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# Contextual variations in calls of two non-oscine birds: the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata*

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

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

# 1. Background

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

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

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

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

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

# 2. Methods

## (a) Studied species and study site

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

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

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

## (b) Playback construction

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

## (c) Playback experiments

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

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

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

## (d) Acoustic analysis

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

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

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

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

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

## (e) Neural Network Approach

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

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

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

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

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

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

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

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

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

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

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

# 3. Results

## (a) Motivation Hypothesis

(i) Call-type discrimination

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

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

In spectral domain, $PCA_F$ results showed that the two first principal components ($PC_F1$, $PC_F2$) were related to fundamental frequency and energy quartiles of syllable and phrase levels, in both blue petrel and Antarctic prion (Table 3). Variables related to $PC_F3$ to $PC_F6$ then varied between the two species. In temporal domain, $PCA_T$ results showed no clear pattern between the two species (Table 3). Detailed results of $PCA_T$ showing variable contributions to each principal component in both species are given in appendix C. Detailed results of binomial GLMM used to compare the call types in both species are presented in appendix D.

(ii) Female-directed vs spontaneous calls

In spectral domain, results in blue petrels showed a decrease of $PC_F4$ and $PC_F5$ (estimate = -0.66, $p < 0.001$; estimate = -1.62, $p < 0.001$). It suggests a broader frequency bandwidth across the phrase in female-directed calls than spontaneous calls on average (Table 3). In Antarctic prions, results showed a decrease of $PC_F1$ and $PC_F2$ (estimate = -0.32, $p = 0.001$; estimate = -0.39, p = 0.03), and an increase of $PC_F5$ (estimate = 0.81, $p = 0.004$). It suggests that female-directed calls were on average higher-pitched than spontaneous calls (Table 3).

In temporal domain, results showed a decrease of $PC_T2$ (estimate = -0.78, $p < 0.001$) in blue petrels, suggesting that the average duration of syllables was longer and the average phrase tempo was

higher in female-directed calls than spontaneous calls (Table 3). In Antarctic prions, female-directed calls were characterized by an increase of $PC_T1$ and $PC_T4$ (estimate = 0.67, $p < 0.001$; estimate = 0.71, $p < 0.001$), suggesting that the average A-syllable duration was longer and the average phrase tempo was higher in female-directed calls than spontaneous calls (Table 3). In both species, the average number of phrases per call was higher in female-directed calls than spontaneous calls (estimate = 3.60, $p < 0.001$; estimate = 1.04, $p < 0.001$). In Antarctic prions, the average number of syllables per phrase was also higher in female-directed calls than in spontaneous calls (estimate = 0.82, p = 0.02; Tables 3, 6).

(iii) Female-directed vs male-directed calls

In spectral domain, results in blue petrels showed an increase of $PC_F1$, $PC_F3$, $PC_F4$ and $PC_F5$ (estimate = 4.24, $p < 0.001$; estimate = 6.00, $p = 0.004$; estimate = 5.63, $p = 0.04$; estimate = 20.47, $p < 0.001$), and a decrease of $PC_F2$ (estimate = -7.07, $p < 0.001$). It suggests that male-directed calls were on average higher-pitched with a narrower frequency bandwidth than female-directed calls in blue petrels. In Antarctic prions, female-directed calls and male-directed calls were not significantly different in spectral domain (Tables 3, 6).

In temporal domain, female-directed calls and male-directed calls were not significantly different in blue petrels (Table 3). In Antarctic prions, results showed a decrease of $PC_T1$ (estimate = -36.21, $p = 0.04$) suggesting that the average duration of syllable A was shorter, and the average phrase tempo was lower in male-directed calls than female-directed calls (Table 3). In both species, the average number of phrases per call was higher in male-directed calls than female-directed calls (estimate = 2.89, $p = 0.001$; estimate = 2.44, $p < 0.001$, Tables 3, 6).

(iv) Male-directed vs spontaneous calls

In spectral domain, results showed an increase of $PC_F1$, $PC_F3$ and $PC_F5$ (estimate = 0.73, $p < 0.001$; estimate = 0.51, $p = 0.01$; estimate = 1.51, $p < 0.001$), and a decrease of $PC_F2$ (estimate = -0.59; $p = 0.002$) in blue petrels; and a decrease of $PC_F1$ and $PC_F2$ in male-directed calls (estimate = -1.82, $p < 0.001$; estimate = -1.77, $p = 0.003$) in Antarctic prions. It suggests that in both species male-directed calls of bachelors were on average higher-pitched than spontaneous calls. In blue petrels, the average frequency bandwidth was tighter in male-directed calls than in spontaneous calls (Tables 3, 6).

