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1 **Contextual variations in calls of two non-oscine birds: the blue petrel**

2 ***Halobaena caerulea* and the Antarctic prion *Pachyptila desolata***

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13 **ABSTRACT.** Bird vocalizations are critical cues in social interactions as they convey temporary information  
14 varying with the social context, such as the motivation of the signaler when facing a rival or a potential mate. To  
15 date, literature mainly focused on learning birds (e.g. passerines and psittaciformes). Burrowing petrels  
16 (Procellariidae) are non-learning birds with a limited vocal repertoire. Bachelor males communicate with  
17 conspecifics with a single major call emitted in three situations: in absence of a certain auditory (spontaneous  
18 calls), towards females (female-directed calls) and toward males (male-directed calls). We first hypothesized  
19 that, although the structure of the call is preserved, temporal and spectral parameters vary between the three call  
20 types of bachelor males, translating different motivations (Motivation Hypothesis). To go further, we  
21 hypothesized that acoustic variations in male-directed calls indicate the signaler's aggressive motivation and  
22 therefore the variations are similar whether calls are produced by breeder or bachelor males (Breeding-Status  
23 Hypothesis). We tested the two hypotheses performing field playback experiments on males of two petrel  
24 species: the blue petrel (*Halobaena caerulea*) and the Antarctic prion (*Pachyptila desolata*). Despite the obvious  
25 call stereotypy, we observed temporal variations but also frequency shifts when males react to a female or a  
26 male. These variations may translate the sexual or aggressive motivation of the caller, as shown in learning birds,  
27 especially oscines. So far, vocal plasticity in non-learning birds have been greatly underestimated. Here, we  
28 highlighted the expression of different motivations through vocal variations and for the first time the ability to  
29 produce frequency variations in non-learning birds.

30

31 **Keywords: acoustic communication, vocal plasticity, motivation, frequency shift, seabirds, petrels**

## 32 **1. Background**

33 In animal communication, the information carried by signals is of two types: stable such as  
34 signaler attributes and identity (e.g. species, group membership, individual identity, phenotypic  
35 characteristics: Searcy and Nowicki 2005); or transient such as emotion (e.g. fear, anxiety, excitement:  
36 Briefer 2012, 2018, 2020) and motivation (i.e. tendencies to perform a rewarding behaviors such as  
37 fighting or mating: Morton 1977; Bradbury and Vehrencamp 2011; Briefer 2020). The transmission of  
38 transient information through vocal signals has been well documented since Darwin hypothesized that  
39 vocal signals are indicators of the signaler's emotions (intense but short-living affective reaction to a  
40 specific event or stimulus: Briefer 2012) and motivation (probability that an animal would perform a  
41 certain behavior: Zahavi 1982). More-recent studies suggest that information about emotions and  
42 motivations of the signaler are carried by acoustic variations: variations between call types may reflect  
43 different arousal valences (positive/negative emotion), whereas the variations within call types may  
44 reflect the arousal degree (Manser 2010).

45 Several stimuli elicit acoustic variations within call types, such as food availability (Proppe and  
46 Sturdy 2009) or the presence of a conspecific. When facing a potential mate, songbirds tend to  
47 vocalize close to their performance limit and exaggerate their sexual motivation by enhancing acoustic  
48 parameters linked to their qualities (Sossinka and Böhner 1980; Podos 1997). For instance, in zebra  
49 finches (*Taeniopygia guttata*), males seeking for mates produce “courtship song” towards females that  
50 are faster, longer and composed of more introductory syllables than “solitary song” (Sossinka and  
51 Böhner 1980). When facing a rival or an intruder, signalers usually vocalize in a way that increases  
52 their perceived competitive potential and willingness (Todt and Naguib 2000; Vehrencamp 2000;  
53 Searcy and Beecher 2009). According to Motivational-Structural Hypothesis (Morton 1977),  
54 contestants produce longer vocal signals, characterized by lower frequencies and wider frequency  
55 bandwidth (Cardoso 2012). In many songbirds, contestants increase their performance level by singing  
56 faster and/or with a broader bandwidth when facing a rival (Searcy and Beecher 2009; Linhart et al.  
57 2013; Funghi et al. 2014)

58 Much of the available literature about acoustic variations related to the social context focuses on  
59 learning birds, especially passerines (Catchpole and Slater 2008). Non-learning birds have received  
60 comparatively little attention, likely because they have less vocal plasticity than learning birds  
61 (Kroodsma 2004). Nonetheless, few studies have investigated temporal variations of male calls in a  
62 territorial context. In common loons (*Gavia immer*), males produce “yodels” with more syllables  
63 repeated when an intruder enters their breeding territory. The more syllables it contains, the higher the  
64 probability of physical fights (Mager et al. 2012). In hoopoes (*Upupa epops*), aggressive males  
65 produce longer strophes (i.e. with more repeated phrases) whereas males with little motivation to fight  
66 produce shorter strophes (Martín-Vivaldi et al. 2004). In the corncrake (*Crex crex*), males produce  
67 calls with syntactic variations encoding the aggressive motivations (Rek 2013, Rek and Osiejuk 2013).  
68 Although temporal variations have been highlighted in non-songbirds, frequency variations in their  
69 calls have not been investigated so far. The understanding of vocal plasticity in non-songbirds thus  
70 remains an open question.

71 Burrowing petrels (Procellariidae, Gmelin 1789) are strong candidates to address this question in  
72 regards of the seeming implication of vocal signals in sexual selection. In these long-lived seabirds,  
73 adults show high mate and nest fidelity through the years. Monogamous pairs take a couple of years to  
74 bond, and divorces are rare (Warham 1990; Warham 1996). After pairing, they lay a single egg per  
75 year, without any possibility of replacement clutch, and both male and female assume parental care.  
76 Mate choice is thus crucial. Signals implied in mate choice may be of two modalities: vocal and  
77 olfactory (Gémard et al. *submitted*; Bretagnolle 1996; Leclaire et al. 2017). Bachelor males and  
78 females call all night long from their self-dug burrow or when overflying the colony. Calls are costly  
79 sexual signals as they attract predators, such as the brown skua *Stercorarius antarcticus* which detects  
80 and locates its preys using their calls (Mougeot and Bretagnolle 2000). After pairing, adults scarcely  
81 call spontaneously as partner and nest recognitions are mainly olfactory (Bonadonna and Nevitt 2004;  
82 Mardon et al. 2010). Both breeder and bachelor males call after being vocally challenged by same-sex  
83 conspecifics (Taoka and Okumura 1989; Bretagnolle and Lequette 1990; Curé et al. 2011). It may be a  
84 way to defend their burrow from intruders and/or rivals (Warham 1996).

85 Petrels' vocal repertoire is limited. It includes up to three major calls according to the genera  
86 (Bretagnolle 1996). Males of the genera *Halobaena* and *Pachyptila* have one single major call,  
87 repetitive and stereotyped, emitted toward males and females (Bretagnolle 1996). Despite this  
88 apparent stereotypy, one may wonder whether the motivation state of the caller may be expressed  
89 through acoustic variation. These two genera are thus good study models to investigate context-  
90 dependent variations in non-songbirds. In our study, we aimed to investigate acoustic variations in  
91 male calls elicited by social interactions with a potential mate or a potential rival. To investigate  
92 context-dependent variations in non-songbirds, we focused on two petrel species: the blue petrel  
93 *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata*. We aimed to assess acoustic  
94 variations in male calls elicited by social interactions with a potential mate or a potential rival. By  
95 playback experiments, we tested in the field the Motivation Hypothesis, i.e. whether sexual and  
96 aggressive motivations of the caller is carried by temporal and/or frequency variations in male-directed  
97 and female-directed calls as shown in oscines. We expected directed calls to be longer and faster than  
98 spontaneous calls based on previous studies in other non-learning bird species. To go further, we  
99 hypothesized that male-directed calls are territorial signals. We thus tested the Breeding-Status  
100 hypothesis by assessing whether bachelor and breeder males vocally react in a similar way when  
101 vocally provoked by another male. Because breeders are attached to their burrow but also defend their  
102 offspring, we expected the breeders' vocal reaction to be stronger, i.e. with longer and faster calls, than  
103 the bachelors' reaction.

