Variation, utilisation, et information contenue dans le chant des pétrels nichant en terrier aux iles Kerguelen

Charlène Gémard

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Variation, use and informative content of burrowing petrels' male calls in Kerguelen

Présentée par Charlène GEMARD
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Sous la direction de
Francesco BONADONNA et Thierry AUBIN

Devant le jury composé de

Dr. Pierrick BOCHER, MCF, LIENSs-CNRS-Université de la Rochelle	Rapporteur
Dr. Charlotte CURE, CR2, CEREMA	Rapportrice
Dr. Claire DOUTRELANT, DR, CEFE-CNRS	Examinatrice, Présidente du jury
Dr. Leonida FUSANI, Prof., Université de Vienne	Examinateur
Dr. Francesco BONADONNA, DR2, CEFE-CNRS	Directeur
Dr. Thierry AUBIN, DR, CNRS	Co-directeur

UNIVERSITÉ DE MONTPELLIER

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“Every answer contains a

new quest”.

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INTRODUCTION

(photo credits: Guilhem Battistella)

ABOUT ANIMAL COMMUNICATION

Animal communication, through amazingly diverse means, is a fascinating and conspicuous aspect of animal behaviour. Because it holds a central place in animal communities, the understanding of how and why animals communicate is a challenge that has never stopped to thrill the scientific community.

Defining animal communication

The term "*communication*" is rather broad and defining animal communication clearly and in exhaustive details is not an easy task. There are still divergences about what should be considered as actual animal communication and what should not. In the "Mathematical Theory of Communication", Shannon and Weaver (1949) originally identified three essential elements for all communication systems: the *emitter* (also called sender or signaller) that sends a signal, the *signal*, and the *receiver* that perceives the signal (Figure A in Box 1). A common definition found in the scientific literature for animal communication is thus "*an exchange of signals produced by a sender, and perceived and decoded by one or several receivers*" (Bradbury & Vehrencamp, 2011). Emitters and receivers are most often from the same species (conspecifics) but not always (Magrath et al., 2015).

The key in animal communication is the signal. However, once again, opinions are not unanimous on its definition. Originally, Shannon and Weaver (1949) defined it as a coded message propagating through a sensory channel from the emitter to the receiver. For instance, goldcrests (*Regulus regulus*) have conspicuous yellow patches on the head. These yellow patches, combined with a head movement, are a visual signal coding information about the willingness of the emitter to attack. The emitter is the individual shaking its head; the receiver is the individual that actually sees it. The concept of coded information is still the basis of many definitions of animal communication (Rendall et al., 2009). Nevertheless, some authors had questioned this approach in the past and proposed adaptationist alternatives to the information-based approach. Smith and Harper (2003) and Scott-Phillips (2008) stated that communication occurs only if the signal induces a change in the receiver's behaviour. They hypothesized that signals are not selected based on the information they carry, but rather on their actual effect on the receiver(s). Using the same example than previously, one would say that the colour patches

and head movements in goldcrests are a signal because they elicit an avoidance response by the receiver. In the vision of Carazo and Font (2010), the definition of animal communication should incorporate both points of view: the information and the effect. A widespread definition of signal is thus "*any behavioural, physiological, morphological characteristics that alter the behaviour of other organisms because they convey information of interest for the receiver*" (see Rendall et al., 2009 for a review). "True" communication may be seen as a trade where both emitter and receiver obtain benefits: "provoked effects" and "information of interest", respectively (Carazo & Font, 2010). A signalling system may be evolutionary stable if it provides respective benefits to both emitter and receiver (Smith & Harper, 2003). Other stimuli used by receiver but that did not evolve for that purpose are defined as "*cues*" (Candolin, 2003). Cues are unbeneficial for the emitter, or even detrimental in cases where the unintended receiver is a predator, a parasite, or a competitor (Searcy & Yasukawa, 2017). For example, the avian predators pied currawongs (*Strepera graculina*) eavesdrop begging calls of their preys, the white-browed scrub wrens (*Sericornis frontalis*), to locate them (Haff & Magrath, 2011).

Signals can be in one or several sensory modalities, such as visual (colour patches, stereotyped movements, displays), olfactory/chemical (body odours, pheromones), acoustic (mating calls, distress calls, songs, vibrations), electrical, and tactile. Signals can also be an extended phenotype; in other words, a part of the phenotype expressed beyond the body (e.g., nest decorations in bower birds, see Schaedelin & Taborsky, 2009 for a review). Communication based on signals of multiple sensory modalities (composite signals) is called multimodal. The main advantage of using simultaneously different sensory modalities is: (i) to be redundant to send the same information in a more reliable way and/or (ii) to multiply the carried information (Partan & Marler, 2005). Since a decade, multimodal communication generated a considerable research interest and a growing number of evidences suggests that it is widespread in animal kingdom. Nonetheless, "widespread" does not mean "ubiquitous" and species that predominantly rely on a single sensory modality are called *sensory specialists*. I will hereafter focus on a single sensory modality: the acoustic communication, and more precisely the vocal communication.

The path between the emission of the vocal signal by the emitter and the induced response of the receiver is not a long, calm river. Endler & Basolo (1998) reviewed nine steps of animal communication (Box 1) simplified in four main steps: (i) emitter must **produce** a signal, then receiver must (ii) **detect** and **perceive** the signal/cue, (iii) **extract and assess** its information, and (iv) **act** accordingly. In the following sections, I shall focus on the first step, the production of vocal signal by emitter, in respect with anatomical, physiological and environmental constraints.

Vocal communication principles

Acoustic communication, when audible, might be one of the most enjoyable and impressive communication channels. It appeared 100-200 million years ago and is now ubiquitous in a vast majority of species, solitary or social. Almost 70% of tetrapod species use acoustic communication, mostly amphibians, mammals, crocodilians, and birds (Chen & Wiens, 2020). Ever since antiquity, Aristotle addresses the question of acoustic communication in animals, and particularly vocal communication. In "*Historia Animālium*", he describes the animal voice "*phônê*", different from the language "*logos*" which is specifically human. However, the structure of vocal signals in animals can be as complex and hierarchical as our own language. Vocal signals (calls, songs) consist of repeated phrases. A phrase is a cluster of unique syllables or elements that can be counted, contrary to trills and warbles which are clusters of elements so fast and so numerous that they cannot be counted. Syllables or elements themselves consist of notes, defined as a continuous line on a sonogram (Figure 1) (Catchpole & Slater, 2008).

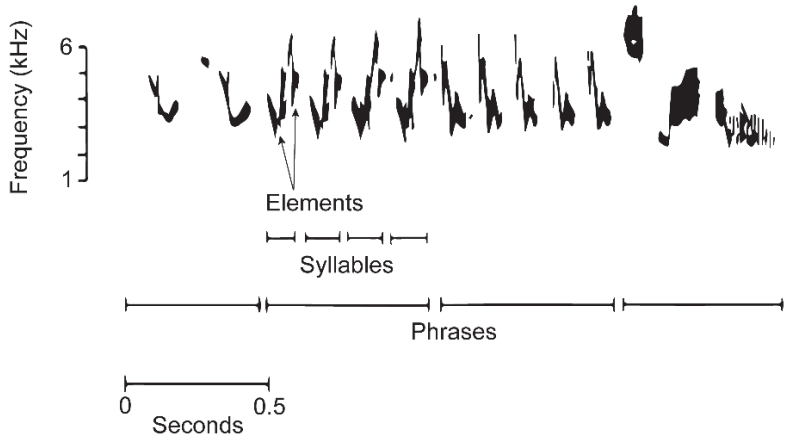


Figure 1. Sonogram of a song from a male chaffinch (*Fringilla coelebs*) showing the syntactic structure of vocalizations in phrases, syllables, and notes (modified from Catchpole & Slater 2008).

BOX 1. The nine communication steps of Endler & Basolo (1998)

Endler & Basolo (1998) described nine steps of animal communication, from the signal emission by the emitter to the elicited response of the receiver (Figure A), while leaving aside the mechanisms of decision, signal generation, and signal emission in signaller:

1. Signal *generation and emission* by the signaller
2. Signal *transmission* through the environment
3. Signal *reception*: i.e., detection and discrimination in the background noise by the receiver
4. Signal *transduction*: i.e., conversion of signal into an electrical impulse by receptor cells, which can be interpreted by the brain
5. Signal *coding*: i.e., processing into the receiver brain
6. Signal *perception*
7. Signal *recognition* and *classification*
8. Signal *interpretation* and *extraction* of its informative content
9. *Decision* and response of the receiver

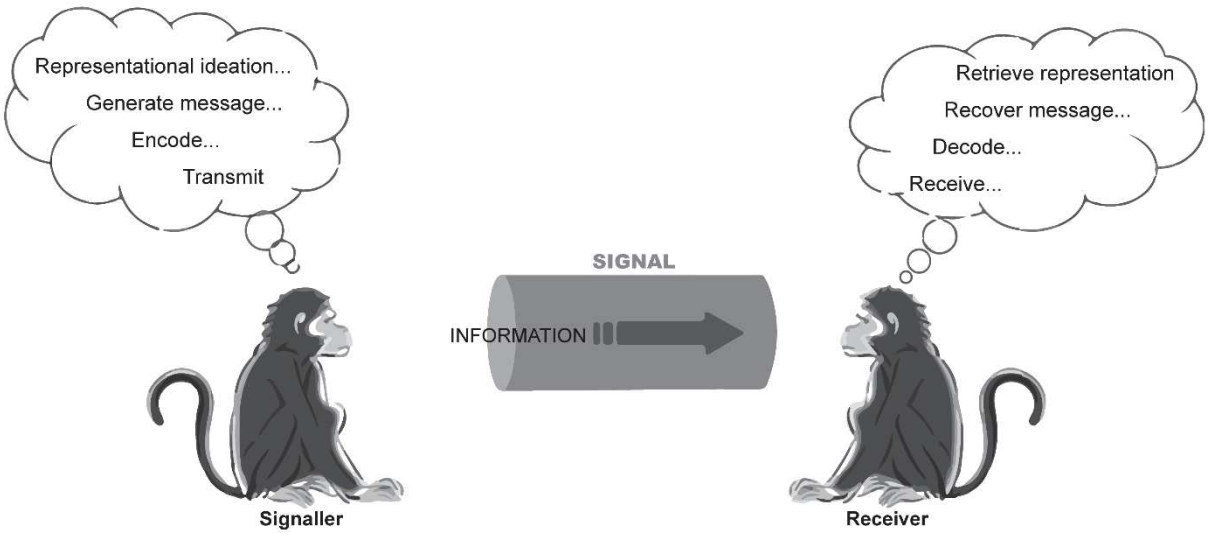


Figure A. Classic schematic of the animal communication principle (from Rendall et al., 2009).

From a physic perspective, acoustic signals are simply the mechanic propagation of sound waves in a medium, that is, gas, liquid or solid (although I will focus on aerial environments hereafter). We distinguish three acoustic signal types: mechanical sounds, calls, and songs (Catchpole & Slater, 2008). Mechanical sounds are produced by different body parts such as legs or wings, but not by a vocal organ contrary to vocalizations. For example, the friction of tymbals in cicadas produces the loud buzzy sound (Young & Bennet-Clark, 1995). Here, I leave aside the mechanical sounds and focus on vocalizations, namely calls and songs. The distinction between calls and songs is not always that clear, and might be a bit subjective (Box 2). Calls are usually short, simple vocalizations emitted in particular contexts. For instance, bird nestlings produce loud, conspicuous, begging calls to encourage their parents to feed them. Songs are long vocalizations produced during the breeding season, usually more complex than calls (Catchpole & Slater, 2008). The production of vocal signals in mammals and birds is quite similar, even though anatomical structures are different. As Zahavi (1982) nicely said, the body of the emitter is like a wind instrument: everything starts with a muscular contraction that pushed the airflow from the lunges (or air sacs in birds) to the vocal organ (larynx/syrinx). When passing through the vocal organ, the airflow induces vibrations in vibrating valves (vocal folds/membranes), generating a sound. The sound is subsequently modified in the vocal tract and the cavity (mouth/beak; Titze, 1994).

