On the contrary, breeders
90 usually have high mate and burrow fidelity over years (Warham 1996, Brooke 2004). Occupied burrows
91 can be equipped with an artificial access to the incubating chamber, by digging a tunnel and closing it
92 with a stone. From this artificial door, birds become easily accessible. For this reason, we worked only
93 on breeding birds. After some infructuous attempts to obtain females' replies to playback, we
94 constrained our study to only on males' calls. According to the literature, very few breeding females
95 react to the playback of bachelor males' calls (Brooke 1978, Bretagnolle and Lequette 1990, Bretagnolle
96 1996). A possible explanation is that, in natural conditions, females call only in flight, whereas males
97 call from their burrow. The study was thus restricted on breeding males of the two petrel species: 31
98 blue petrels (16 in 2017 and 15 in 2018) and 24 Antarctic prions (16 in 2017 and 8 in 2018). Mates take
99 a shift every eight to ten days incubating the eggs (Warham 1990), and occasions when both mates are
100 present in the nest at the same time are quite rare. This enabled us to record the male alone. Petrels well
101 tolerate weak human disturbance (Bergès et al. 2019), allowing us to conduct several recording sessions
102 on the same individuals to assess the individual signature. All the birds were metal ringed and
103 individually identifiable.

104 **Study location**

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

109 blue petrels; December 23rd 2017 to January 16th 2018 and December 25th 2018 to January 13th 2019 for
110 Antarctic prions).

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

112 During incubation, breeding petrels are silent in the colony, rarely calling spontaneously,
113 seemingly to avoid predation (Mougeot and Bretagnolle 2000). However, it is possible to elicit vocal
114 responses by broadcasting calls of same-gender conspecifics (Taoka et al. 1989, Bretagnolle & Lequette
115 1990, Curé et al. 2011). Petrel calls consist of a repetition of distinct sections called “phrases”,
116 themselves composed of indivisible elements called syllables (see Catchpole and Slater 2008 for
117 definition, see Fig. 2a and Bretagnolle 1996 for sonograms). Signals to broadcast were graphically
118 synthesized from spontaneous calls of nine bachelor male blue petrels and five bachelor male Antarctic
119 prions recorded in the same colonies in 2013 and 2017 (i.e. series of phrases, themselves constituted of
120 syllables). We used the signal processing software Avisoft–SASLab Pro v 5.2.11 (Specht 2017). Each
121 synthesized call consisted in a two-phrase call of a single blue petrel or Antarctic prion male, separated
122 by a silence of 200 ± 60 ms (5.5 ± 1.6 s and 3.43 ± 0.85 s, respectively; mean \pm SD). To avoid
123 pseudoreplication (McGregor et al. 1992), nine blue petrel call series and five Antarctic prion call series
124 were played-back.

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

135 The recording equipment was composed of an omnidirectional Sennheiser K6-ME62 microphone
136 (frequency response: 20-20 000 Hz \pm 2.5 dB) connected to a Marantz PMD 660 digital recorder
137 (sampling frequency: 44.1 kHz, dynamic: 16 bits). The microphone was positioned on the ground, at the
138 burrow entrance, and one randomly selected synthesized call was broadcast at a natural sound pressure
139 level (\pm 67 dB, measured on 111 calls from 54 males with a sound level meter) using a TASCAM DR-
140 07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). Calls emitted in reply by the
141 burrow owner were recorded during the playback and two minutes after the end of the playback stimulus.
142 If the focal individual did not reply, the playback was repeated every 30 seconds, up to three times.

143 **Morphometric measurements**

144 Soon after recording, the identity of the bird was checked by capturing the birds and reading the
145 metal ring. The day after, birds were caught again in order to take a blood sample from the brachial vein
146 (0.2 mL in Queen lysis buffer, Seutin et al. 1991) and the following seven morphometric measurements
147 (some shown in Fig. 1, Cramp and Simmons 1977): bill length (CL), from edge of implantation of
148 feathers to the bill tip; bill depth (BD), from angle of gonys to dorsal surface of hook; head length (HL),
149 from supraoccital to front edge of bill; tarsus length (TL), from middle of mid-tarsal joint to distal end
150 of tarso-metatarsus; wing chord length (WL), maximum flattened chord, from carpal joint to tip of
151 longest primary; mass (MS); wing area (WA).