## 104 **2. Methods**

### 105 (a) Studied species and study site

106 In blue petrels (*Halobaena caerulea*) and Antarctic prions (*Pachyptila desolata*), both males and  
107 females vocalize at night and maintain a high vocal activity during the entire breeding season (from  
108 October to February in blue petrels, from December to March in Antarctic prions: Warham 1990).  
109 Bachelor males and females spontaneously call from their burrow and while flying, respectively.  
110 Breeder males also call when vocally stimulated by a same-sex conspecific whereas breeding females  
111 scarcely call, even when vocally stimulated by playback (Bretagnolle 1996). For these reasons, we

112 only focused on males hereafter. We conducted the study on 56 male blue petrels (40 bachelors, 16  
113 breeders) and 50 male Antarctic prions (33 bachelors, 17 breeders) in total.

114 We performed the fieldwork on blue petrels' and Antarctic prions' colonies, on a small sub-  
115 Antarctic island within the Kerguelen Archipelago (Ile Verte, 49°51' S, 70°05' E), southern Indian  
116 Ocean during the birds' breeding season (November 25 to December 12 on blue petrels, and  
117 December 23 to January 16 on Antarctic prions). We tested the "Breeding-Status Hypothesis" and the  
118 "Motivational Hypothesis" on breeder and bachelor males facing another male during the 2013 and  
119 2017 breeding seasons, and on bachelors facing females during the 2018 breeding season.

## 120 (b) Playback construction

121 For playback experiments, we built 24 playbacks from 24 isolated spontaneous calls of bachelor  
122 males and females of both blue petrels and Antarctic prions (nine male and five female blue petrels;  
123 five male and five female Antarctic prions) using the signal processing software Avisoft-SASLab Pro  
124 v 5.2.11 (Specht 2017). To do so, we recorded spontaneous calls of bachelor males and females in the  
125 same colonies in 2013 and 2017. Males were recorded when calling spontaneously from their burrow,  
126 using an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20-20 000 Hz  $\pm$  2.5  
127 dB, all uncertainties in SD units unless otherwise stated). Females were recorded when spontaneously  
128 calling while flying, using a directional Sennheiser K6-ME66 microphone (frequency response: 40-  
129 20 000 Hz  $\pm$  2.5 dB). Both microphones were connected to a Marantz PMD 660 digital recorder  
130 (sampling frequency: 44.1 kHz, dynamic: 16 bits). In both blue petrel and Antarctic prion, there is a  
131 vocal sexual dimorphism mainly based on the call syntax. Male calls played-back consisted of two  
132 phrases separated by a silence of  $200 \pm 60$  ms (total duration:  $5.5 \pm 1.6$  s in blue petrel, and  $3.43 \pm 0.85$   
133 s in Antarctic prion), extracted from the call of a male blue petrel or a male Antarctic prion. Female  
134 calls played-back consisted of a mean complete female flight call (i.e. three-phrase calls, total  
135 duration:  $12.4 \pm 2.2$  s in blue petrels and  $6.2 \pm 2.1$  s in Antarctic prions).

## 136 (c) Playback experiments

137 To limit background noises, we performed playback experiments in quiet weather conditions  
138 (wind speed  $< 4$  km.h<sup>-1</sup> and no rain). To mimic the natural conditions of a vocal exchange, we carried

139 out playback sessions in dark nights between 22:00-02:00, which is the period of maximal vocal  
140 activity in the colony (Mougeot and Bretagnolle 2000).

141 Prior to each experiment, we randomly located vocally active bachelor males in the colony (40  
142 blue petrels and 33 Antarctic prions) and we located breeder males (16 blue petrels and 17 Antarctic  
143 prions) by controlling the monitored burrows of the colony. The recording equipment was composed  
144 of an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20-20 000 Hz  $\pm$  2.5 dB)  
145 connected to a Marantz PMD 660 digital recorder. The microphone was positioned on the ground, at  
146 the burrow entrance. We waited a few minutes before starting the experiment to ensure that the tested  
147 individual did not vocally react to our presence, i.e. bachelor males kept a steady call rate and breeder  
148 males stayed silent. We recorded spontaneous calls from bachelor males during four minutes. When  
149 we detected a silence longer than about 10 seconds between two spontaneous calls, we then  
150 broadcasted either a male or a female call, randomly-selected among the built playbacks, at a natural  
151 sound pressure level, i.e. maximum SPL at 70 dB (blue petrels:  $66.3 \pm 9.6$  dB, measured on 115 calls  
152 from 14 males; and Antarctic prions:  $68.1 \pm 11.0$  measured on 443 calls from 40 males with a sound  
153 level meter) using a TASCAM DR-07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic:  
154 16 bits) at the entrance of the burrow. We recorded the vocal reaction during the playback and two  
155 minutes after it ended. Because breeders do not spontaneously vocalize (Bretagnolle 1996; Warham  
156 1990, 1996), we recorded only male-directed calls using the same male playbacks and the same  
157 experimental protocol performed in bachelor males. Each male - bachelor or breeder - was tested only  
158 once. To avoid testing males twice, the nest entrance was labelled by a colored marker.

#### 159 (d) Acoustic analysis

160 The structure of a petrel call consists of a repetition of distinct phrases, themselves composed of  
161 syllables (Bretagnolle 1996). There are four types of syllables discernible by their frequency  
162 modulation shape, hereafter mentioned as A, B, C, and D. In blue petrels and Antarctic prions, the  
163 number of syllables C varies depending on the individuals (mean  $\pm$  SD:  $4.7 \pm 2.1$  and  $1.8 \pm 0.8$   
164 syllables, respectively). The first and last phrases are sometimes incomplete, i.e. syllables C and D are  
165 missing. Hereafter, we considered only complete phrases in our analyses. In total, we obtained N =



166 678 phrases of blue petrels (117 on breeders and 561 on bachelors) and 428 phrases of Antarctic  
167 prions (71 on breeders and 357 on bachelors).

168 Tested individuals might return to a spontaneous vocal behavior before the end of the experiment.  
169 To limit bias related to a behavioral change, we restricted our analyses to the last spontaneous calls  
170 before playback and the first directed calls after playback.

171 Although vocalizations are often described at the call or phrase levels in the literature, syllable  
172 types might be subjected to particular social or environmental cues (Proppe and Sturdy 2009). We thus  
173 aimed to describe the calls at different syntactic levels and in two physical domains. We measured 14  
174 acoustic parameters in the temporal domain and 20 in spectral domain that may encode motivational  
175 information (see Kroodsma and Miller 1982 for a review) on syllables and on phrases (classification,  
176 description and abbreviations are provided in Table 1).

177 To increase the accuracy of frequency measurements, we preliminarily downsampled recorded  
178 calls from 44.1 to 11.025 kHz using the automatic “Sampling Frequency Conversion” functionality of  
179 Avisoft. We also high-passed filtered (cutting frequency: 0.10 kHz, FFT filter) recorded calls to  
180 remove low-frequency background noise, which does not affect recordings. We counted the number of  
181 syllables and phrases on sonograms. We did not analyze syllables  $C_2$  to  $C_n$  as they are not present in  
182 all individuals. We automatically extracted temporal variables on the amplitude envelopes using the  
183 software functionality “Pulse Train Analysis”, with a resolution of 11.6 ms. This functionality  
184 automatically measures the temporal structure of waveforms using pulse recognition algorithms. We  
185 automatically extracted fundamental frequencies and variables describing energy spectral distribution  
186 on linear amplitude spectrum with a resolution of 22 Hz. Automatic extractions were based on similar  
187 pre-sets for all birds to ensure replicable measurements.