In temporal domain, results showed an increase of $PC_T5$ (estimate = 0.92, $p$ = 0.01), and a decrease of $PC_T2$ and $PC_T6$ (estimate = -0.75, $p$ = 0.02; estimate = -2.02, $p$ < 0.001; respectively) in blue petrels; and a decrease of $PC_T1$ (estimate = -1.28, $p$ < 0.001) and an increase of $PC_T2$ (estimate = 0.52, $p$ = 0.002) in Antarctic prions. It suggests that in both species, the average duration of phrases was longer, the average phrase tempo was lower, and the average duration of syllable was longer in male-directed calls than spontaneous calls (Table 3). In both species, the average number of phrases per call was higher in male-directed calls than spontaneous calls (estimate = 3.48, $p$ < 0.001; estimate = 9.00, $p$ = 0.004, Tables 3, 6).

## (b) Breeding-Status Hypothesis

### (i) Breeding-status discrimination

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

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

In spectral domain, results of PCA on bachelors' and breeders' male-directed calls were similar to PCA on different calls of bachelors', in both species (Tables 3, 4). In temporal domain, $PCA_T$ showed no clear pattern between the two species on temporal variables (appendix E). Details of variable contribution to each principal component in both species are given in appendix E. Detailed results of binomial GLMM used to compare bachelors' and breeders' male-directed calls are presented in appendix F in both species.

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

In spectral domain, results in blue petrels showed an increase of $PC_F2$, $PC_F4$ and $PC_F5$ (estimate = 0.92, $p$ = 0.001; estimate = 1.13, $p$ = 0.009; estimate = 6.30, $p$ < 0.001) and a decrease of $PC_F3$ and

$PC_F6$ (estimate = -0.76, $p$ = 0.02; estimate = -1.65, $p$ = 0.02). In Antarctic prions, results showed an increase of $PC_F1$, $PC_F3$, $PC_F4$ (estimate = 0.33, $p < 0.001$; estimate = 0.62, $p$ = 0.006; estimate = 0.73, $p$ = 0.02, respectively); and a decrease of $PC_F6$ (estimate = -1.16, $p$ = 0.001). It suggests that on average, breeders produced lower-pitched calls than bachelors in blue petrels, while breeders produced higher-pitched calls than bachelors in Antarctic prion (Tables 5, 6).

In temporal domain, results in blue petrels showed a decrease of $PC_T2$, $PC_T3$, $PC_T4$, $PC_T5$ (estimate = -0.77, $p < 0.001$; estimate = -0.93, $p < 0.001$; estimate = -0.85, $p < 0.001$; estimate = -0.38, $p$ = 0.01), and an increase of $PC_T6$ (estimate = 0.41, $p$ = 0.01). It suggests that the average rhythm and tempo were higher, and the average duration of syllable (except D) was shorter in breeder calls than bachelor's. In Antarctic prions, results showed a decrease of $PC_T3$ and an increase of $PC_T6$ (estimate = -0.44, $p$ = 0.003; estimate = 0.92, $p$ = 0.001), suggesting that the difference between bachelors and breeders was coded at the syllable level: the average durations of syllable A and interval between syllables B and $C_1$ was longer in breeder calls than bachelor's. In both species, the average number of phrases per call was lower in breeder calls than bachelor's (estimate = -0.13, $p < 0.001$; estimate = -0.16, $p < 0.001$, Tables 5, 6).

# 4. Discussion

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

## (a) Motivation Hypothesis

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

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

(i) Female-directed calls

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

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

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

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

(ii) Male-directed calls

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

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

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

## (b) Breeding-Status Hypothesis

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

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

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

### (c) Conclusion

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

## Ethics statement

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

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# Figure captions

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

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

# Tables

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

| class | abbreviation | description |
|---|---|---|
| **syntax** | Call.NbPh | Number of phrases in a call |
| | Ph.NbSyll | Number of syllables in a phrase |
| **temporal** | 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-$C_1$ duration |
| | D.Int | Inter-syllable $C_{cie}$-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 |
| **spectral** | A.F0 | Fundamental frequency of A syllable |
| | 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 $C_1$ syllable |
| | C1.Q25 | $C_1$ upper quartile |
| | C1.Q50 | $C_1$ medium quartile |

| | |
|---|---|
| C1.Q75 | $C_1$ 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 |

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

| species | actual | prediction | | |
|---|---|---|---|---|
| | | **spontaneous** | **female-directed** | **male-directed** |
| **blue petrels** | | | | |
| | 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) |
| **Antarctic prions** | | | | |
| | 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) |

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

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

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

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

| species | actual | prediction | |
|---|---|---|---|
| | | bachelor | breeder |
| **blue petrels** | | | |
| | bachelor | 67.5% (3.8) | 0.5% (0.8) |
| | breeder | 0.6% (0.8) | 31.4% (3.9) |
| **Antarctic prions** | | | |
| | bachelor | 57.2% (6.4) | 3.7% (3.1) |
| | breeder | 3.2% (3.5) | 38% (6.2) |

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

| | | **breeders' male-directed calls (vs bachelors')** |
|---|---|---|
| **blue petrels** | | |
| **frequency variables** | | |
| 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 | ↘ |
| **temporal variables** | | |
| 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 | ↘ |
| **syntax** | | |
| | Call.NbPh | ↘ |
| | Ph.NbSyll | ↗ |
| **Antarctic prions** | | |
| **frequency variables** | | |
| 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 |

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

Variable abbreviations given in Table 1.

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

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