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

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

162 Head size has been used as an indicator of body size in swallows (Winkler and Allen 1996, Patel et al.
163 2010) and nestling growth in blue tits (Plummer et al. 2013). Similarly, tarsus and wing lengths are good
164 indicators of body size in passerines (Senar and Pascual 1997, Gosler et al. 1998), although it has not
165 been documented if these indicators are suitable in seabirds. Bill is considered as the end of the vocal
166 tract and its morphology (length and depth) may influence sound production. Bill is also the small
167 petrels' feeding means (Warham 1996), as they filter small crustaceans at the surface of the water. Wing
168 area seems a relevant morphological trait because petrels are a soaring species and travel great distances
169 at sea to feed (Cherel et al. 2002).

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

176 Birds were genetically sexed following methods for non-ratite birds (Fridolfsson and Ellegren
177 1999).

178 **Acoustic analysis**

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

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

193 **Statistical Analysis**

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

196 ***Relating acoustic parameters and morphological traits***

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

204 We investigated covariance among morphometric measurements and acoustic parameters with
205 a Co-Inertia Analysis (CIA), an ordination method designed to reveal the co-structures among two data
206 tables (Dolédéc and Chessel 1994, Dray et al. 2003). A summary table of acoustic and morphometric
207 data are given in Appendices I and II, respectively. We first summarized the morphometric measurement
208 table with the two first axes of a normed Principal Component Analysis (PCA₁), which explained
209 together 55.6 % for blue petrel (32.2 and 23.3 % for PC₁₁ and PC₁₂, respectively) and 60.6% of total
210 inertia for Antarctic prion (34.6 and 26.0 % for PC₁₁ and PC₁₂, respectively). We ordinated the acoustic
211 parameters table with a Between-Class Analysis (PCA₂), a PCA which accounts for the clustering of
212 object (here phrases) by a grouping factor (here individuals), similarly as in a redundancy analysis
213 (Dolédéc and Chessel 1987). We retained the two first axes of the PCA₂ in both species (28.2% and
214 24.7% of variance explained by PC₂₁ and PC₂₂, respectively, in blue petrel; 34.6% and 24.9% in
215 Antarctic prion). We built the CIA as an ordination of PCA₁ and PCA₂. Overall similarity between the

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

218 *Individual signature*

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

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

236 **Results**

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

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

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

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

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

254 **Individual signature**

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

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

262 The PIC values of each of the 11 acoustic parameters used to describe blue petrel and Antarctic
263 prion calls are presented in Fig. 4. All values in both species are higher than one, suggesting that all
264 acoustic parameters considered here may bear the vocal signature (Robisson et al. 1993). Eight out of
265 11 parameters are higher than two, suggesting they potentially code more than others for individual
266 information (Robisson et al. 1993). In both species, acoustic parameters with highest PIC values are
267 upper energy quartiles in spectral domain, duration, and phrase rate in time domain (Table 2). BCA and
268 PIC methods gave similar results.

269 **Discussion**

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

273 **Relationship between acoustic parameters and morphological traits**

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

278 Specifically, frequency parameters (i.e. fundamental frequency and energy quartiles) are related
279 to bill morphology, especially head-bill length, in both species even though the relationship is weak in
280 blue petrels. Males with a short head and bill produce low-pitched calls in blue petrels whereas they
281 produce high-pitched calls in Antarctic prions. Relationship between bill morphology and frequency is
282 unclear in birds and both opposite patterns have been observed in many species (e.g. Palacios and Tubaro
283 2000, Laiolo and Rolando 2003, Christensen et al. 2006). Other studies have found no relationships
284 between frequencies and bill morphology (e.g. Garcia and Tubaro 2018).

285 Head-bill length is also a body size indicators, suggesting frequencies are related to body size.
286 This frequency-body size relationship has been illustrated in many species at the light of the source-
287 filter theory (e.g. Taylor & Reby 2010). This theory states that vocal signals result from a two-stage
288 production: the source signal is generated by membrane vibrations in the vocal organ (larynx in
289 mammals or syrinx in birds), and subsequently filtered by the vocal tract and the mouth/nostrils (Fant
290 1960). Consequently, the anatomy of the “source”, particularly the length and mass of vibrating
291 membranes, shapes the fundamental frequency. Muscular interactions changes the airflow in the
292 “source” and thus influence temporal parameters such as rhythm, duration and amplitude. The “filter”
293 influences the formants, i.e. the resonant frequencies (Titze 1994, Taylor and Reby 2010). Although this
294 theory is valid in mammals, the relationships between frequencies and body size remains unclear in

295 birds (Galeotti et al. 1997, Mager et al. 2007, Favaro et al. 2017, Kriesell et al. 2018 but see Patel et al.
296 2010).