## 188 (e) Neural Network Approach

189 We tested each of the hypotheses, Motivation Hypothesis and Breeding Status Hypothesis,  
190 independently, and both problems were stated as a supervised learning problem. Each procedure was  
191 repeated identically for Antarctic prions and blue petrels.

192 To discriminate the three call types, spontaneous calls, male-directed calls, and female-directed  
193 calls, we used a Supervised Machine Learning algorithm (SML). We here used algorithms based on a  
194 Neural Network (NN). NN relaxes linearity assumptions and thus provides a flexible framework for  
195 the analysis of acoustic signals (Lek et al. 1996; Olden et al. 2008). In comparison with other machine  
196 learning methods such as random forests, NN exhibit higher predictive power, better flexibility and  
197 stability (Kotsiantis 2007; Olden et al. 2008).

198 We tested different NN architectures. Shallow networks (no hidden layers) showed poorer  
199 performance (in terms of accuracy) than NN with hidden layers. We finally used a two hidden layers  
200 architecture (with 10 and 5 nodes respectively) since more complex architectures did not improve the  
201 out of sample accuracy, and were slower to train.

202 To avoid overfitting, we performed a Cross Validation procedure (CV), in which we randomly  
203 split the data in two groups called “training” (70% data) and “test” (30% remaining data). After the  
204 training, we evaluated the NN performance by comparing the prediction on the test data and  
205 computing the confusion matrix,  $M$ , where the element  $m_{i,j}$  provides the number of cases predicted  
206 with label  $i$  that are actually in the class  $j$ . We then calculated the accuracy, defined as the sum of the  
207 diagonal elements of the confusion matrix divided by the total number of cases, and that corresponds  
208 to the proportion of well-identified labels by the algorithm. The procedure split-training-evaluation  
209 was repeated ( $N=1000$ ) to obtain an average and standard deviation for each of the entries of the  
210 confusion matrix, and for the accuracy.

211 To estimate the weight of the variable classes (frequency parameters, temporal variables, and  
212 syntactic variables), we trained a NN for each class. As the NN did not converge with only two  
213 syntactic variables, we also trained a NN using both temporal and syntax variables. We then  
214 graphically compared the accuracy of the three NN with each other, and with the full NN as well.

## 215 (f) Generalized Linear Mixed Model (GLMM) approach

216 In a first phase, we aimed to assess whether the different call types (spontaneous, male-directed,  
217 and female-directed), and the calls of males with different breeding status (bachelor or breeder) can be  
218 discriminated. In a second phase, we aimed to highlight the acoustic parameters that significantly vary

219 between the three call types or according to the breeding status, and how they vary. We tested each  
220 hypothesis, Motivation Hypothesis and Breeding-Status Hypothesis, independently and similarly.

221 We preliminary performed a standard correlation analysis that shown that frequency parameters  
222 are independent from temporal and syntactic parameters (appendices A and B). We thus analyzed the  
223 three classes of acoustic parameters independently. Each procedure was repeated identically for blue  
224 petrels and Antarctic prions.

225 We used Principal Components Analysis (PCA) to reduce the dimensionality of the frequency  
226 class and the temporal class, consisting of 20 and 12 variables respectively, for both species and both  
227 hypotheses independently (Table 1). In both species, PCA performed on the frequency class and  
228 temporal class are respectively called  $PCA_F$  and  $PCA_T$  hereafter. For each of the four PCA, we first  
229 calculated a correlation matrix and we kept the six first Principal Components (PC) that explained  
230 between 83 and 91% of the total variance depending on the parameter class and the species. PCA  
231 results are available in appendices C and D. We did not need to perform a PCA in syntactic class as it  
232 consisted of only two variables.

233 To test the Motivation Hypothesis, we used Generalized Linear Mixed Models (GLMM) to model  
234 the call type as a function of the six principal components of  $PCA_F$  or  $PCA_T$  independently. As the  
235 response variable has to be binomial, we used three GLMMs to compare spontaneous calls vs male-  
236 directed calls, spontaneous calls vs female-directed calls, and male-directed calls vs female-directed  
237 calls. To incorporate the dependency among calls of the same male, we used “male ID” as random  
238 factor. When we similarly modelled the call type as a function of call syntax, covariates were the  
239 number of syllables per phrase and the number of phrases per call. To test the Breeding-Status  
240 Hypothesis, we similarly modelled the breeding status as a function of the six principal components of  
241  $PCA_F$  or  $PCA_T$  independently using a binomial GLMM. We similarly modelled the breeding status as  
242 a function of the number of syllables per phrase and the number of phrases per call. When models  
243 failed to converge with the six principal components as covariates, we used fewer principal  
244 components (Tables 3,5).

### 245 **3. Results**

246 (a) Motivation Hypothesis

247 (i) Call-type discrimination

248 NN discriminated the three call types of blue petrels and Antarctic prions with an accuracy of  
249  $90.6 \pm 2.3\%$  and  $79.8 \pm 3.8\%$ , respectively. In both species, spontaneous calls and female-directed  
250 calls were more similar to each other than to male-directed calls (Table 2).

251 In both species, the accuracy of call-type discrimination based on temporal parameters and syntax  
252 only was close to the discrimination accuracy when considering all parameters, and higher than  
253 discrimination accuracy when considering temporal parameters or frequency parameters only (Figure  
254 2a,b). In blue petrels, discrimination accuracy when considering only frequency parameters was  
255 similar to discrimination accuracy when considering only temporal parameters, whereas it was lower  
256 in Antarctic prions (Figure 2a,b).

257 In spectral domain, PCA<sub>F</sub> results showed that the two first principal components (PC<sub>F1</sub>, PC<sub>F2</sub>)  
258 were related to fundamental frequency and energy quartiles of syllable and phrase levels, in both blue  
259 petrel and Antarctic prion (Table 3). Variables related to PC<sub>F3</sub> to PC<sub>F6</sub> then varied between the two  
260 species. In temporal domain, PCA<sub>T</sub> results showed no clear pattern between the two species (Table 3).  
261 Detailed results of PCA<sub>T</sub> showing variable contributions to each principal component in both species  
262 are given in appendix C. Detailed results of binomial GLMM used to compare the call types in both  
263 species are presented in appendix D.

264 (ii) Female-directed vs spontaneous calls

265 In spectral domain, results in blue petrels showed a decrease of PC<sub>F4</sub> and PC<sub>F5</sub> (estimate = -0.66,  
266  $p < 0.001$ ; estimate = -1.62,  $p < 0.001$ ). It suggests a broader frequency bandwidth across the phrase in  
267 female-directed calls than spontaneous calls on average (Table 3). In Antarctic prions, results showed  
268 a decrease of PC<sub>F1</sub> and PC<sub>F2</sub> (estimate = -0.32,  $p = 0.001$ ; estimate = -0.39,  $p = 0.03$ ), and an increase  
269 of PC<sub>F5</sub> (estimate = 0.81,  $p = 0.004$ ). It suggests that female-directed calls were on average higher-  
270 pitched than spontaneous calls (Table 3).