The “HOW” question leads to the “WHY”. From a behavioural ecologist perspective, vocal communication has several advantages: (i) vocal signals travel great distances despite obstacles contrary to tactile and visual signals; (ii) they are used in low visibility conditions such as fogginess and darkness contrary to visual signals; (iii) they may have low energy costs although this point is poorly documented and controversial; and (iv) vocal signals are transient contrary to some chemical signals (Catchpole & Slater, 2008). Vocal signals are ubiquitous and regulate many social behaviours directly affecting the survival or the reproduction of the caller and its offspring. For instance, it is broadly admitted that the two main functions of birdsong are to seduce potential mates and to dissuade rivals or intruders (*dual function hypothesis*, Catchpole & Slater, 2008). Further social behaviours also rely on exchange of vocal signals, including parent-offspring recognition, predator-avoidance strategies, group cohesion and coordination, and resource and territorial defence (Bradbury & Vehrencamp, 2011).

BOX 2. To call or to sing?

As I was asked at a congress once, "can we say that non-songbirds "sing"?" The matter deserves to be addressed and I briefly reviewed here some definitions of the terms "*song*" and "*call*".

"Song" originally describes complex vocalizations of oscine passerines, also called "true songbirds" (Catchpole & Slater, 2008) but it has evolved over the years. Spector (1994) reviewed different song concepts in birds, based on different criteria such as the structure, function, social context, and taxonomy. In the oldest definitions, songs are different from calls based on their length (at least three notes in songs), complexity and/or amplitude (Spector, 1994). Other definitions in the 70's and 80's use the concept of song learning as the discriminant criteria. The term "song" was thus restricted to learning species, namely the songbirds, parrots, and hummingbirds.

Nottebohm (1972) relied on two main criteria to describe songs and calls: function and production context. He defined songs as seasonal vocalizations, usually produced by males with a breeding or courting territory, which ensure the functions of attracting females and repelling rivals. Songs can be produced spontaneously or in response to social stimuli. As for calls, they refer to shorter and simpler vocalisations than songs, produced by both sexes all year long or seasonally. A few years later, Dobson and Lemon (1977) introduced the concept of syntax complexity in the definition of "song". Hence, songs are generally "series of complex syllables increasing in frequency with significant individual variation in syllable types and order".

More recently, Catchpole and Slater (2008) recognized that the distinction between songs and calls is "both traditional and arbitrary". Current definitions include the syntactic structure, function and production context, similarly to Nottebohm's (1972). More precisely, songs are "long, complex, vocalizations produced by males in the breeding season", produced spontaneously and with a diurnal rhythm. On the other hand, calls are "shorter, simpler and produced by both sexes throughout the year". Calls are less spontaneous than songs, as calls are usually associated with a particular context (e.g., begging call, alarm call, flight call, etc.).

Based on these most recent definitions, it appears that vocalizations of males during the breeding season in burrowing petrels, studied here, could be defined as songs. Nevertheless, to avoid lexical troubles and mostly to stay consistent with previous studies on similar species, I will keep using the term "call" throughout the manuscript.

INFORMATIVE CONTENT OF VOCAL SIGNALS

Communicating information is the key in animal social interactions. The "Mathematical Theory of Communication" states that vocal signals encode a wide but finite range of information (Shannon & Weaver, 1949). After signal reception, the receiver extracts and assesses the information (Box 1), eventually leading to a behavioural response.

Coding information

Vocal signals have a hierarchical structure. Songs, calls, phrases, motifs, even the simplest notes, can be characterized and described by a wide range of acoustic parameters. Any variations, between or within individuals, of one or few parameters associated with the emitter condition is an information (Bradbury & Vehrencamp, 2011). For example, we consider two male red deers (*Cervus elaphus*) from the same population: a large male produces low-pitched roars and a thin male produces high-pitched roar (Reby & McComb, 2003). The associated variations of frequency and mass give an information about the male body condition. The wording *hierarchical mapping* may sound a little far-fetched but it simply means that the degree of signal variations codes different information. Large variations of a given parameter may code for one information such as the species identity, while small variations may code for individual identity among members of a given species (Bradbury & Vehrencamp, 2011).

In theory, there are endless possibilities of combinations between parameter variations and emitter conditions. However, not all combinations are actually possible due to physiological, developmental, and morphological factors constraining the signal production. As a reminder, the vocal production is a two-step process. First, the airflow expelled from lunges passes through the vocal organ (syrinx/larynx), in a space called the glottis between membranes (e.g., vocal folds in mammals). When passing through the glottis, airflow causes membrane vibrations with a particular rate depending on the air pressure and the membrane stiffness. Second, the resulting glottal waveform then passes through the supra-laryngeal vocal tract (Titze, 1994). The *source-filter theory* states that the anatomy of the vibrating membranes and of the supra-laryngeal vocal tract shapes the signal. The membranes are the "source": the opening-closure rate determines the fundamental frequency and the harmonics of vocal signals. The vocal tract

is the "filter": its length and its resonant properties shape the formant frequencies of vocal signals (Fant, 1960). Therefore, the anatomy of the vocal organ and tract is a major morphological constraint on temporal parameters, energy spectrum, and amplitude of the signal, particularly described in mammals (Charlton et al., 2020). Another well-known example of vocal constraints is the Podos triangle in songbirds *Emberizidae* (buntings). Podos (1997) described a clear negative relationship between trill rate and frequency bandwidth (i.e., *vocal performance*). The faster songbirds sing, the tighter the frequency band, forming a graphic triangle in scatter plot. Physiological and/or developmental constraints make impossible for birds to sing fast and with wide frequency gaps between successive notes. Signals so constrained that they poorly vary are defined stereotyped.

One way of classifying the signal-condition association is to determine whether it is discrete (with independent conditions, e.g., sex which can be either male or female) or graded (with continuity between conditions, e.g., aggressiveness). In the latter case, the degree of variations of the signal is related to continuous conditions of the emitter (Bradbury & Vehrencamp, 2011). For instance, males in African painted reed frogs (*Hyperolius marmoratus*) react gradually to vocalizations of their rivals: the longer the calls, the more aggressive the emitter (Grafe, 1995). Information can also be classified based on its longevity. Static information is related to particular idiosyncratic characteristics and identity of the emitter whereas dynamic information is related to context-dependant internal states of the emitter.

Static information about emitter's attributes

Information is said to be static when it is consistent over the long term. In most cases, static information is about discrete conditions of the emitter. For instance, very common conditions are species and sex of the emitter: most species have a distinct vocal repertoire, preventing hybridization, and a sexual vocal dimorphism. Vocal signals give additional information about the identity of the emitter, including its group membership or geographical origin through geographical variations and particular dialects (e.g., bearded seals *Erignatus barbatus*: Charrier et al., 2013; sperm whales *Physeter microcephalus*: Rendell & Whitehead, 2003; St. Lucia parrots *Amazona versicolor*: Kleeman & Gilardi, 2005; yellowhammers *Emberiza citronella*: Petrusková et al., 2014). It allows group cohesion and

recognition of familiar or related individuals. Within groups, vocalizations also carry information about kinship and dominance status (see Laidre & Johnstone, 2013 for a review).

At a smaller scale, vocal signals may provide the individual identity of the emitter (Falls, 1982; Lambrechts & Dhondt, 1995). When an individual identifies another according to the distinctive characteristics of its vocalizations (i.e., *vocal signature*), the term *recognition* is used (Falls, 1982; Dale et al., 2001). Vocal signature and its role in mate recognition and parent-offspring interactions have been highlighted in many colonial species, such as pinnipeds (Charrier et al., 2003, 2009; Pitcher et al., 2012) and seabirds (Charrier et al., 2001; Curé et al., 2011; Jouventin et al., 1999; Mathevon et al., 2003), especially species with no nest site to meet at (Aubin & Jouventin, 2002; Robisson et al., 1993). Nonetheless, vocal signature does not obligatory imply individual recognition (Townsend et al., 2010).

Lastly, emitter's attributes such as its physic characteristics, sometimes related to qualities, may be encoded in vocalizations. For instance, in swamp sparrows (*Melospiza georgiana*), size and age of males are related to vocal performance and reproductive success. Large males and older males, which have a better reproductive success, produce faster trills with a wider frequency band than young males (Ballentine, 2009). One of the most-known examples is the relationship between the emitter body size and the fundamental frequency F0: the larger the emitter, the larger the vocal tract and thus the lower the frequencies (see source-filter theory in the previous sub-section; Fant, 1960). The relationship is explicit in several mammal species. A convincing example is the African elephants (*Loxodonta africana*) calling at about 17 Hz while house mice (*Mus musculus*) call about 5700 times higher (see Charlton et al., 2020 for the most recent review and further examples). Nonetheless the fundamental frequency-body size relationship remains unclear in other taxa including birds (Favaro et al., 2017; Galeotti et al., 1997; Kriesell et al., 2018; Mager et al., 2007; but see Patel et al., 2010).

Dynamic information

Context-dependant information relates to a temporary internal state of the emitter in a particular environmental context. As early as in the year 1872, Darwin hypothesized that vocalizations are vocal indicators of the motivational state of the emitter. Ever since, many studies assessed that vocalizations

also convey transient information about the internal states of the emitter according to the environmental context. Particular ecological (e.g., food availability: Proppe & Sturdy, 2009) or social (e.g., presence of a potential mate or a rival) stimuli affect the physiological state of the emitter. Because physiological factors constrain vocal production, physiological changes affect the design of vocal signals (Briefer, 2012, 2018, 2020). Acoustic variations are thus vocal indicators of the emotional state of the caller.

According to the conceptual framework of Mendl et al. (2010), a simple bi-dimensional space represents emotional states, with the emotion valence (positive/negative) as the first dimension and the emotion intensity (degree of "arousal") as the second. A high negative arousal may represent fear, stress, whereas a high positive arousal may represent excitation. High arousals may lead to different motivations, i.e. the probability that the emitter would perform a certain rewarding behaviour (Zahavi, 1982). As an example, aggressive motivation is the probability that the emitter would fight and thus gets reduction of a threat or territory maintenance as a reward; sexual motivation is the probability that the emitter would mate and thus get access to mates and mating as a reward.

Acoustic variations in agonistic context have been well documented in birds after the naturalist Gilbert White (1789) reported in the late 1780's that rivalry for space between males is the most important function of birdsongs (Catchpole & Slater, 2008). Ever since, numerous experiments established a relationship between aggressiveness and acoustic variations including amplitude variations (Beebee, 2004; Szipl et al., 2017; Zollinger & Brumm, 2015), increase of temporal parameters and number of syntactic elements (Funghi et al., 2014; Mager et al., 2012; Martín-Vivaldi et al., 2004; Szipl et al., 2017; Szymkowiak & Kuczyński, 2017), and spectral variations (DuBois et al., 2009; Szipl et al., 2017). In mammals and birds, the *Motivational-Structural Rules* state that vocalizations emitted in a hostile social context are characterized by long durations, low frequencies, wide frequency bandwidth, and little frequency modulations (Briefer, 2012, 2020; Morton, 1977). In sexual context, emitters tend to exaggerate their sexual motivation by varying acoustic parameters linked to their qualities (Podos, 1997). For instance, they vocalize close to the performance limit (trade-off between trill rate and frequency bandwidth). In zebra finches (*Taeniopygia guttata*), courtship songs addressed to females are faster, longer and composed of more syllables than solitary songs (Sossinka & Böhner, 1980).

VOCAL COMMUNICATION IN NOISY ENVIRONMENTS

Many studies in the past focused on the informative content of calls; but when an animal produces a vocal signal, its intention is first to be reliably detected by potential receivers. Nonetheless, abiotic and biotic environmental factors impair vocal communication, especially in noisy environments (Brumm & Slabbekoorn, 2005). As Endler & Basolo (1998) wisely reminded us, the signal design and the environmental constraints that apply to it are important to consider when studying a signalling system.