297 Our results show some temporal parameters are related to body size in both species, suggesting
298 big males produce more challenging songs than small males. More precisely, in blue petrels, males with
299 a long head, wings and tarsus produce long, fast calls with many syllables. In Antarctic prions, males
300 with long wings produce short, fast calls. In many species, females are more attracted by males
301 performing physically challenging songs/calls (e.g. high rate, long duration), likely because they reflect
302 male characteristics linked to qualities such as endurance (Ballentine et al. 2004), survival (Byers et al.
303 2016), age, and size (Ballentine 2009).

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

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

323 rely on attractive and reliable cues to evaluate the quality of a potential partner (Darwin 1871, Smith
324 1991). As in many bird species, males' calls are likely to be sexual signals that attract and/or stimulate
325 a potential mate (Bretagnolle 1990). Especially as they are highly vocal, despite the predation cost, and
326 as living in burrows prevents visual communication on long-range. We hypothesize, thus, that the
327 information contained in male calls about the caller body size may have a significant role in sexual
328 selection. In blue petrels, bigger males at the beginning of the breeding season have a higher breeding
329 success (Chastel et al. 1995). Moreover, calls contain information about wing morphology, which may
330 be linked to reproductive success in these soaring birds (Saether et al. 1993, Weimerskirch et al. 1995,
331 Navarro and Gonzáles-Solís 2007).

332 **Individual signature**

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

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

350 does not seem to be involved in mate reunion. Vocal signatures do not systematically imply recognition
351 (Townsend et al. 2010). So far, there is no clear evidence that burrowing petrels vocally recognize
352 conspecifics as shown in other seabird families (e.g. Spheniscidae: Robisson et al. 1993, Jouventin et al.
353 1999, Aubin and Jouventin 2002, Procellariidae: Barbraud et al. 2000, Curé et al. 2011, Stercorariidae:
354 Charrier et al. 2001, Laridae: Mathevon et al. 2003). Nonetheless, vocal signature could be used in
355 neighbour/stranger discrimination processes. Indeed, blue petrel and Antarctic prion males call from
356 their burrow in crowded colonies (respectively up to 0.7 and 1.4 burrows/m² according to Croxall and
357 Prince 1980). The significant costs of calling behaviour (Mougeot and Bretagnolle 2000) suggests that
358 males should call only when necessary, for instance in the presence of a stranger male not belonging to
359 the neighbouring community, to avoid higher predation risks and useless energy expenditures. This
360 “dear-enemy phenomenon” (Fisher 1954) has been documented in many territorial songbirds where
361 males are less aggressive with neighbours than with strangers when defending their breeding territory
362 (Temeles 1994). One hypothesis is that territory owners adjust their aggressive behaviour according to
363 the familiarity and/or threat degrees and thus minimizes fighting costs (Temeles 1994).

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

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

387

388 *Acknowledgments* – We thank all people who kindly helped us in the field, especially Jean-Yves Barnagaud,
389 Guilhem Battistella, Matthieu Bergès, Samuel Perret and the French polar institute IPEV which provided logistic
390 support in the field. We are very grateful to Jean-Yves Barnagaud and Pierre Legendre for their sound advices and
391 guidance on statistical analyses. We are also grateful to Jessica Graham for her comments and English
392 improvement of the paper.

393 *Conflict of interest* – The authors declare no conflicts of interest associated with this study.

394 *Funding* – This work was supported by the French Polar Institute Paul Emile Victor (IPEV, program no. 354).

395 *Permits* – This study was performed according to guidelines established by both IPEV and CNRS for the Ethical
396 Treatment of Animals. All experiments comply with the current laws of the country where they were performed.

397

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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 |
| Temporal analysis | |
| 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) |
| Frequency analysis | |
| 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 | 2.24 | 2.52 |
| NbSy | 2.05 | 2.24 |
| Duration | 2.44 | 2.27 |
| Interphrase | 2.17 | 2.10 |
| Rhythm | 1.63 | 1.65 |
| SyllRate | 1.79 | 2.07 |
| PhRate | 2.32 | 3.97 |
| q25 | 2.01 | 1.95 |
| q50 | 2.33 | 2.76 |
| q75 | 3.15 | 3.22 |
| F0 | 1.56 | 1.28 |

619

620 **Figure captions**

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

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

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

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