271 In temporal domain, results showed a decrease of PC<sub>T2</sub> (estimate = -0.78,  $p < 0.001$ ) in blue  
272 petrels, suggesting that the average duration of syllables was longer and the average phrase tempo was

273 higher in female-directed calls than spontaneous calls (Table 3). In Antarctic prions, female-directed  
274 calls were characterized by an increase of PC<sub>T</sub>1 and PC<sub>T</sub>4 (estimate = 0.67,  $p < 0.001$ ; estimate = 0.71,  
275  $p < 0.001$ ), suggesting that the average A-syllable duration was longer and the average phrase tempo  
276 was higher in female-directed calls than spontaneous calls (Table 3). In both species, the average  
277 number of phrases per call was higher in female-directed calls than spontaneous calls (estimate = 3.60,  
278  $p < 0.001$ ; estimate = 1.04,  $p < 0.001$ ). In Antarctic prions, the average number of syllables per phrase  
279 was also higher in female-directed calls than in spontaneous calls (estimate = 0.82,  $p = 0.02$ ; Tables 3,  
280 6).

### 281 (iii) Female-directed vs male-directed calls

282 In spectral domain, results in blue petrels showed an increase of PC<sub>F</sub>1, PC<sub>F</sub>3, PC<sub>F</sub>4 and PC<sub>F</sub>5  
283 (estimate = 4.24,  $p < 0.001$ ; estimate = 6.00,  $p = 0.004$ ; estimate = 5.63,  $p = 0.04$ ; estimate = 20.47,  $p$   
284  $< 0.001$ ), and a decrease of PC<sub>F</sub>2 (estimate = -7.07,  $p < 0.001$ ). It suggests that male-directed calls  
285 were on average higher-pitched with a narrower frequency bandwidth than female-directed calls in  
286 blue petrels. In Antarctic prions, female-directed calls and male-directed calls were not significantly  
287 different in spectral domain (Tables 3, 6).

288 In temporal domain, female-directed calls and male-directed calls were not significantly different  
289 in blue petrels (Table 3). In Antarctic prions, results showed a decrease of PC<sub>T</sub>1 (estimate = -36.21,  $p$   
290 = 0.04) suggesting that the average duration of syllable A was shorter, and the average phrase tempo  
291 was lower in male-directed calls than female-directed calls (Table 3). In both species, the average  
292 number of phrases per call was higher in male-directed calls than female-directed calls (estimate =  
293 2.89,  $p = 0.001$ ; estimate = 2.44,  $p < 0.001$ , Tables 3, 6).

### 294 (iv) Male-directed vs spontaneous calls

295 In spectral domain, results showed an increase of PC<sub>F</sub>1, PC<sub>F</sub>3 and PC<sub>F</sub>5 (estimate = 0.73,  $p <$   
296  $0.001$ ; estimate = 0.51,  $p = 0.01$ ; estimate = 1.51,  $p < 0.001$ ), and a decrease of PC<sub>F</sub>2 (estimate = -0.59;  
297  $p = 0.002$ ) in blue petrels; and a decrease of PC<sub>F</sub>1 and PC<sub>F</sub>2 in male-directed calls (estimate = -1.82,  $p$   
298  $< 0.001$ ; estimate = -1.77,  $p = 0.003$ ) in Antarctic prions. It suggests that in both species male-directed  
299 calls of bachelors were on average higher-pitched than spontaneous calls. In blue petrels, the average  
300 frequency bandwidth was tighter in male-directed calls than in spontaneous calls (Tables 3, 6).

301 In temporal domain, results showed an increase of PC<sub>T</sub>5 (estimate = 0.92,  $p = 0.01$ ), and a  
302 decrease of PC<sub>T</sub>2 and PC<sub>T</sub>6 (estimate = -0.75,  $p = 0.02$ ; estimate = -2.02,  $p < 0.001$ ; respectively) in  
303 blue petrels; and a decrease of PC<sub>T</sub>1 (estimate = -1.28,  $p < 0.001$ ) and an increase of PC<sub>T</sub>2 (estimate =  
304 0.52,  $p = 0.002$ ) in Antarctic prions. It suggests that in both species, the average duration of phrases  
305 was longer, the average phrase tempo was lower, and the average duration of syllable was longer in  
306 male-directed calls than spontaneous calls (Table 3). In both species, the average number of phrases  
307 per call was higher in male-directed calls than spontaneous calls (estimate = 3.48,  $p < 0.001$ ; estimate  
308 = 9.00,  $p = 0.004$ , Tables 3, 6).

## 309 (b) Breeding-Status Hypothesis

### 310 (i) Breeding-status discrimination

311 NN discriminated the two breeding status (bachelor vs breeder) in blue petrels and Antarctic  
312 prions with an accuracy of  $98.9 \pm 1.1\%$  and  $94.6 \pm 3.9\%$ , respectively (Table 4).

313 In blue petrels, the accuracy of breeding-status discrimination based on frequency parameters  
314 only was close to the maximum discrimination accuracy when considering all parameters (Figure 2c).  
315 In Antarctic prions, discrimination accuracy when considering temporal and syntactic parameters was  
316 close to the maximum discrimination accuracy when considering all parameters (Figure 2d).  
317 Discrimination accuracy when considering only frequency parameters was the lowest, similarly to  
318 results of call-types discrimination (Figure 2).

319 In spectral domain, results of PCA on bachelors' and breeders' male-directed calls were similar to  
320 PCA on different calls of bachelors', in both species (Tables 3, 4). In temporal domain, PCA<sub>T</sub> showed  
321 no clear pattern between the two species on temporal variables (appendix E). Details of variable  
322 contribution to each principal component in both species are given in appendix E. Detailed results of  
323 binomial GLMM used to compare bachelors' and breeders' male-directed calls are presented in  
324 appendix F in both species.

### 325 (ii) Bachelors' vs breeders' male-directed calls

326 In spectral domain, results in blue petrels showed an increase of PC<sub>F</sub>2, PC<sub>F</sub>4 and PC<sub>F</sub>5 (estimate =  
327 0.92,  $p = 0.001$ ; estimate = 1.13,  $p = 0.009$ ; estimate = 6.30,  $p < 0.001$ ) and a decrease of PC<sub>F</sub>3 and

328 PC<sub>F6</sub> (estimate = -0.76,  $p = 0.02$ ; estimate = -1.65,  $p = 0.02$ ). In Antarctic prions, results showed an  
329 increase of PC<sub>F1</sub>, PC<sub>F3</sub>, PC<sub>F4</sub> (estimate = 0.33,  $p < 0.001$ ; estimate = 0.62,  $p = 0.006$ ; estimate = 0.73,  
330  $p = 0.02$ , respectively); and a decrease of PC<sub>F6</sub> (estimate = -1.16,  $p = 0.001$ ). It suggests that on  
331 average, breeders produced lower-pitched calls than bachelors in blue petrels, while breeders produced  
332 higher-pitched calls than bachelors in Antarctic prion (Tables 5, 6).

333 In temporal domain, results in blue petrels showed a decrease of PC<sub>T2</sub>, PC<sub>T3</sub>, PC<sub>T4</sub>, PC<sub>T5</sub>  
334 (estimate = -0.77,  $p < 0.001$ ; estimate = -0.93,  $p < 0.001$ ; estimate = -0.85,  $p < 0.001$ ; estimate = -0.38,  
335  $p = 0.01$ ), and an increase of PC<sub>T6</sub> (estimate = 0.41,  $p = 0.01$ ). It suggests that the average rhythm and  
336 tempo were higher, and the average duration of syllable (except D) was shorter in breeder calls than  
337 bachelor's. In Antarctic prions, results showed a decrease of PC<sub>T3</sub> and an increase of PC<sub>T6</sub> (estimate =  
338 -0.44,  $p = 0.003$ ; estimate = 0.92,  $p = 0.001$ ), suggesting that the difference between bachelors and  
339 breeders was coded at the syllable level: the average durations of syllable A and interval between  
340 syllables B and C<sub>1</sub> was longer in breeder calls than bachelor's. In both species, the average number of  
341 phrases per call was lower in breeder calls than bachelor's (estimate = -0.13,  $p < 0.001$ ; estimate = -  
342 0.16,  $p < 0.001$ , Tables 5, 6).