Problem of signal detectability

Although vocal signals propagate on great distances and are widely used in long-range communication, receivers cannot hear them from anywhere and at any time. The maximum distance from the source at which the signal is differentiated from the background noise is called *detectability threshold*. In the literature, the terms "*propagation distance*" (Morton, 1975), "*effective range*" (Heuwinkel, 1990), and mostly "*active space*" (Larsen, 2020; Marten et al., 1977) are also used. The *signal-to-noise ratio* (S/N) is the difference between a signal amplitude and the background amplitude. The higher the S/N ratio, the better the signal detectability. On the opposite, if the S/N ratio is small, the background masks the signal and impairs its detection. Signal detectability does not systematically imply signal discrimination, nor recognition (Larsen, 2020). At farthest distances, receivers may detect a vocal signal without extracting any information from it. At shorter distances, emitter may detect the vocal signal and discriminate whether it comes from a heterospecific or a conspecific and in the latter case, to discriminate the signal type. Thus, the closest the receiver from the sound source, the more information it may be able to extract from the signal (Larsen, 2020).

Natural processes impair the signal detection and discrimination, either by diminishing the intensity of the signal (*attenuation*) or by modifying spectral, temporal and structural patterns of the signal (*degradation*) (Marler & Slabbekoorn, 2004). Naguib & Wiley (2001) reviewed six processes of attenuation and degradation: spherical spread, medium absorption, scattering, reverberation, amplitude fluctuations, and diffraction.

- Spherical spread, spreading loss, or spherical attenuation: in theory, the signal intensity drops by six decibels each doubling distance in open habitats, resulting in an overall attenuation of the signal (Wiley & Richards, 1982).
- Attenuation by medium absorption: the medium (for instance the atmosphere) absorbs the signal energy and thus decreases signal intensity. Absorption is frequency-dependant and particularly affects high frequencies. Consequently, low frequencies propagate further than high frequencies. Absorption is also temperature-dependant: the higher the temperature, the higher the absorption (Wiley & Richards, 1982).
- Attenuation by scattering (also called "excess attenuation"): heterogeneities and obstacles in propagation path of vocal signals reflect the signal in all directions. Vegetation, animals, atmospheric gradients (humidity, temperature) and bad weather (rain, wind) are the main causes of scattering.
- Reverberation: obstacles in the propagation path of vocal signals may reflect an attenuated and degraded signal in several direction. A well-known example of reverberation is the echo, i.e., a reverberated signal whose temporal characteristics and amplitude have been modified (tailing effect) when the signal struck the obstacle.
- Amplitude fluctuations due to turbulences in the atmosphere, such as wind turbulences.
- Diffraction of sound by temperature gradients and velocity of air in the environment.

Scattering and absorption are both frequency-dependant processes and mostly affect high frequencies above 2 kHz. Nonetheless, other processes such as the *ground effect* affect low frequencies. The ground effect is a sound attenuation mainly caused by reflection of the sound on the ground. It particularly affects the frequencies between 0.5 and 2 kHz in sound propagating closer to the ground than 1 m. This effect occurs in all habitats, from forests to open habitats (Marten et al., 1977; Morton, 1975) but the attenuation intensity depends on the ground surface (e.g. hard, porous, soft) and vegetation (Hannah, 2006). For instance, grass particularly attenuates frequencies around 500 Hz (Wiley & Richards, 1982).

Signal masking and vocal interferences

Animals do not live in a silent word. Besides attenuation and degradation, a third environmental source of signal distortion is the addition of *noise* (i.e. interfering abiotic and biotic sounds that may blur or mask the signal: Brumm & Zollinger, 2013). Noise, usually quite low, adds new low frequencies to the signal and amplifies energy to existing components. Different sources, abiotic (e.g., wind, rain, running water) or biotic (e.g., conspecifics, heterospecifics, and anthropogenic noise), generate an ambient noise and interferences, masking the signal. Air movements and wind turbulences are the main abiotic sources of noise: even a slight breeze in open grasslands generate as much noise as a whisper (about 30 dB: Brumm & Zollinger, 2013). Insects, especially hemipterans and orthopterans, are particularly good at generating interferences. Some birds for instance avoid singing at the same time than insect choruses, but we shall come back to that later. Conspecifics' vocalizations are the most masking interferences as individuals all vocalize within the same frequency band (Aubin & Jouventin, 1998). Vocal communication in dense aggregations is thus especially difficult and constrained.

Improving signal detectability and discrimination

By increasing the detectability of vocal signals, the chance of being detected and reliably discriminated – and consequently chosen – by potential mates increases too. Selective pressures may thus favour signals propagating efficiently on great distances (Marten et al., 1977). Wiley and Richards (1982) suggested three vocal strategies to improve the signal detectability: attention-alerting signals, reduction of signal diversity (stereotypy) and signal repetition (redundancy). The emission of an attention-alerting signal before the informative signal aims to draw receivers' attention. The first attention-alerting signal must thus be easily detectable and do not need to carry precise information. For example, the "Puget sound" of white-crowned sparrow (*Zonotrichia leucophrys pugetensis*) starts with an alerting pure whistle. This whistle of greater amplitude has a better transmission and suffers less from degradation than the other song parts, which carry information about the caller's motivation, geographic origin and identity (Nelson, 2017). The reduction in the diversity of alternative signals consists in limiting the vocal repertoire to only a few calls and songs and allows a more reliable detection by

conspecifics (Price, 2013). The signal-repetition strategy consists in the emission of the exact same signal and/or particular patterns of the signal in a redundant manner.

Besides the three strategies described by Wiley and Richards (1982), Aubin and Mathevon (1995) hypothesized that increasing the signal duration and vocalizing within a wide frequency band – in the limitations of the emitter physiological constraints – improves the signal propagation and its detectability. On the contrary, Bradbury and Verhencamp (2011) suggested that the overall structure of signal in a restricted bandwidth would be less degraded because frequencies are differentially degraded. Another strategy to avoid frequency-dependant interferences is to vocalize within a frequency range not used by other signallers (both conspecifics and heterospecifics), nor within frequency range of background noise (Goodwin & Podos, 2013; Slabbekoorn & Peet, 2003). Nonetheless, the diverse strategies listed above affect the temporal, spectral and structural patterns of the signal, and may thus conflict with the information encoding.

Further strategies optimize signal detectability without any loss of information, such as sending composite signals providing the same information with different sensory channels (Partan & Marler, 2005) or increasing the amplitude according to the background amplitude. Besides the improvement of signal detectability, composite signals with redundant information clarify the message and limit habituation of the receiver (Partan & Marler, 2005). The adjustment of signal amplitude with the background amplitude, called the Lombard Effect, has been observed in birds and mammals, in non-urban (Pytte et al., 2003) and urban areas (Brumm & Zollinger, 2013).

At the right place, at the right time

The design of a signal affects its propagation and thus its detectability in the environment. Besides different vocal strategies and adjustments, the choice of appropriate signalling sites and/or moments may be crucial to optimize signal detectability without modify the signal structure. Signalling sites close to boundaries (canopy, ground, etc.) would constrain vocal communication because boundaries reflect signals and thus attenuate it (Wiley & Richards, 1982). Holland et al. (1998) noticed that wrens *Troglodytes troglodytes* singing from high perches have better chances to be detected than their

conspecifics perching on low perches where the vegetation is dense. Another strategy consists in choosing signalling sites with particular structures that amplify all or part of an emitted signal. In anurans, frogs of the genus *Eusophus* vocalize from burrows that amplify their own vocalizations by 5 dB, but also the incoming vocalizations of conspecific males (Muñoz & Penna, 2016; Penna & Solís, 1996, 1999). Male frogs of the genus *Heleiporous* call from burrows which resonate at the same frequencies than their calls (Bailey & Dale Roberts, 1981). In mammals, male Spix's disc-winged bats *Thyroptera tricolor* use tubular leaves that amplify perceived calls (Chaverri & Gillam, 2013). In birds, burrows of male Manx' shearwaters (*Puffinus puffinus*) act as a natural amplifier for females at the entrance of the burrow (Storey, 1984).

Besides particular signalling sites, certain times of the day are favourable to acoustic communication. To counter the effect of signal degradation and masking interferences, the temporal avoidance strategy consists in vocalizing outside periods of high-intensity noise and when the environmental conditions are the most favourable to sound propagation. For example, one of the explanations for the impressive dawn choruses in birds is that sound transmission is better at this time of the day. Indeed, the particular atmospheric conditions at dawn, such as lower temperatures and fewer air turbulences than during the day, are more favourable to sound propagation (Henwood & Fabrick, 1979; but see Gil & Llusia, 2020 for a critic and 11 alternative hypotheses). Birds also avoid vocalizing during bad weather, as shown in avian dawn choruses (Bruni et al., 2014) and in tawny owls (*Strix aluco*) which do not vocalize during rainy periods (Lengagne & Slater, 2002).

SELECTIVE PRESSURES ON VOCAL SIGNALS

Vocal communication in animals is quite complex and holds a fundamental place in animal social life. Therefore, selective pressures should applied on the signalling system as a whole and should shape the mechanisms at each stage of the communication, i.e. emission, detection and perception, extraction and assessment, and receiver's response (simplified from Endler & Basolo, 1998; see Box 1 for further details). There is a growing interest for signal evolution, which generated considerable models and theories, sometimes divergent.

Acoustic window

We have previously seen the effect of physical properties of the habitat and background noise on signal transmission. Further biotic and abiotic factors, including the phylogenetic history, the morphology, and the neurology of both emitter and receiver, also constrain the production and perception of vocal signals. Consequently, vocal signals have evolved in a delimited parameter space called the *acoustic window*. This space is defined by the intersection of three factors: the acoustic space actually available in the community, the optimal transmission space based on habitat properties and the physiological limits of emitters and receivers (Figure 2). Any changes on these factors affect the acoustic window and thus the possible directions for signal evolution. Signal evolution within the acoustic window may occur through several processes. I will detailed hereafter the *sensory drive* and *sexual selection*, although other pressures apply, such as random genetic drift and recurrent mutations.

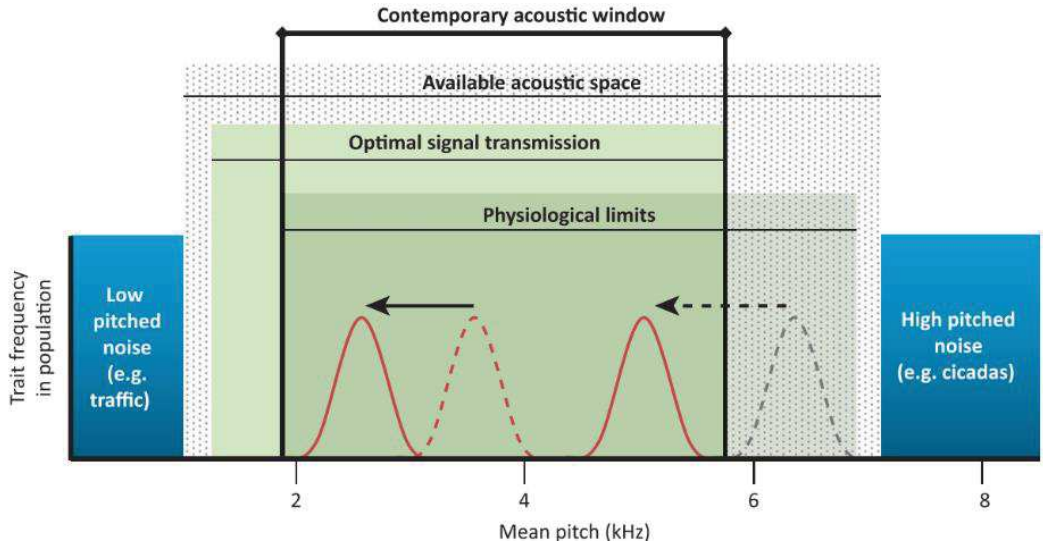


Figure 2. Example of an acoustic window delimited by the intersection of three factors: the available acoustic space (blue-dotted square), the optimal signal transmission (green square) and the physiological limits (shaded square). Arrows indicate a signal evolution between ancestral populations (dotted curves) to contemporary populations (solid-line curves). More precisely, dotted arrow represents signal evolution into a new acoustic window from a different habitat through sensory drive. Solid-line arrow represents signal evolution within the contemporary acoustic window through other processes, e.g., sexual selection, drift (from Wilkins et al., 2013).