#### 343 **4. Discussion**

344 The aim of this study was to compare the acoustic structure of males' calls in different social  
345 contexts in two burrowing-petrel species. We first compared the three call types of bachelor males  
346 (Motivation Hypothesis): spontaneous, male-directed, and female-directed. We then compared  
347 whether male-directed calls emitted by breeders and bachelors present the same acoustic variations  
348 (Breeding-Status Hypothesis).

##### 349 (a) Motivation Hypothesis

350 In both blue petrels and Antarctic prions, calls emitted by bachelors in different social situations  
351 (spontaneous, female-directed, and male-directed calls) are discriminable based on their acoustic  
352 parameters. Although temporal parameters are the most discriminant due to their great variations  
353 between call types, our results showed significant frequency shifts between the different call types as  
354 well. For the first time in two non-songbirds, we observed context dependent frequency shifts at the

355 fine scale of syllables within phrases. Thus, in blue petrels and Antarctic prions, the presence of  
356 conspecifics, either male or female, influences the vocal performance of callers, resulting in acoustic  
357 variations in both temporal and spectral domains.

358 (i) Female-directed calls

359 Female-directed calls and spontaneous calls were more similar to each other than to male-directed  
360 calls. In songbirds, spontaneous songs have two main functions: to attract potential mates and to repel  
361 rivals (“Dual-Function Hypothesis”: Catchpole and Slater 2008). Our results support the hypothesis  
362 that male calls in burrowing petrels have the same functions: attracting flying females into the burrow  
363 and repelling other males. The greater similarity between spontaneous and female-directed calls, in  
364 both species, suggests that spontaneous calls, resounding at night in the colony, may primarily be  
365 sexual signals addressed to flying females susceptible to detect the signal (Gémard et al. *submitted*;  
366 Bretagnolle 1996), even though they are potentially emitted in absence of an audience.

367 When vocally reacting to a female call, bachelors of both species produce calls characterized by  
368 temporal variations. In blue petrels, female-directed calls consist of more, longer, and slower (lower  
369 phrase tempo) phrases. In Antarctic prions, female-directed calls are faster (higher phrase tempo), and  
370 consist of more phrases and more syllables than spontaneous calls. These results are consistent with  
371 previous studies on temporal variations in female-directed songs in songbirds (Sossinka and Böhner  
372 1980; Sakata et al. 2008). In both blue petrels and Antarctic prions, an increase in call duration and/or  
373 syllable number may thus indicate a higher vocal investment and a greater sexual motivation when a  
374 male perceives the presence of a female, in spite of an increased risk of predation (Mougeot and  
375 Bretagnolle 2000). This suggests that spontaneous calls may have a trade-off between advertising  
376 potential for females flying over the burrow and self-protection against predators.

377 When vocally reacting to a female call, bachelors of both species produce calls characterized by  
378 spectral variations. In blue petrels, our results showed a broader frequency bandwidth due to frequency  
379 shifts in syllables. More precisely, the first syllable (A) was higher-pitched and the last syllable (D)  
380 was lower-pitched in female-directed calls than in spontaneous calls. In Antarctic prions, female-  
381 directed calls consisted of higher-pitched phrases than spontaneous ones. When reacting to a potential  
382 mate, males usually enhance the acoustic parameters related to their qualities (Sossinka and Böhner



383 1980; Podos 1997). In previous studies on blue petrels, we showed that large males produce long and  
384 high-pitched calls (Gémard et al. 2019), and that females are more attracted by high-pitched calls  
385 (Gémard et al. *submitted*). In Antarctic prions, large males produce low-pitched calls (Gémard et al.  
386 2019) and we do not know female preferences for acoustic parameters. One hypothesis may be that  
387 male blue petrels exaggerate acoustic parameters related to their morphology when vocally reacting to  
388 a female. This may not be the case in Antarctic prions, although we cannot exclude that further  
389 relationships between male qualities and acoustic parameters have not been highlighted yet.

#### 390 (ii) Male-directed calls

391 After being vocally challenged by another male, bachelors of both species produced male-directed  
392 calls that are longer (with more phrases) and slower (lower syllable and phrase tempos) than  
393 spontaneous calls. This result is consistent with previous studies showing that lengthening  
394 vocalizations is an aggressive signal in learning and non-learning birds (Martín-Vivaldi et al. 2004;  
395 Mager et al. 2012; Balsby et al. 2017). In both blue petrels and Antarctic prions, male-directed calls  
396 also consist of longer syllables than in spontaneous calls. Similar results have been found in a  
397 territorial passerine, the skylark (*Alauda arvensis*): when vocally challenged by another male, skylark  
398 males produce longer syllables separated by shorter silences within songs (Geberzahn and Aubin  
399 2014). Further studies in songbirds also show that vocal performance and song complexity increase in  
400 aggressive contexts (DuBois et al. 2009; Kareklas et al. 2019). We did not find similar results in blue  
401 petrels and Antarctic prions, as challenged males produced calls with lower syllable and phrase  
402 tempos, and with a steady number of syllables. Unlike songbirds, burrowing petrels produce  
403 stereotyped calls with a limited number of syllable types. In these species, the increase of vocal  
404 performance and of song complexity in an aggressive context shown in songbirds may thus be  
405 impossible (Searcy and Beecher 2009). Alternatively, non-learning birds may have evolved a different  
406 signaling system compared to learning species, where motivation is not coded by vocal performance.

407 Although temporal variations in male-directed calls are described in both songbirds and non-  
408 songbirds, spectral variations have never been described in non-songbirds to our knowledge. Our  
409 results show that male-directed calls have a higher fundamental frequency than spontaneous calls in  
410 both species. Although energy quartiles also increased in Antarctic prions, they decreased in blue

411 petrels suggesting a tighter frequency bandwidth than in spontaneous calls. According to the  
412 Motivational-Structural Hypothesis, vocalizations emitted in an aggressive social context are  
413 characterized by long durations, low frequencies, wide frequency bandwidth, and little frequency  
414 variations (Morton 1977). Our results in burrowing petrels show an opposite pattern, which is not so  
415 surprising. The Motivational-Structural Hypothesis has been first described in mammals. Although  
416 some songbirds such as ravens (Szipl et al. 2017) and swamp sparrows (DuBois et al. 2009) follow the  
417 rules, many do not (see Cardoso 2012 for a review). Producing long high-pitched-calls while being  
418 vocally challenged by another male at the entrance of the burrow may thus be an aggressive signal in  
419 territory tenure.

#### 420 (b) Breeding-Status Hypothesis

421 Our results show that calls emitted by bachelors and breeders toward males are discriminable  
422 based on their acoustic parameters. When stimulated by another male, breeders produce lower-pitched  
423 calls than bachelors in blue petrels and higher-pitched calls in Antarctic prions. In burrowing petrels,  
424 breeder and bachelor males do not differ morphologically but breeders coming back from their feeding  
425 trips at sea are heavier than bachelors (Chaurand and Weimerskirch 1994; Appendix G). Large  
426 individuals produce high-pitched calls in blue petrels and low-pitched calls in Antarctic prions  
427 (Gémard et al. 2019). Here we observed the opposite pattern, suggesting that weight variation is thus  
428 not a sufficient explanation for spectral variations in male-directed calls produced by breeders.  
429 Frequency shifts between bachelors and breeders may thus be related to the motivation of the caller.

430 In both species, breeders' calls consisted of fewer phrases than bachelors' and are thus shorter.  
431 One hypothesis is that breeders have less endurance than bachelors do, as they fast in the burrow for  
432 several days when incubating the egg (Chaurand and Weimerskirch 1994). Another hypothesis is that,  
433 in species vulnerable to predation (Mougeot and Bretagnolle 2000), producing short calls may be a  
434 trade-off between self-protection from predators and repelling intruders. A short call by the resident  
435 male might be enough to immediately scare the intruder that, outside the burrow, would be the first to  
436 be caught by a predator possibly attracted by that call.

437 The acoustic variations related to the breeding status of the caller are not similar to the variations  
438 between spontaneous and male-directed calls of bachelors. Therefore, differences between bachelors'  
439 and breeders' calls may not be related to the territorial-response intensity of the caller only, contrary to  
440 our hypothesis.

#### 441 (c) Conclusion

442 In many species, males use long-distance vocal signals to attract mates and/or to regulate the  
443 spacing between competitors. In blue petrels and Antarctic prions, we showed that conspecifics  
444 vocally stimulating a male at the entrance of its burrow induce temporal variations, but also frequency  
445 shifts in the burrow-owner calls. These acoustic variations differ according to the conspecific sex, and  
446 are thus likely to convey different motivations, such as aggressive motivation when facing another  
447 male and sexual motivation when facing a female. Both bachelors and breeders intensively react to the  
448 presence of a conspecific male, but the acoustic variations related to the breeding status of the caller  
449 are not explained by a difference in the territoriality intensity. So far, expression of motivation in vocal  
450 signals have been highlighted in very few non-songbirds, and this is the first time that a study  
451 describes spectral variations related to the signaler motivation in non-songbirds. It opens new leads in  
452 the assessment of vocal plasticity in non-oscine species.

#### 453 **Ethics statement**

454 All experiments were approved by the French Ethical Committee (APAFIS#9496-201707131540776)  
455 after favourable recommendation of Comité d'Ethique pour L'Expérimentation Animale Languedoc-  
456 Roussillon (CEEA-LR), C2EA n°36, and by the Ethical Committee of Reserve Naturelle des Terres  
457 Australes et Antarctiques Françaises (TAAF). Experiments were made in full conformity with  
458 guidelines established by both IPEV and CNRS for the Ethical Treatment of Animals. All experiments  
459 comply with the current laws of the country where they were performed.

#### 460 **References**

461 Balsby TJ, Eldermire ER, Schnell JK, Poesel A, Walsh RE, Bradbury JW. . 2017. Function of vocalization  
462 length and warble repertoire size in orange-fronted conures, *Anim Behav.* 134: 301–310.  
463 doi:10.1016/j.anbehav.2017.10.025

464 Bonadonna F, Nevitt GA. 2004. Partner-specific odor recognition in an Antarctic seabird. *Science* (80- ).  
465 306(5697):835. doi:10.1126/science.1103001.

466 Bradbury JW, Vehrencamp SL. 2011. *Principles of animal communication*.

467 Bretagnolle V. 1996. Acoustic communication in a group of nonpasserine birds, the petrels. In: Kroodsma DE,  
468 Miller EH, editors. *Ecology and Evolution of Acoustic Communication in Birds*. Cornell Un. New York. p.  
469 160–177.

470 Bretagnolle V, Lequette B. 1990. Structural variation in the call of the Cory's shearwater (*Calonectris diomedea*,  
471 Aves, Procellariidae). *Ethology*. 85:313–323. doi:10.1111/j.1439-0310.1990.tb00410.x.

472 Briefer EF. 2012. Vocal expression of emotions in mammals: Mechanisms of production and evidence. *J Zool*.  
473 288(1):1–20. doi:10.1111/j.1469-7998.2012.00920.x.

474 Briefer EF. 2018. Vocal contagion of emotions in non-human animals. *Proc R Soc B Biol Sci*.  
475 285(1873):20172783. doi:10.1098/rspb.2017.2783.  
476 <http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2017.2783>.

477 Briefer EF 2020. Coding for 'Dynamic' Information: Vocal Expression of Emotional Arousal and Valence in  
478 Non-human Animals. In *Coding Strategies in Vertebrate Acoustic Communication*. Springer, Cham. p. 137–  
479 162.

480 Cardoso GC. 2012. Paradoxical calls: the opposite signaling role of sound frequency across bird species. *Behav*  
481 *Ecol*. 23(2):237–241. doi:10.1093/beheco/arr200.

482 Catchpole CK, Slater PJB. 2008. *Bird song: biological themes and variations*.

483 Chaurand T, Weimerskirch H. 1994. Incubation routine, body mass regulation and egg neglect in the blue petrel  
484 *Halobaena caerulea*. *Ibis* (Lond 1859). 136(3):285–290. doi:10.1111/j.1474-919X.1994.tb01097.x.

485 Curé C, Aubin T, Mathevon N. 2011. Sex discrimination and mate recognition by voice in the yelkouan  
486 shearwater *Puffinus yelkouan*. *Bioacoustics*. 20:235–250. doi:10.1080/09524622.2011.9753648.

487 Darwin C. 1871. *The descent of man, and selection in relation to sex*. Murray, editor. London.

488 DuBois AL, Nowicki S, Searcy WA. 2009. Swamp sparrows modulate vocal performance in an aggressive  
489 context. *Biol Lett*. 5(2):163–165. doi:10.1098/rsbl.2008.0626.  
490 <http://rsbl.royalsocietypublishing.org/cgi/doi/10.1098/rsbl.2008.0626>.

491 Funghi C, Cardoso GC, Mota PG. 2014. Increased syllable rate during aggressive singing in a bird with complex  
492 and fast song. *J Avian Biol*. 46(3):283–288. doi:10.1111/jav.00480.

493 Geberzahn N, Aubin T. 2014. How a songbird with a continuous singing style modulates its song when  
494 territorially challenged. *Behav Ecol Sociobiol.* 68(1):1–12. doi:10.1007/s00265-013-1616-4.

495 Gémard C, Aubin T, Bonadonna F. 2019. Males' calls carry information about individual identity and  
496 morphological characteristics of the caller in burrowing petrels. *J Avian Biol.*:jav.02270.  
497 doi:10.1111/jav.02270. <https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02270>.

498 Gémard C, Aubin T, Reboud EL, Bonadonna F. Call rate, fundamental frequency and syntax determine male-  
499 call attractiveness in blue petrels *Halobaena caerulea*. *Submitted*.

500 Kareklas K, Wilson J, Kunc HP, Arnott G. 2019. Signal complexity communicates aggressive intent during  
501 contests, but the process is disrupted by noise. *Biol Lett.* 15(4). doi:10.1098/rsbl.2018.0841.

502 Kotsiantis SB. 2007. Supervised machine learning: a review of classification techniques. *Informatica.* 31:249–  
503 268.

504 Kroodsma DE. 2004. The diversity and plasticity of birdsong. In: *Nature's Music: The Science of Birdsong*. p.  
505 108–131.

506 Kroodsma DE, Miller EH. 1982. *Acoustic communication in birds*. Academic P. Ouellet H, editor.

507 Leclaire S, Strandh M, Mardon J, Westerdahl H, Bonadonna F. 2017. Odour-based discrimination of similarity at  
508 the major histocompatibility complex in birds. *Proc R Soc B Biol Sci.* 284(1846):2016–20466.  
509 doi:10.1098/rspb.2016.2466.

510 Lek S, Delacoste M, Baran P, Dimopoulos I, Lauga J, Aulagnier S. 1996. Application of neural networks to  
511 modelling nonlinear relationships in ecology. *Ecol Modell.* 90(1):39–52. doi:10.1016/0304-3800(95)00142-  
512 5.

513 Linhart P, Jaška P, Petrusková T, Petrusek A, Fuchs R. 2013. Being angry, singing fast? Signalling of aggressive  
514 motivation by syllable rate in a songbird with slow song. *Behav Processes.* 100:139–145.  
515 doi:10.1016/j.beproc.2013.06.012.