Sensory drive model

Factors of the environment in which signals transit affect signal propagation, transmission and perception. Theoretical framework to study signal evolution through environmental pressures includes several concepts such as the acoustic adaptation hypothesis (Morton, 1975), environmental selection hypothesis (Hansen, 1979) and sensory drive model (Endler, 1992).

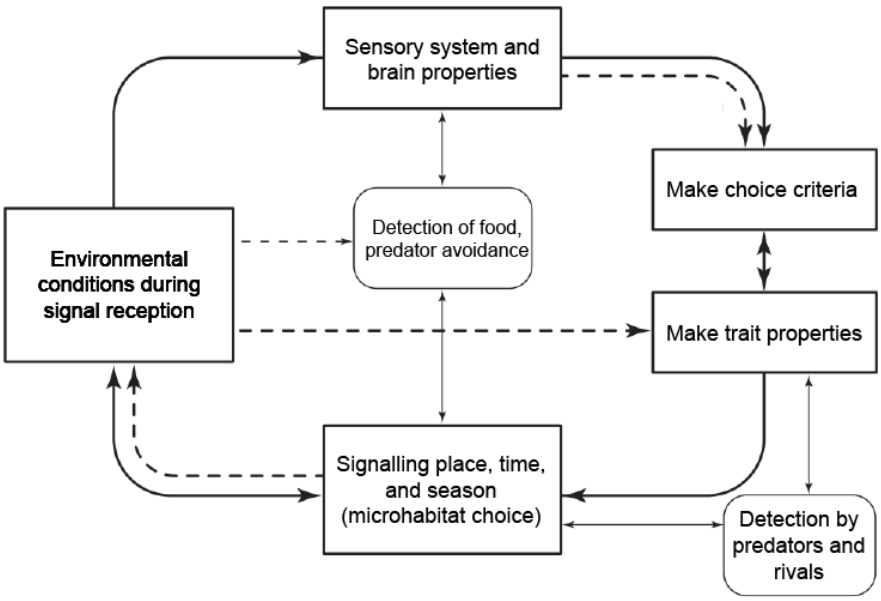


Figure 3. Main evolutionary interactions (large unbroken arrows), immediate effect (large broken arrows), evolutionary effect of predation (small unbroken arrows) and immediate effects of predation (small broken arrows) emphasizing signal evolution according to the sensory drive model (from Endler & Basolo, 1998).

Morton (1975) hypothesized that a given signal do not propagate similarly in all habitats. Because habitat characteristics affect signal propagation, they represent a selective force on acoustic parameters of vocal signals. Similarly, the acoustic adaptation hypothesis of Hansen (1979) stated that structural differences of habitats affect the signal transmission and will lead to the optimisation of signal design for transmission. Endler (1992) went further and developed a model called “sensory drive” (Figure 3). He considered that signal design, reception system of the receiver, and signalling behaviour (time and place to signal) are functionally jointed and define how signal will eventually be perceived. Consequently, any changes in one of these three mechanisms will lead to evolutionary changes in the other two. Endler called these three mechanisms and their functional relationships the sensory system. He hypothesized that the characteristics of the sensory system coevolve under selective pressures of

environmental conditions called sensory drive. Sensory drive includes physical properties of the habitat, background noise, and presence of predators, prey and parasitoids (Figure 3). This model thus emphasizes that the sensory drive selects signals that propagate efficiently and emitters providing efficient signals.

In the early 90's, there was a growing interest in developing models of signal evolution completely different from Endler's model. The emergent models relied on receiver biases. For example, Ryan (1990) developed a model of signal evolution called sensory exploitation. He emphasised that acoustic traits in male calls evolve to "exploit" latent preferences of females for signals ("pre-existing bias"). Consequently, traits stimulating females provide an advantage to the emitter and may evolve as a new signal, even if the stimulation was not sexual at first (Ryan, 1990). For example, in Lebinthine crickets, females are attracted by males producing high-frequency sounds, which is an anti-predator behaviour (Ter Hofstede et al., 2015). Receiver-bias models rely on biases in mate attraction rather than on environmental constraints. On this specific point, these models are close to the concept of sexual selection.

Sexual selection theory

The sexual selection theory states that certain individuals have a reproductive advantage over others, resulting in a differential reproductive success among individuals (Darwin, 1871). Sexual selection operates through two mains mechanisms: intra- and intersexual competitions. Intrasexual competition is a competition between same-gender individuals to get access to breeding resources (e.g., nest sites) and/or potential mates. The inter-sexual competition is a choice of mate made by the choosy sex, usually females but not always (*parental investment theory*: Trivers, 1972). These two mechanisms imply an assessment of rivals and potential mates, based on information about the emitter provided by signals, including vocal signals. Hence, vocal signals influence competition outcome and mating decisions. Individuals with the most preferred signals are selected by the choosy sex, and consequently gain a fitness advantage (Andersson & Simmons, 2006). Choosy individuals looking for mates would rather mate with high-quality individuals, resulting in a high-quality progeny, and thus a fitness increase (good gene model). For instance, in red deer *C. elaphus*, females are preferentially attracted by high

roaring rate and low-pitched roars, emitted by large males, because large males have a better reproductive success than others (Charlton et al., 2007; McComb, 1991; Reby et al., 2010). Similarly, in anurans, females are preferentially attracted by low-pitched calls produced by large males, which have a better reproductive success than small males (Forester & Czarnowsky, 1985; Giacoma et al., 1997; Schwartz, 1986).

In its assessment of signal evolution, Burley (1985) distinguished the processes affecting signal design and those based on signal informative content. He emphasized that selective pressures affecting design and information act concurrently. Endler (1998) shared this point of view and stated that sexual selection theory differs from sensory drive model because the former emphasizes the informative content of the signal while the later emphasizes the signal detectability. The difference may be a bit more subtle than that as selective pressures are intimately mixed and their isolated effects are poorly understood. As Endler and Basolo (1998) said, we should stand back to take a broader picture and to incorporate ecological factors in our future investigations. Nonetheless, vocal signal functions and evolution have been well studied in the framework of sexual selection.

SEABIRDS AS MODELS OF SEXUAL VOCAL INTERACTIONS

Past studies on the implications and determinisms of vocal communication in sexual selection originally focused on passerines called “true songbirds”. However, non-songbirds, such as seabirds, offer a remarkable example of a signalling system at the heart of sexual selection mechanisms, in a colonial environment with strong biotic and abiotic constraints. Underestimated for a long time, non-songbirds may share more vocal affinities with songbirds than previously thought.

Songbird predominance

Song learning is the main criteria to discriminate songbirds and non-songbirds: birds of the orders Passeriformes (perching birds) and Psittaciformes (parrots), and of the family Trochilidae (hummingbirds) learn how to sing, whereas birds of other orders do not (non-songbirds). Among Passeriformes, the so-called “true songbirds” consist in two large sub-orders called Oscines (or Passeri) and Sub-Oscines (or Tyranni) (Hackett et al., 2008). In scientific literature, they hold a central place in

the study of animal communication. For instance, in a recent study on acoustic communication origins, a quarter of the sampled bird families and one-fifth of the sampled bird species are songbirds (Chen & Wiens, 2020). Songbirds represent almost half of all bird species (Kroodsma, 2004), but broadness and ubiquity is not the only reason of their predominance in bioacoustics. An undeniable advantage of songbirds is their extraordinary vocal diversity, plasticity, and abilities. Vocal repertoires in songbirds can reach dozens of vocalizations, even though some are very small. The "top four of the biggest song repertoires" includes song sparrows *Melospiza melodia* with more than 10 songs; marsh wrens *Cistothorus palustris* with 100 to 200 songs; sedge wrens *Cistothorus platensis* with 300 to 400 songs; and brown thrashers *Toxostoma rufum* with more than 1000 songs (Kroodsma, 2004). Songbirds memorize and learn the vocal repertoire by imitating conspecifics when nestling, but they have the particularity to learn new songs for all ("open-ended learners") or part ("close-ended learners") of their life. Consequently, within and between individuals of a given songbird species, songs progressively change. This learning process may give a selective advantage to songbirds that can vocally adapt to new environments faster than non-learning birds (Kroodsma, 2004). Suthers (2001) compared the mechanisms of sound production in songbirds and non-songbirds. He reviewed two major differences between these two taxa. The syrinx of non-songbirds is less muscled than the one of songbirds. Having a more complex and developed syringeal musculature allow songbirds to have a better control of sound production than non-songbirds. Moreover, songbirds are able to precisely coordinate and rapidly alternate respiration and phonation, giving them a better motor control than non-songbirds.

The so-called "non-songbirds" are characterized by an absence of song learning (although this is not true in hummingbirds and parrots), a vocal organ with fewer muscles than oscines, and vocalizations usually less complex than oscines (Catchpole & Slater, 2008; Suthers, 2001). Vocalizations of non-songbirds may not have the panache and the complexity of songbird vocalizations but some sound production processes are present in both songbirds and non-songbirds (Catchpole & Slater, 2008; Suthers, 2001). For instance, songbirds control independently the two side parts of the syrinx and thus produce two distinct sounds simultaneously (Greenwalt, 1968). This "two-voice" phenomenon is present in non-songbirds as well (Suthers, 2001). Another example is the mini-breath respiratory pattern,

which is present in very few non-oscines too (Suthers, 2001). Moreover, vocal signals in non-songbirds are implied in many social behaviours, as shown in songbirds (Catchpole & Slater, 2008). Some social behaviours are actually well studied in non-songbirds, such as the two-voice phenomenon, the sexual and vocal signatures, and their implications in familiar-individual recognition, studied in penguins since the 90's (Aubin & Jouventin, 2002; Favaro et al., 2015; Jouventin et al., 1999; Kriesell et al., 2018; Lengagne et al., 1997, 1999; Robisson et al., 1993). There is thus a growing research interest for non-songbirds, although songbirds are still predominant.

Implication of vocal signals in seabirds' mate choice

Over the past 30 years, seabirds (or marine birds) have generated considerable research interest, including in bioacoustics. They are one of the most endangered taxa of birds, with more than 31% species threatened (Dias et al., 2019), and their particular life history traits make them remarkable. Seabirds are, par excellence, colonial: 93% of seabird species are colonial (Bried & Jouventin, 2001). Coloniality provides many benefits, including decrease of predation risk based on dilution effect, but also costs such as spread of parasites and diseases. Costs associated with coloniality are among them: dozens, hundreds or thousands of aggregated individuals vocalizing simultaneously generate strong masking interferences and signal scattering by conspecifics' bodies. Moreover, seabirds usually settle on seashores or near the sea, mostly in open habitats. One may guess that the openness and the absence of filtering vegetation are favourable conditions for vocal communication. However, oceanic climate combines wind turbulences, rains, temperature gradients and humidity, inducing signal attenuation, degradation and interferences. These climatic factors, combined with biotic factors, constrain vocal signals. In spite of strong environmental constraints, sex advertising relies on vocal displays in most species, although visual (e.g., courtship dance in albatrosses), tactile (e.g., billing in shearwaters), and olfactory displays can also play a role (Nelson & Baird, 2001).

In seabirds, mate choice has a crucial and significant impact on the individual fitness. It can take several years for pairs to bond and seabirds are predominantly socially and genetically monogamous (Lack, 1968), meaning that one male restricts his mating to one female and vice versa. Both sexes usually share parental duties during incubation and fledging (Bried & Jouventin, 2001; Schreiber & Burger,

2001). It is noteworthy, however, that a few species may be polygynous and polyandrous under some circumstances (e.g., brown skua *Stercorarius antarcticus*: Phillips, 2002; common tern *Sterna hirundo*: Ludwigs, 2004; red-footed booby *Sula sula*: Cao et al., 2010). Not all seabirds are monogamous for life but they are known for their long-term partnership because partner changing is a loss of breeding opportunities. Breeding success is thus higher when seabirds retain the same mate year after year (Brooke, 1978; Guillotin & Jouventin, 1980). Therefore, divorces and extra-pair copulations are rare depending on species (see Quillfeldt et al., 2012 for a review). In seabirds, clutches are small-sized (e.g., only one egg in petrels, one to two in penguins, three to four in cormorants, see Bried & Jouventin, 2001 for a review), but the parental investment during incubation and chick rearing by both sexes is very high, and cooperative breeding has never been observed (Bried & Jouventin, 2001). According to the energy-limitation hypothesis, these particular life-history traits have evolved as a result of dispatched resources and energetic constraints (Lack, 1968).