516 Mager JN, Walcott C, Piper WH. 2012. Male common loons signal greater aggressive motivation by lengthening  
517 territorial yodels. *Wilson J Ornithol.* 124(1):73–80. doi:10.1676/11-024.1.  
518 <http://www.bioone.org/doi/abs/10.1676/11-024.1>.

519 Manser MB. 2010. The generation of functionally referential and motivational vocal signals in mammals. In:  
520 *Handbook of Behavioral Neuroscience*. Vol. 19. p. 477–486.  
521 <https://linkinghub.elsevier.com/retrieve/pii/S1569733910700588>.

522 Mardon J, Saunders SM, Anderson MJ, Couchoux C, Bonadonna F. 2010. Species, gender, and identity:  
523 Cracking petrels' sociochemical code. *Chem Senses*. 35(4):309–321. doi:10.1093/chemse/bjq021.

524 Martín-Vivaldi M, Palomino JJ, Soler M. 2004. Strophe length in spontaneous songs predicts male response to  
525 playback in the hoopoe *Upupa epops*. *Ethology*. 110(5):351–362. doi:10.1111/j.1439-0310.2004.00971.x.

526 Morton ES. 1977. On the occurrence and significance of Motivation-Structural Rules in some bird and mammal  
527 sounds. *Am Nat*. 111(981):855–869. doi:10.1086/283219.  
528 <http://www.journals.uchicago.edu/doi/10.1086/283219>.

529 Mougeot F, Bretagnolle V. 2000a. Predation risk and moonlight avoidance in nocturnal seabirds. *J Avian Biol*.  
530 31(3):376–386. doi:10.1034/j.1600-048X.2000.310314.x. <http://doi.wiley.com/10.1034/j.1600->  
531 [048X.2000.310314.x](http://doi.wiley.com/10.1034/j.1600-048X.2000.310314.x).

532 Mougeot F, Bretagnolle V. 2000b. Predation as a cost of sexual communication in nocturnal seabirds: an  
533 experimental approach using acoustic signals. *Anim Behav*. 60(5):647–656. doi:10.1006/anbe.2000.1491.  
534 <http://linkinghub.elsevier.com/retrieve/pii/S000334720091491X>.

535 Olden JD, Lawler JJ, Poff NL. 2008. Machine Learning methods without tears: a primer for ecologists. *Q Rev*  
536 *Biol*. 83(2):171–193. doi:10.1086/587826.

537 Podos J. 1997. A Performance Constraint on the Evolution of Trilled Vocalizations in a Songbird Family  
538 (Passeriformes: Emberizidae). *Evolution (N Y)*. 51(2):537–551. doi:10.2307/2411126.  
539 <https://www.jstor.org/stable/2411126?origin=crossref>.

540 Proppe DS, Sturdy CB. 2009. The effect of schedules of reinforcement on the composition of spontaneous and  
541 evoked black-capped chickadee calls. *J Exp Biol*. 212(18):3016–3025. doi:10.1242/jeb.031724.

542 Ręk P. 2013. Corncrake males learn new signal meanings during aggressive interactions. *Anim. Behav*. 86(2):  
543 451–457. doi: 10.1016/j.anbehav.2013.05.042.

544 Ręk P, Osiejuk TS. 2013. Temporal patterns of broadcast calls in the corncrake encode information  
545 arbitrarily. *Behav. Ecol*. 24(2): 547–552. doi: 0.1093/beheco/ars196.

546 Sakata JT, Hampton CM, Brainard MS. 2008. Social modulation of sequence and syllable variability in adult  
547 birdsong. *J Neurophysiol*. 99(4):1700–1711. doi:10.1152/jn.01296.2007.

548 Searcy WA, Beecher MD. 2009. Song as an aggressive signal in songbirds. *Anim Behav*. 78(6):1281–1292.  
549 doi:10.1016/j.anbehav.2009.08.011.

550 Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deception in signaling  
551 systems. Princeton.

552 Sossinka R, Böhner J. 1980. Song types in the zebra finch. *Z Tierpsychol.* 53:123–132.

553 Szipl G, Ringler E, Spreafico M, Bugnyar T. 2017. Calls during agonistic interactions vary with arousal and  
554 raise audience attention in ravens. *Front Zool.* 14(1):1–13. doi:10.1186/s12983-017-0244-7.

555 Taoka M, Okumura H. 1989. Sexual dimorphism of chatter-calls and vocal sex recognition in Leach's storm-  
556 petrels (*Oceanodroma leucorhoa*). *Auk.* 106:498–501.

557 Todt D, Naguib M. 2000. Vocal interactions in birds: the use of song as a model in communication. *Adv Study*  
558 *Behav.* 29(C):247–296. doi:10.1016/S0065-3454(08)60107-2.

559 Vehrencamp SL. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal signals:*  
560 *signalling and signal design in animal communication.*

561 Warham J. 1990. *The petrels: their ecology and breeding systems.* Press A, editor. London.

562 Warham J. 1996. Behaviour and vocalizations of Procellariidae, Hydrobatidae and Pelecooididae. In: *The*  
563 *Behaviour, Population Biology and Physiology of the Petrels.* Elsevier.  
564 <https://linkinghub.elsevier.com/retrieve/pii/B9780127354156500193>.

565 Zahavi A. 1982. The pattern of vocal signals and the information they convey. *Behaviour.* 80(1–2):1–8.  
566 doi:10.1163/156853982X00409. [https://brill.com/view/journals/beh/80/1-2/article-p1\\_1.xml](https://brill.com/view/journals/beh/80/1-2/article-p1_1.xml).

567

568 **Figure captions**

569 **Figure 1.** Spectrograms of calls from a bachelor male of blue petrel *H. caerulea* and Antarctic prion *P. desolata*  
570 (Blackman window, FFT length: 512): (a) spontaneous blue petrel call; (b) spontaneous Antarctic prion call; (c)  
571 male-directed blue petrel call; (d) male-directed Antarctic prion call.

572 **Figure 2.** Accuracy of NN trained to discriminate the three call types of bachelor males based on their acoustic  
573 parameters in (a) blue petrel *H. caerulea* and (b) Antarctic prion *P. desolata*. Accuracy of NN trained to  
574 discriminate male-directed calls of bachelors and breeders in (c) blue petrels and (d) Antarctic prions.



575 **Tables**

576 **Table 1.** Summary of the 34 syntactic, temporal and spectral parameters and their abbreviations used to describe  
 577 calls of male blue petrels *H. caerulea* and Antarctic prions *P. desolata*.

<b>class</b>	<b>abbreviation</b>	<b>description</b>
<b>syntax</b>	Call.NbPh	Number of phrases in a call
	Ph.NbSyll	Number of syllables in a phrase
<b>temporal</b>	A.Du	A syllable duration
	B.Du	B syllable duration
	C1.Du	Duration of the first syllable C
	D.Du	D syllable duration
	B.Int	Inter-syllable A-B duration
	C1.Int	Inter-syllable B-C <sub>1</sub> duration
	D.Int	Inter-syllable C <sub>cie</sub> -D duration
	Syll.Tempo	Syllable tempo (number of syllables per second for each phrase)
	Ph.Tempo	Phrase tempo (number of phrases per second for each call)
	Ph.Rhythm	Phrase rhythm (ratio between syllable and silence durations)
	Ratio.Du	Ratio between syllable and phrase durations
	Ph.Du	Phrase duration
	<b>spectral</b>	A.F0
A.Q25		A upper quartile (frequency at the upper limit of the 25% energy of A syllable)
A.Q50		A medium quartile (frequency at the upper limit of the 50% energy of A syllable)
A.Q75		A lower quartile (frequency at the upper limit of the 75% energy of A syllable)
B.F0		Fundamental frequency of B syllable
B.Q25		B upper quartile
B.Q50		B medium quartile
B.Q75		B lower quartile
C1.F0		Fundamental frequency of C <sub>1</sub> syllable
C1.Q25		C <sub>1</sub> upper quartile
C1.Q50		C <sub>1</sub> medium quartile