Most seabirds have two well-distinct breeding and feeding areas: they breed on land while they forage resources at sea. Consequently, pairs synchronously alternate foraging trips and fasting periods while incubating the egg. The shifts last from a day to three weeks depending on the species, and the distance travelled by these long-ranged feeders may be particularly impressive, from hundreds of meters in small species to thousands of kilometres in large species. For instance, wandering albatrosses *Diomedea exulans* forage in an average range of 1300 km at the beginning of the incubation (Weimerskirch et al., 1993). This particular breeding system is a major evolutionary constraint in seabirds. It implies a perfect synchrony between partners, highlighting once again the importance of mate choice and efficient communication between partners.

Vocal signals involved in mate choice code for a wide range of information for potential mates, about the caller species, sex (Bretagnolle, 1996; Curé et al., 2011; Warham, 1996), body size and condition (Genevois & Bretagnolle, 1994), and individual identity (Aubin et al., 2007; Aubin & Jouventin, 2002; Charrier et al., 2001; Favaro et al., 2017; Robisson et al., 1993). Vocal strategies and adaptations of the production and reception mechanisms increase the detectability of vocal signals, and thus ensure that potential mates get the message across the colony hubbub. For instance, call redundancy

increases the chances of the emitter to be detected and/or to vocalize during a silence window. Vocal individuality and call stereotypy increase the chance of being discriminated because familiar sounds are easier to discriminate in background noise (*cocktail party effect*: Aubin & Jouventin, 1998; Cherry, 1957). Producing vocalizations with a wide spectrum limits signal degradation because all frequencies are not similarly degraded and/or attenuated (Aubin & Mathevon, 1995; Bretagnolle, 1996; Wiley & Richards, 1982). Besides coding strategies, highly sensitive perception mechanisms have evolved in seabirds. For example, seabirds can detect and discriminate a signal in a conspecific crowd due mainly to the redundancy of the signal. In king penguins *Aptenodytes patagonicus,* only a small syllable fraction is needed to elicit recognition and this small fraction is repeated in the different syllables of the vocal signal (Aubin & Jouventin, 2002).

THE SPECIAL CASE OF BURROWING PETRELS

Among seabirds, petrels offer a good opportunity to assess the implication of vocal signals in mate choice due to their breeding ecology and associated constraints, including coloniality, social and genetic monogamy, extreme weather and burrow-nesting.

Breeding ecology of petrels

"Petrels" is the common term used to refer to seabirds of the Procellariiformes order, recognizable by their tubular nostrils atop the bill. They consist in three families representing a third of seabirds: Procellariidae, Hydrobatidae, Pelecanoididae. I here voluntarily considered "petrels" in the narrow sense and thus excluded the albatrosses (family Diomedeidae).

Petrels mostly live in high latitudes of the south hemisphere. Although they are mainly solitary and diurnal at sea, they are colonial and mostly nocturnal on land during the breeding season. Depending on species, breeding colonies form near to the sea, on cliffs or open habitats, such as beaches, coastal slopes, and tussock flats. They are usually dense, especially in small species (e.g., density about 1.4 nest/m² in Antarctic prion *Pachyptila desolata*, and inter-nest distance about 5-10 meters in giant petrel *Macronectes giganteus*; Warham, 1996). Colonies consist in a mix of adults at different breeding stages: pre-breeders (adults that have not reached the sexual maturity, yet), non-breeders or bachelors (sexually

mature adults looking for a mate), and breeders (Warham, 1996). Most petrels are philopatric, meaning that they settle in the colony they were born after reaching the sexual maturity (two to twelve years according to species: Warham, 1996). On their breeding ground, few species are surface nesters (e.g., giant petrel) or crevice nesters (e.g., Wilson's storm petrel *Oceanites oceanicus*) but petrels are mostly burrow nesters (Warham, 1996). Petrels usually establish breeding stations consisting in close or mixed colonies of several petrel species (Warham, 1996).

Petrels are socially and genetically monogamous, and divorces and extra-pair copulations are infrequent (Quillfeldt et al., 2012). After pairing, pairs lay a single egg per year, with no possibilities of replacement clutch. Although clutch size is very small, it requires a high parental investment during the incubation. Only one partner fasts in the nest and incubates the egg, while the second partner forages at sea. Partners shift regularly and the shift duration depends on the species size: the bigger the individuals, the longer the shift (Warham, 1996). In long-lived monogamous species with high parental investment and bi-parental responsibilities, mate choice is expected to be extremely important and adults particularly choosy. Mate choice, in fact, takes several years (Warham, 1990, 1996).

Burrow-nesting

The main advantage of studying this particular order lays in their burrowing-habit: 65% of petrels are burrow-nesters (Warham, 1990). Moreover, burrow-nesting is the ancestral condition in petrels, while surface-nesting, for instance in fulmars *Fulmarus* spp. and giant petrels *Macronectes* spp., is a subsequent independent radiation (Van Buskirk & Nevitt, 2008). Burrows vary in shape and material, depending on the size and habitat of the species. In medium-sized petrels, approximately close to the size of a pigeon, burrow measures 0.3 to one meter long (Brothers, 1984). Males dig burrows themselves using their beak and legs, or squat existing unoccupied burrows. After pairing, pairs are faithful to their burrow and occupy the same, year after year. Burrow provides several advantages to the owner. First, it protects against predators including gulls, feral cats, and skuas, although brown skua sometimes excavate burrows (Mougeot & Bretagnolle, 2000). It also protects from bad weather, especially from frequent winds and rains in areas exposed to oceanic climate where petrels breed (Warham, 1990). In addition, burrow preserves its occupants from temperature fluctuations. Chamber, where egg is laid, acts

as an incubator. It keeps the heat when an adult is present, and the inside temperature varies little with outside temperature (Pefaur, 1974; Warham, 1990). Although burrow is a real shelter providing safeness to its occupants, it may also constraint social interactions in the colony, including vocal interactions between bachelors.

Communication and environmental constraints in burrowing petrels

Walking in the colony, we can hear females calling in flight, and males calling from underground burrows. Hence, vocal signals were considered historically the main channel for males and females to communicate, while olfactory signals were assumed unlikely. In early 2000's, studies in burrowing petrels focused on the use of olfactory signals in social interactions within breeding colonies. Results showed that olfactory abilities of these birds were greatly underestimated. Olfactory signals, such as body odour in blue petrels and Antarctic prions, provide information about the sex, genetic compatibility through MHC (Major Histocompatibility Complex), identity, and kinship (Bonadonna et al., 2009; Bonadonna & Sanz-Aguilar, 2012; Mardon et al., 2010; Strandh et al., 2012). Moreover, burrowing petrels discriminate their nest odour, their own odour, their partner's odour and unfamiliar conspecifics' odours, and they are preferentially attracted by the odour of non-kin (Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Mardon & Bonadonna, 2009). Further sensory channels, beyond vocal and chemical signals, do not seem to be used in long-range signalling. The burrow represents a visual barrier preventing the use of visual signals, and the absence of sexual dimorphism and the low visual capacities of petrels in the dark (Warham, 1990) are consistent with this hypothesis. The distance between males in burrows and females in flight prevents the use of tactile signals.

Burrowing petrels can mainly use thus two sensory modalities to communicate within the colony: olfactory and acoustic. There is no evidence so far that predator birds use olfactory signals to locate their prey petrels (Mougeot & Bretagnolle, 2000). Contrarily vocal communication is associated with high predation costs. In medium-sized burrowing petrels, calling in the colony increases the risks of being predated. For example, the brown skua *S. antarcticus* is a terrestrial predator that hunts on the ground using its preys' calls to locate them and sometimes to excavate them (Mougeot & Bretagnolle, 2000). I shall not deal with the matter of energetic costs of vocal communication, still debated (Catchpole &

Slater, 2008), but there are other constraints to consider for vocal communication, such as climatic conditions, vegetation, vocal interferences from conspecific and from other petrels. In burrowing petrels, the burrow, from where males vocalize, is an additional constraint to ongoing and outgoing vocalisations. The burrow dimensions and the grassy vegetation at the entrance may degrade and change significantly the signal structure even before its propagation in the air. In spite of the mentioned costs and constraints, burrowing petrels intensely vocalize in the colony, meaning that vocalizations should provide significant advantages to the caller, but to date these advantages remain unknown. One may thus wonder what are the implications and determinisms of vocalizations in petrel social interactions.

Implication of male calls in burrowing petrels' mate choice

Callers are mainly bachelors: males looking for a mate vocalize from their burrow while female vocalize when flying over the colony, at night. Male calls are likely to attract females (Bretagnolle, 1996; Warham, 1996). After hearing a male call, females land, walk toward the burrow using male calls to locate the entrance, and penetrate the burrow (Bretagnolle, 1996; Storey, 1984). Once inside, both adults perform extensive duet (Bretagnolle, 1996; Warham, 1996). It suggests that vocal interactions between males and females are restricted to mate choice. After pairing, adults rarely vocalize, likely to minimize predation risks, except in few species (e.g., flesh-footed shearwaters *Puffinus carneipes*, short-tailed shearwaters *P. tenuirostris*; Warham, 1996). Both breeder and bachelor males inside their burrow vigorously vocally react to calls of conspecifics at the entrance, and breeder females sometimes tend to respond to other females only (Bretagnolle, 1996; Bretagnolle & Lequette, 1990; Curé et al., 2011). Vocalizations are thus likely to be implied in burrow defence. Hence, petrel calls may ensure the functions of attracting mates and deterring rivals, as in songbirds (dual-function hypothesis).

As for most non-songbirds, there is no vocal learning in burrowing petrels and their vocal repertoire is poor (Bretagnolle, 1996). It consists in one to two "major" calls, and one to five "minor" calls, respectively defined as calls emitted in sexual and agonistic interactions, and calls emitted in other situations (e.g., contact, distress, copulation; Bretagnolle, 1996). In species with two major calls, different calls may independently ensure sexual and agonistic functions whereas in species with a single major call, it may ensure the dual function. Major calls of burrowing petrels provide information for

potential mates and/or competitors such as species, sex, individual identity, geographic origin, motivation, and body condition. Species signature avoids misrecognition as several petrel species nest in close proximity in breeding stations (Warham, 1996; e.g., Yelkouan *Puffinus yelkouan* and Balearic *P. mauretanicus* shearwaters: Curé et al., 2010, 2012). Most petrels also have a vocal sexual dimorphism coded by spectral, temporal, or syntactic parameters depending on species (Bretagnolle, 1996). This sexual signature allows sexual recognition, implied in sexual and male territorial interactions (Curé et al., 2011; Taoka et al., 1989). Petrel calls also code the caller individual identity (Bretagnolle, 1996; Curé et al., 2011), as shown in many other seabirds (e.g., Spheniscidae: Aubin & Jouventin, 2002; Favaro et al., 2015, 2017; Jouventin et al., 1999; Robisson et al., 1993; Stercorariidae: Charrier et al., 2001 ; Laridae: Mathevon et al., 2003). In few petrel species, relationships between temporal parameters of male calls and body condition of the emitter have been highlighted (blue petrels: Genevois & Bretagnolle, 1994; Cory's shearwater: Bretagnolle, 1996). So far, whether and how females use this information in male calls has not been tested experimentally. Finally, besides static information, burrowing petrels' calls provide dynamic information. Frequency shifts related to aggressiveness have been reported in Wilson's storm petrel (Bretagnolle, 1989) and Cory's shearwater (Bretagnolle & Lequette, 1990), and their existence have been suggested but not demonstrated in most shearwaters and prions (Bretagnolle, 1996).

THESIS AIMS & HYPOTHESES

Main goals

In species with proved olfactory abilities, environmental constraints on sound propagation, and high predation pressures related to vocal production, the use of vocal signals might seem surprising at first. Nonetheless, in burrowing petrels, vocal signals seem to have an important role to play in sexual interactions among bachelors, including mate choice. The available literature on vocal communication in burrowing petrels is restricted to papers between the 80's to the 2000' reviewed in Warham (1996) and Bretagnolle (1996). They depict the background of vocal communication in burrowing petrels, mostly focusing on the presumed territorial and sexual functions, but we still ignore whether and how male calls affect female mate choice. Moreover, emission of vocal signals from burrows or hollow

structures is still poorly investigated in birds, likely because among the numerous species breeding in cavities, very few species vocalize inside it. Burrowing petrels thus represent a thrilling signalling system in constrained environments, in which there remains a need for investigations. The goal of the present thesis is to investigate the determinisms and implications of male calls in bachelor interactions, focusing on the two most predated species, the blue petrel (*Halobaena caerulea*) and the Antarctic prion (*Pachyptila desolata*) as biological models.

Thesis organization

In a first chapter, I explored the informative content of male vocalizations. Although it is a bit descriptive, this chapter provides the necessary background for the successive chapters. In burrowing petrels, males vocally advertise to stimulate and attract females in their burrow. I hypothesized that male calls give females the opportunity: (i) to evaluate reliably the caller as a prospective life partner; and (ii) to discriminate between each other bachelor males. Calls should thus carry information about intrinsic qualities and identity of the caller. Literature on this particular point focuses on the relationship between mass and call rhythm (Bretagnolle, 1996). In species with a particular breeding ecology that implies fasting periods – and consequently large variations of mass in the same individual over time (Chaurand & Weimerskirch, 1994) – I humbly doubted the relevance of choosing this particular variable. I thus tested the existence of a vocal individual signature, and the relationships between the caller morphology and the particular physical properties of its calls.

The second chapter concentrates upon the male vocal plasticity. After exploring the stable informative content of male calls, the logical continuation was to tackle the transient information carried by these calls. I thus assessed the acoustic modulations induced by the presence of conspecifics, either males or females. To go further, I also tested whether the vocal response of males hearing a female is the same regardless of the female flight path and/or proximity; or whether males vocally react more strongly to a close female. This chapter has an interest wider than the framework of petrels' mate choice because potential vocal plasticity related to motivation in non-songbirds has been understudied so far.

The third chapter focuses on the influence of vocal signals in female mate choice. Knowing that particular acoustic parameters of male calls carry information about the caller identity, morphology, and sexual motivation, I hypothesized that parameters highlighted in the previous chapters should affect female mate choice. I specifically tested by playback experiments whether females are preferentially attracted by calls whose acoustic parameters indicate a sexually motivated and/or good-quality caller. In a second time, I tested whether females are preferentially attracted by males calling in proximity or by lone callers. I hypothesized that females should be more attracted by grouped callers, which are more detectable.

Finally, the fourth chapter deals with the burrow effect on call propagation and its implication in female mate choice. The originality of burrowing petrels is that males actually call from the burrow chamber. From a physic point of view, it seems intuitive that a sound signal emitted from a cavity will be affected by the cavity properties such as frequency filtration, resonant properties, etc. Few researchers have addressed this question in anurans, insects, and bats, but it remains poorly studied in birds. To go further, I also assessed whether, in addition to intrinsic morphological characteristics of the caller, characteristics of its burrow affect female mate choice.

GENERAL METHODS

(photo credits: Jean-Yves Barnagaud)

STUDIED SPECIES

Generalities

To study the vocal communication system in burrowing petrels, I focused on two species: the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata* formerly called dove prion (Animalia, Chordata, Aves, Procellariforms, Procellariidae: Gmelin 1789). Both species are medium-sized burrowing petrels, although Antarctic prions are slightly smaller than blue petrels (Table 1). They both have a blue-grey plumage on the back, white on the belly. They are recognizable by the coloured band at the extremity of the tail feathers, white in blue petrels, black in Antarctic prions; and by the coloured M-mark across upperparts, visible when birds are in flight. Legs and bill are bluish. There is no visible sexual dimorphism (Figure 4, Table 1).

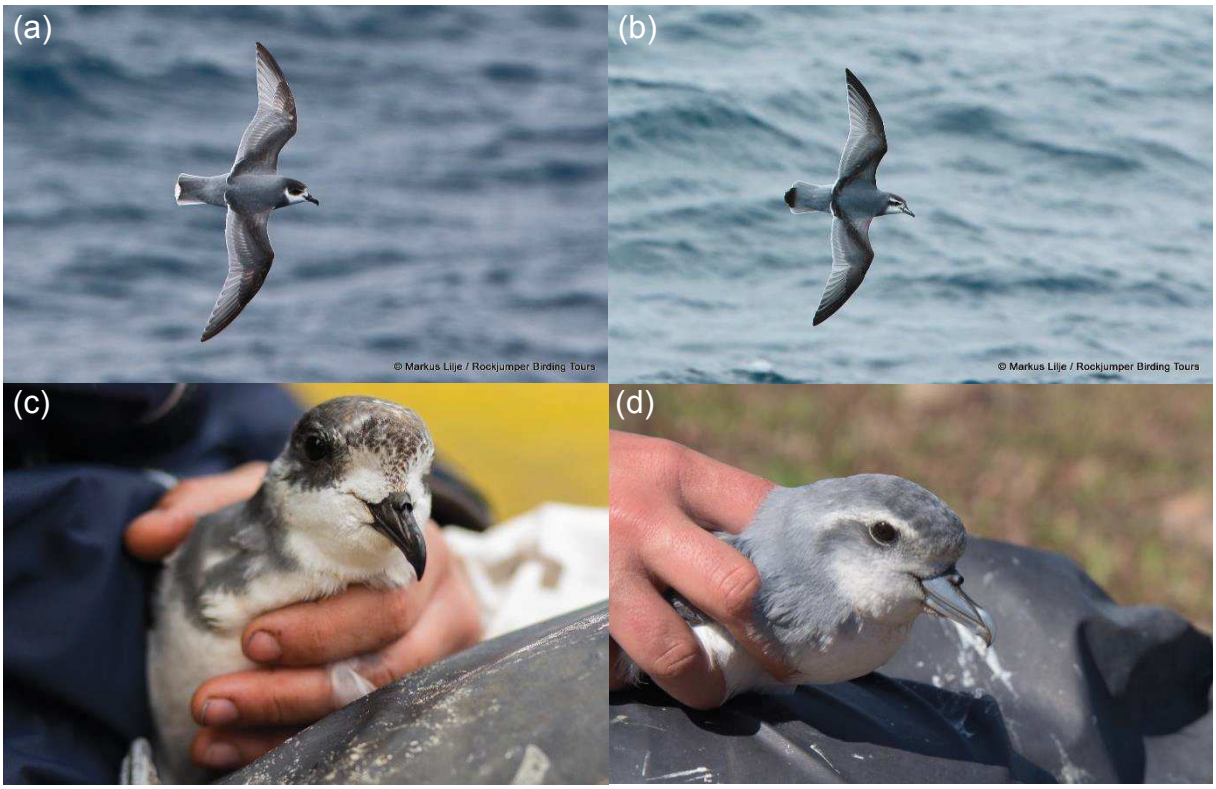


Figure 4. Pictures of (a) a blue petrel in flight; (b) an Antarctic prion in flight (photo credits: Markus Lilje); (c) a blue petrel (photo credits: Guilhem Battistella); and (d) an Antarctic prion (photo credits: Jean-Yves Barnagaud).

Table 1. Morphometric measurements of blue petrels (N = 718 adults, including 159 males and 160 females) and Antarctic prions (N = 537 adults, including 123 males and 118 females) in the population of Île Verte, Kerguelen.

		Tarsus (mm)	Wing (mm)	Weight (g)
Blue petrels	males	33.7 ± 3.9	215.8 ± 24.5	194.7 ± 29.0
	females	33.4 ± 2.9	216.7 ± 17.9	183.8 ± 31.4
	population mean	*33.5 ± 2.8*	*216.1 ± 17.3*	*184.4 ± 25.8*
Antarctic prions	males	32.7 ± 6.3	190.8 ± 19.8	154.3 ± 22.0
	females	33.1 ± 4.6	190.7 ± 19.8	158.5 ± 22.5
	population mean	*32.0 ± 6.7*	*189.9 ± 11.1*	*154.6 ± 19.9*

These two species breed on remote locations very close to the Antarctic Convergence. Blue petrels breed only in six locations: Macquarie Island; Kerguelen archipelago; Crozet archipelago; Marion and Prince Edward Islands; South Georgia; Diego Ramirez, Cape Horn, and nearby islands. Antarctic prions also breed on Aucklands, Scott, Heard, South Sandwich, South Orkney, and South Shetland (Figure 5). On their breeding sites, they occupy self-dug underground burrows in coastal grass slopes, but Antarctic prions tend to occupy stony areas while blue petrels do not (Warham, 1990). They feed at sea from pelagic resources from Antarctic and sub-Antarctic waters (mainly copepods, amphipods, euphausiids; but also fish, insects, and cephalopods) by surface-seizing, surface-filtering, hydroplaning and dipping (Warham, 1990). They reach the sexual maturity around six years. Both species are long-lived with lifespan up to 22 years contrary to others burrowing petrels that live shorter (Warham, 1996).

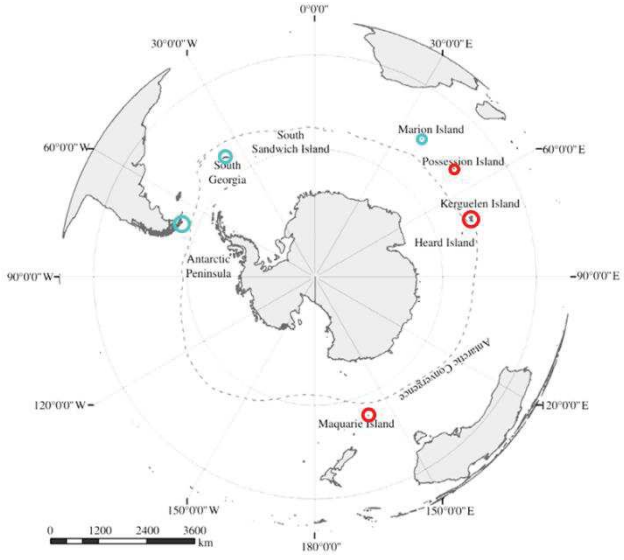


Figure 5. Distribution maps of breeding colonies of blue petrels and Antarctic prions according to Warham (1990). Blue circles indicate colonies of blue petrels, red circles indicate colonies where both species breed. Map of Antarctica and surrounding Southern Ocean Islands modified from Mortimer et al. (2011).

Why these two species?

I think that blue petrels and Antarctic prions are relevant models for two main reasons. First, these two species basically contributed to our understanding and knowledge about the use of olfactory signals in non-foraging behaviours in birds (see Bonadonna & Mardon, 2013 for a review). Second, blue petrels and Antarctic prions are the main preys of the brown skua in Kerguelen archipelago, representing respectively 88% and 5% of the skua diet (Moncorps et al., 1998). They thus suffer from the highest predation pressure among burrowing petrels. As skuas use male vocalizations to locate their preys (Mougeot & Bretagnolle, 2000), calling in the colony increases the predation risk. Despite high predation risks, bachelor males and females in blue petrels and Antarctic prions are highly vocal. It suggests that call production is associated with higher benefits outweighing the predations costs, but so far unknown. These two species are thus the perfect models to investigate the implication of vocal communication in burrow-nesters.

Conducting experiments on two species allow a comparison of the use, informative content, and design of vocal signals. Blue petrels and Antarctic prions are ideally comparable as they are quite similar at different levels. Both species have a similar external morphology (Figure 4). Plumage coloration, pattern, and structure is similar between the two species. Internally, they have similar osteology and myology (Warham, 1990). Genetic studies based on different analyses, such as allelic frequency (Barrowclough et al., 1981) and microsatellite markers (Moodley et al., 2015), showed the genetic proximity between the two species. Unsurprisingly, the monotypic genus *Halobaena* is usually placed close to the *Pachyptila* genus in phylogenetic trees (Figure 6). Blue petrels and Antarctic prions also share behavioural similarities, listed in the previous sub-section (Bretagnolle, 1990; Warham, 1990).