C1.Q75	C <sub>1</sub> lower quartile
D.F0	Fundamental frequency of D syllable
D.Q25	D upper quartile
D.Q50	D medium quartile
D.Q75	D lower quartile
Ph.F0	Mean fundamental frequency of the phrase
Ph.Q25	Phrase upper quartile
Ph.Q50	Phrase medium quartile
Ph.Q75	Phrase lower quartile

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578

579

580 **Table 2.** Mean accuracy and standard deviation of the classification of three call types of bachelor males in blue  
 581 petrels *H. caerulea* and Antarctic prions *P. desolata*.

species	actual	prediction		
		spontaneous	female-directed	male-directed
<b>blue petrels</b>				
	spontaneous	25.4% (3.6)	7.8% (2.7)	1.0% (1.1)
	female-directed	8.0% (2.5)	28.7% (3.8)	0.0% (0.2)
	male-directed	1.6% (1.2)	0.1% (0.4)	27.4% (3.9)
<b>Antarctic prions</b>				
	spontaneous	24.3% (2.7)	3.5% (1.5)	1.3% (1.1)
	female-directed	3.1% (1.7)	21.2% (2.6)	0.3% (0.4)
	male-directed	1.4% (1.0)	0.2% (0.5)	44.5% (3.1)

582

583

584 **Table 3.** Variations of acoustic parameters between the three different call types of bachelor males in blue  
585 petrels *H. caerulea* and Antarctic prions *P. desolata*. Acoustic parameters given here are the most correlated with  
586 the principal components (but see appendix C for the contribution of each acoustic parameter in each principal  
587 component).

		female-directed calls (vs spontaneous)	male-directed calls (vs spontaneous)	male-directed calls (vs female-directed)
<b>blue petrels</b>				
<b>frequency variables</b>				
PC1	all F0, all Q25	NS	↗	↗
PC2	all Q50, all Q75	NS	↘	↘
PC3	A.Q50, C.Q50, A.Q75, C.Q75	NS	↗ ↘	↗ ↘
PC4	A.F0, A.Q25 A.Q50, D.F0, D.Q25, D.Q50	↗ ↘	NS	↘ ↗
PC5	B.Q75	↘	↗	↗
PC6	B.Q50, B.Q75	NS	NS	NA
<b>temporal variables</b>				
PC1	Ph.Rhythm, Ratio.Du	NS	NS	NS
PC2	B.Du, Ph.Du, Ph.Tempo	↗ ↘	↗ ↘	NS
PC3	Syll.Tempo	NS	NS	NS
PC4	C1.Du, D.Du	NS	NS	NS
PC5	D.Du	NS	↘	NA
PC6	A.Du	NS	↗	NA
<b>syntax</b>				
	Call.NbPh	↗	↗	↗
	Ph.NbSyll	NS	NS	NS

---

### Antarctic prions

#### frequency variables

PC1	all F0, all Q25, all Q50	↗	↗	NS
PC2	A.Q75, B.Q75, C.Q75, Ph.Q75	↗	↗	NS

PC3	A.Q50	NS	NS	NS
PC4	B.F0	NS	NS	NS
PC5	A.F0	↗	NS	NS
PC6	B.F0	NA	NA	NA

**temporal variables**

PC1	A.Du, Ph.Tempo	↗	↘	↘
PC2	B.Du, D.Du	NS	↗	NS
	Syll.Tempo		↘	
PC3	B.Int	NS	NS	NS
PC4	C.Int	↘	NS	NA
PC5	C1.Du	NS	NS	NA
PC6	C1.Int	NS	NS	NA

**syntax**

	Call.NbPh	↗	↗	↗
	Ph.NbSyll	NS	↗	NA

588 NS: non-significant; NA: non-applicable; ↗ indicates an increase and ↘ a decrease. Variable abbreviations given  
589 in Table 1.

590 **Table 4.** Mean accuracy and standard deviation of the classification of bachelor and breeder males in blue  
 591 petrels *H. caerulea* and Antarctic prions *P. desolata*.

species	actual	prediction	
		bachelor	breeder
<b>blue petrels</b>			
	bachelor	67.5% (3.8)	0.5% (0.8)
	breeder	0.6% (0.8)	31.4% (3.9)
<b>Antarctic prions</b>			
	bachelor	57.2% (6.4)	3.7% (3.1)
	breeder	3.2% (3.5)	38% (6.2)

592

593

594 **Table 5.** Variations of acoustic parameters between the male-directed calls of bachelor and breeder males in blue  
 595 petrels *H. caerulea* and Antarctic prions *P. desolata*. Acoustic parameters given here are the most correlated with  
 596 the principal components (but see appendix E for the contribution of each acoustic parameter in each principal  
 597 component).

<b>breeders' male-directed calls (vs bachelors')</b>		
<b>blue petrels</b>		
<b>frequency variables</b>		
PC1	all F0, all Q25	NS
PC2	all Q75, B.50, C1.50	↘
PC3	C1.50	↗
	C1.Q75	↘
PC4	A.Q50	↘
PC5	Ph.Q75	↘
PC6	B.Q75	↗
	D.Q75	↘
<b>temporal variables</b>		
PC1	Ph.Du, Syll.Tempo, Ph.Tempo	NS
PC2	Ph.Rhythm, Ratio.Du	↗
PC3	B.Int	↘
PC4	A.Du	↘
PC5	B.Du	↘
PC6	C1.Du	↗
	D.Du	↘
<b>syntax</b>		
	Call.NbPh	↘
	Ph.NbSyll	↗
<b>Antarctic prions</b>		
<b>frequency variables</b>		
PC1	F0, Q25, Q50	↗
PC2	A.F0, Q75	NS
PC3	all F0	↗

PC4	B.F0	↘
	D.F0	↗
PC5	B.Q25, C.F0	NS
PC6	A.F0	↘

**temporal variables**

PC1	B.Du	NS
PC2	Ph.Du, Ph.Tempo	NS
PC3	A.Du	↗
PC4	C1.Du	NS
PC5	D.Int	NS
PC6	C.Int	↗

**syntax**

	Call.NbPh	↘
	Ph.NbSyll	NS

---

598 NS: non-significant; NA: non-applicable; ↗ indicates an increase and ↘ a decrease.

599 Variable abbreviations given in Table 1.

600



601 **Table 6.** Summary table of the acoustic variations characterizing directed calls emitted by males stimulated by a  
 602 conspecific, according to the sex of the conspecific and the reproductive status of the signaler.

	<b>bachelor males' calls</b>		<b>breeder males' calls</b>
	<b>female-directed</b>	<b>male-directed</b>	<b>male-directed</b>
	(vs spontaneous)	(vs spontaneous)	(vs bachelors' male-directed calls)
<b>blue petrels</b>			
<b>frequency variables</b>	- higher pitched - shifts on syllables	- higher pitched - narrower bandwidth	- narrower bandwidth
<b>temporal variables</b>	- longer phrases - lower tempo	- longer phrases - lower tempo	- shorter syllables - higher rhythm
<b>syntax</b>	- more phrases per call	- more phrases per call	- more syllables per phrase - less phrases per call
<b>Antarctic prions</b>			
<b>frequency variables</b>	- higher pitched	- higher pitched	- higher pitched
<b>temporal variables</b>	- higher tempo	- lower tempo - longer syllables - shorter silences	- longer syllables A
<b>syntax</b>	- more phrases per call	- more phrases per call	- less phrases per call

603