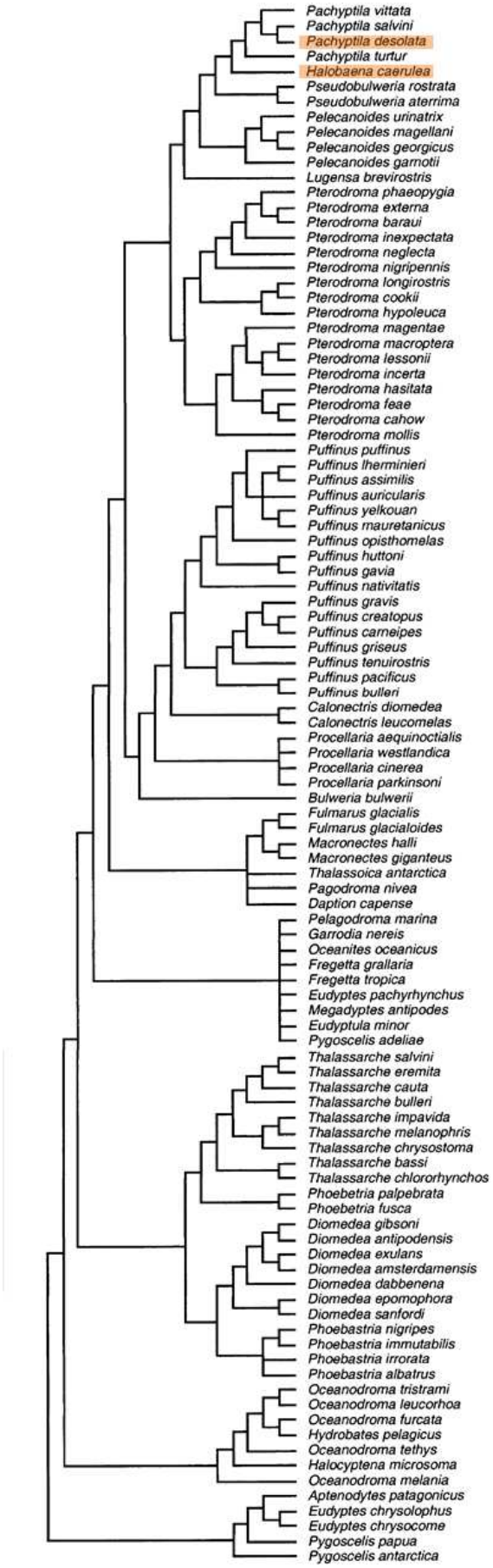


Figure 6. Phylogenetic super trees of seabirds, modified from Kennedy & Page (2002).

Why only males?

Both sexes in blue petrels and Antarctic prions intensely vocalize during the breeding period. Nonetheless, I focused my research on male calls only for biological and practical reasons. Historically in the Darwin's vision of mate choice, males are the advertising sex while females are the choosy sex. Although we now know that this is not true in an unneglectable number of species, we have to admit that in many species, males conspicuously advertise while females do not. A wide variety of references thus focus on males only and offer more points of comparison. Focusing on males was also easier because it allowed to easily catch and ring them in their burrow, and thus to record identified individuals. It would have been much more difficult with bachelor females flying over the colony. I might have worked on breeding females, easily catchable in the safeness of the burrow. However, according to previous studies, very few breeding females react to playback stimulations (Bretagnolle, 1996; Bretagnolle & Lequette, 1990; Brooke, 1978). One of my supervisors would say that I am stubborn and proud, but after many infructuous attempts to obtain female calls, I had to recognize my defeat. Moreover, in blue petrels and Antarctic prions, males do not go outside their burrow to meet with females, but on the contrary, females join males into their burrow. It suggests that, even though the mate choice is likely to be mutual in these species (Trivers, 1972), the first step of mate choice seems to consist of a female choice when still flying, based on male vocalizations.

Description of vocalizations

Acoustically, blue petrels and Antarctic prions are comparable and thus relevant models. They have the smallest vocal repertoire among burrowing petrels, with only one major call type, emitted towards males and females during the breeding season (Bretagnolle, 1996). Both species are vocally sexually dimorphic on the syntactic structure of calls (Bretagnolle, 1996). In both species, the male major call is short and stereotyped, with a similar and simple syntax (Figure 7). Warham (1990) defined the major call of blue petrel males as a "low-pitched cooing". Major call of Antarctic prion males is a bit harsher and lower-pitched. The main frequency range is between 300 and 1000 Hz in both species. Major call consists of a repetition of phrases made of short, staccato syllables. In both species, four syllable types are easily discriminable based on their spectral and temporal characteristics. All syllable types appear

only once per phrase, except syllable C, which is repeated (Figure 7). The intra- and interspecific variability lies in the number of repetitions of syllable "C" (blue petrels: 4.7 ± 2.1, Antarctic prions: 1.8 ± 0.8, all uncertainties in mean ± SD except if stated otherwise).

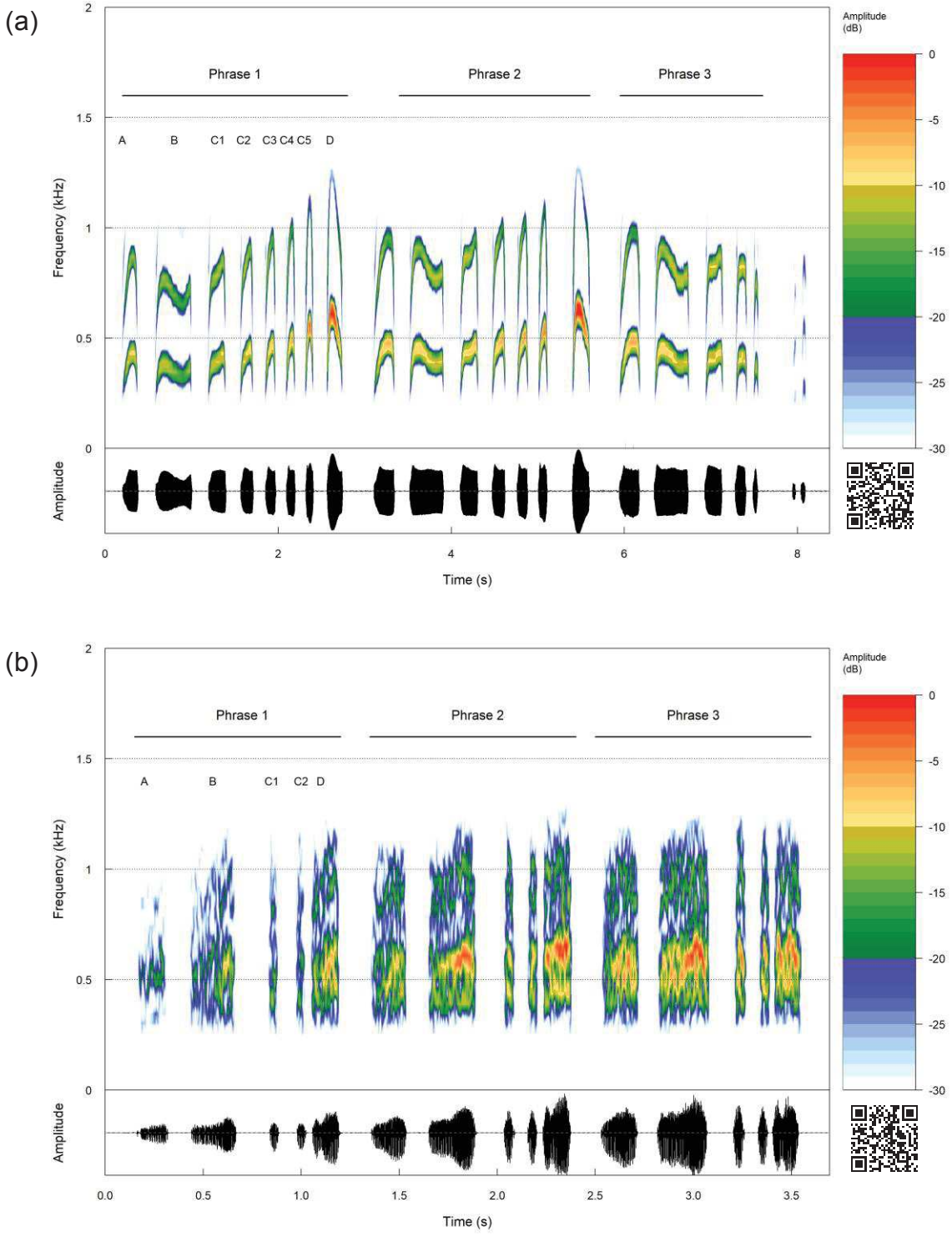


Figure 7. Sonogram (top) and oscillogram (bottom) of spontaneous calls from a male (a) blue petrel; and (b) Antarctic prion.

STUDY SITE

Fieldwork was performed on a sub-Antarctic island called “Île Verte” (literally “green island”; 49°51′S, 70°05′E), in the Golfe du Morbihan (“Morbihan Gulf”), in the East of Kerguelen archipelago, Southern Indian Ocean (Figure 8). Kerguelen is one of French Southern Territories (“Terres Australes et Antarctiques Françaises”: TAAF), known to have an oceanic climate particularly windswept and rainy. To give you an indication, the archipelago is exposed to wind gusts over 16 m/s 314.1 days per year. The monthly mean temperature during the burrowing petrels’ breeding season (November to January) is 5.5°C, 7.2°C and 8.2°C, respectively. The mean daily amount of precipitation per month is 49.4 mm, 55.8 mm and 51.1 mm, respectively (data collected in Port-aux-Français between 1950 and 2020, source: Météo France). These conditions are ideal to study vocal communication in constrained habitats, although makings recordings in such windy areas might seem a bit discouraging at first.

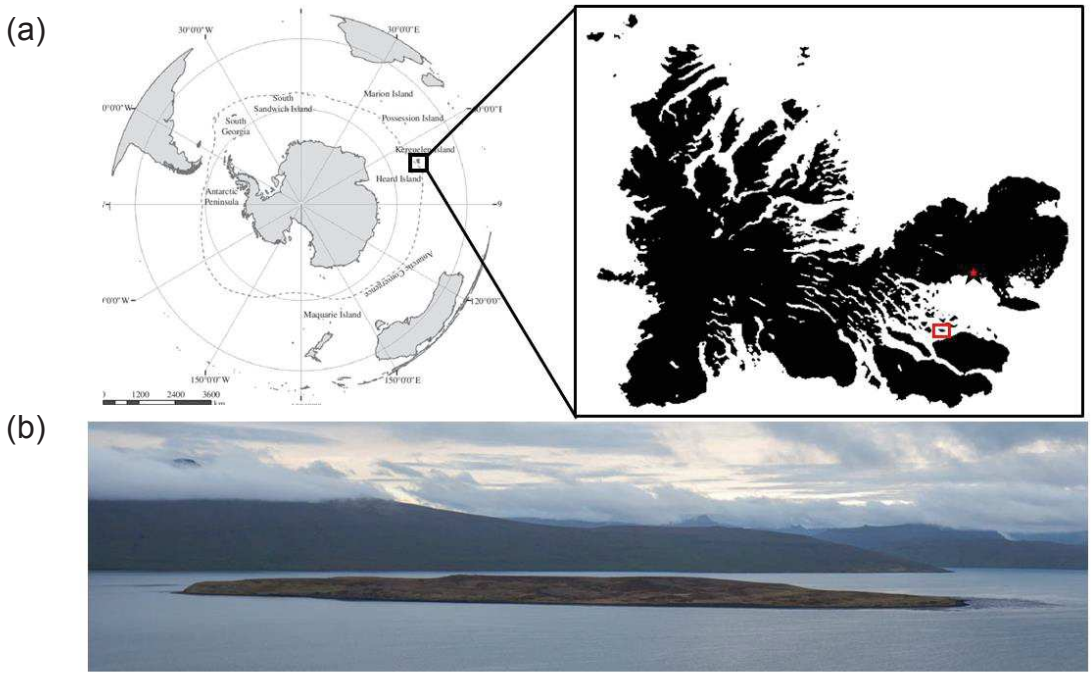


Figure 8. (a) Location and map of the Kerguelen archipelago. The red square indicates the Île Verte, the red star the base of Port-Aux-Français. (b) Picture of the Île Verte (photo credits: Guilhem Battistella).

The Golfe du Morbihan hosts many small islands, including Ile Verte, where both blue petrels and Antarctic prions are abundant and live in sympatry. Aside from its obvious and convenient flatness (maximum elevation: 48 m; Figure 8), Île Verte was a relevant study site due to its location in the gulf and the presence of both studied species. Researchers have monitored the colonies of both species

annually since early 2000's, as a part of the French Polar Institute (Institut Polaire Français Paul Emile Victor: IPEV) program no. 354 ETHOTAAF. A recent study showed that human disturbances in the colony have no effect on the breeding success in blue petrels (Bergès et al., 2019).

STUDY PERIOD

I studied blue petrels and Antarctic prions during their breeding period, more precisely during the incubation, when breeders are in their burrow, one at the time, and can thus be easily, individually caught and/or stimulated with playbacks. In the meantime, bachelor males and females are very active and call from their burrow and in flight, respectively. Incubation starts in late October in blue petrels and mid-December in Antarctic prions, and it lasts about 45 days (means: 49.0 and 44.8 days, respectively; Warham, 1990). After hatching, nestlings spend about 50 days in the burrow before fledgling (means: 53.0 and 50.2, respectively) but parents are absent, except when briefly feeding the chick at night.

Blue petrels and Antarctic prions are nocturnal on their breeding area. For both species, I described the daily vocal activity of four groups of bachelors using Song Meter SM2+ automatic recording units (Wildlife Acoustic, 2009). Activity diagrams show that both species are mainly vocally active between 10:00 pm to 02:00 am with a peak of activity at 11:00 pm (Figure 9). Consequently, all experiments described below were conducted during this time slot.

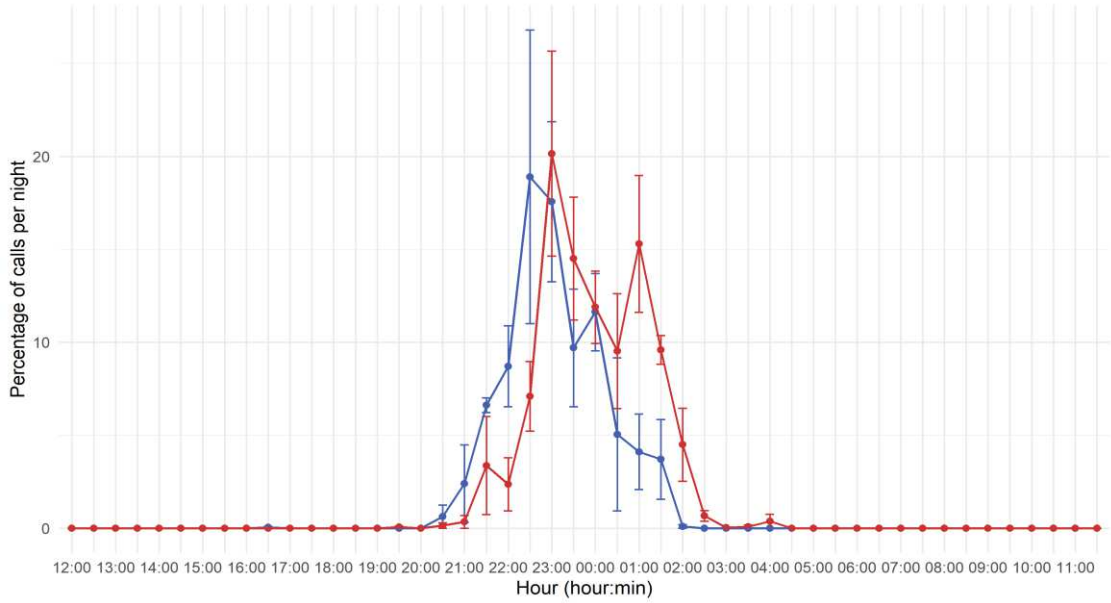


Figure 9. Temporal pattern of vocal activity in blue petrels (blue) and Antarctic prions (red). In both species, 24-hour recordings were made in small groups of three to four bachelor males, using continuous recorders SM2+.

ACOUSTIC EXPERIMENTS AND ANALYSES

Playback experiments

Most records made on the field (except recordings of spontaneous calls) have been obtained by playback stimulation. This experimental approach consists in broadcasting natural or synthetic signals (stimuli) to subjects in order to elicit a behavioural response (including the vocal response). Observing the subject's response helps understand the function of the broadcast signals (McGregor, 1992). I carried out two kinds of playback experiments in the field, either to directly elicit a vocal response from the focal individual (playback stimulations), or to simulate a bachelor males vocalizing from its burrow to assess the attractiveness of different acoustic parameters and burrow characteristics. Playback stimulations with similar protocols have been used in previous studies to describe call structure, to estimate populations, and to highlight vocal identity in several petrel species, including blue petrels (Barbraud & Delord, 2006), prions (Bretagnolle et al., 1998), gadfly petrels (McKown, 2008), shearwaters (Bretagnolle & Lequette, 1990; Brooke, 1978; Curé et al., 2009, 2011, 2012), and storm petrels (Bolton, 2007; Ratcliffe et al., 1998; Taoka et al., 1989; Taoka & Okumura, 1989). I used playbacks to simulate natural interactions in the birds' natural habitat between: (i) bachelor male and bachelor female; (ii) two bachelor males; and (iii) bachelor male and breeding male.

Sound representations and measurements

From recordings made in the field, I sought for answers to my specific questions on the temporal, spectral, syntactic structure of petrel calls. To do so, I relied on sound representations using the signal-processing software Avisoft–SASLab Pro v5.2.11 (Specht, 2017). A sound wave, such as bird vocalizations, can be quantified in two physical domains (spectral and temporal) and visually represented by:

- the oscillogram, representing the time domain of a sound, and plots the amplitude versus time. (Figure 10a). The envelope representation is derived from this representation and corresponds to a smooth curve outlining the extremes of the oscillating amplitude (Figure 10b).

- the spectrogram (or spectrum), representing the frequency domain of a sound, plotted as amplitude versus frequency (Figure 10c)

- the sonogram, which is a mix between the two previous visualisations. It plots the waveform in its three main dimensions: frequency versus time and the amplitude levels are indicated by a colour scale (usually from warm colours for intense sounds to cold colours for weak sounds). It is maybe the most widespread representation (Figure 10d). This visualisation clearly shows the frequency modulations and the shape of notes composing the signal. I used the following settings (otherwise stated in chapters): FFT length: 512; Blackman window; 50% overlap.

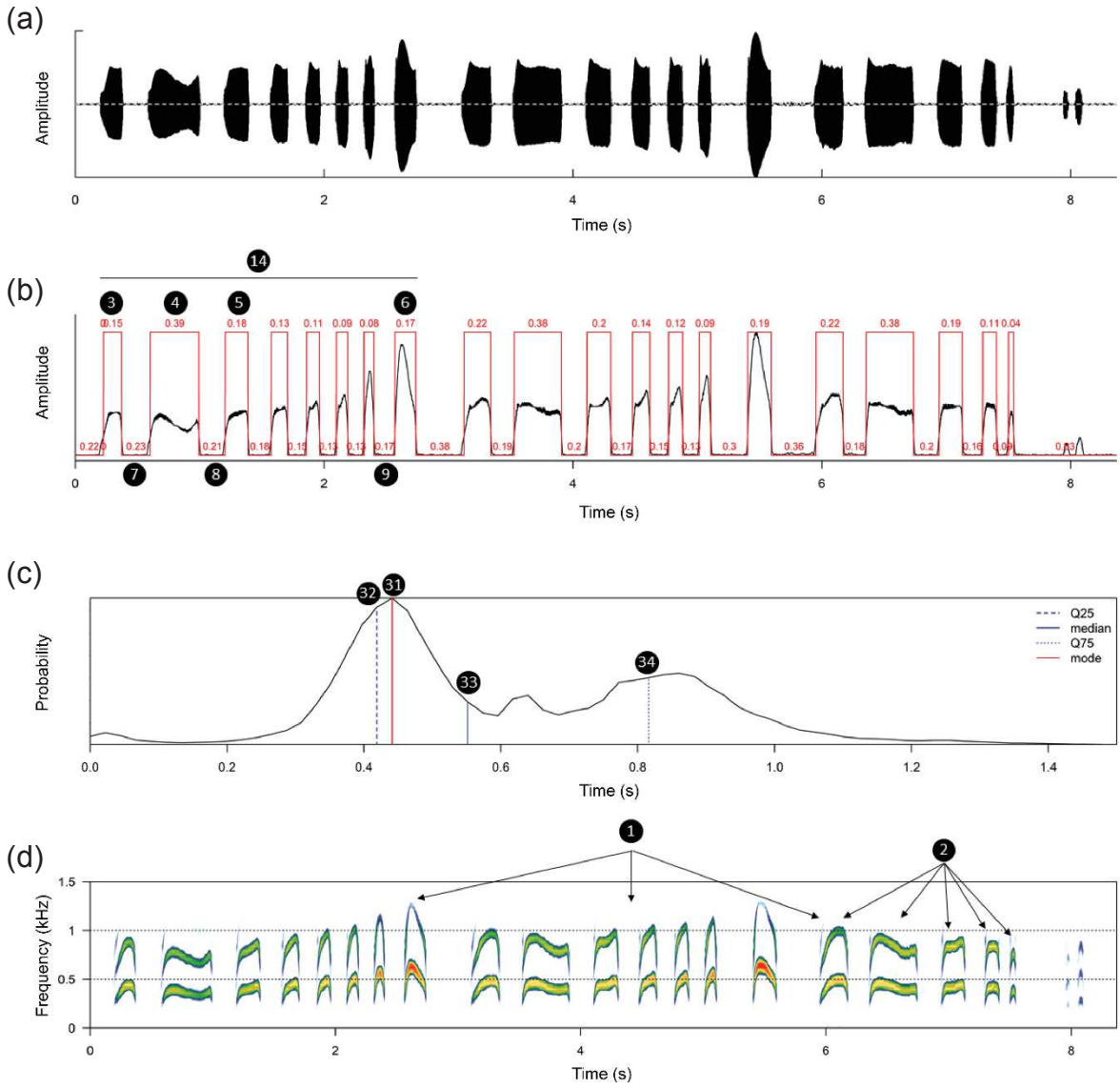


Figure 10. Acoustic measurements and sound representations of a blue petrel call: (a) oscillogram, (b) envelop, (c) amplitude spectrum, (d) sonogram. Circled numbers refer to the acoustic parameters given in Table 2.

Acoustic data extraction

To answer my questions, I measured chosen acoustic parameters on sound representations. I started with a pre-treatment in two steps. In noisy environments, like in a seabird colony exposed to wind, the ambient noise can be significant. I thus removed this noise by high-pass filtering at 110 Hz. This cut-frequency value is below the lowest frequencies of male calls in both species. Then, to increase the accuracy of frequency measurement, I sub-sampled recordings from 44.1 to 11.025 kHz. After this pre-treating phase, acoustic parameters were measured on the three sound graphic representations. All acoustic parameters measured are presented in Table 2 and illustrated on Figure 10. To limit observer bias and ensure replicable measurements, I used the automatic functions of Avisoft whenever it was possible.

As seen previously, vocal signals have a hierarchical syntax. Calls or songs consist of phrases, themselves consisting of syllables or elements. Trying to be the most accurate possible, I described petrel calls at two syntactic levels, phrases and syllables, in both physical domains: time and frequency. Temporal and syntactic parameters were automatically extracted on the amplitude envelopes. I used the function "*Pulse Train Analysis*" with the method "*Peak Search with Hysteresis*", which uses a pulse recognition algorithm to detect waveforms. It then extracts selected measurements, including pulse count, as well as start time, duration, interval, for each one of them (Figure 10). Syntactic parameters were counted directly and visually on sonograms.

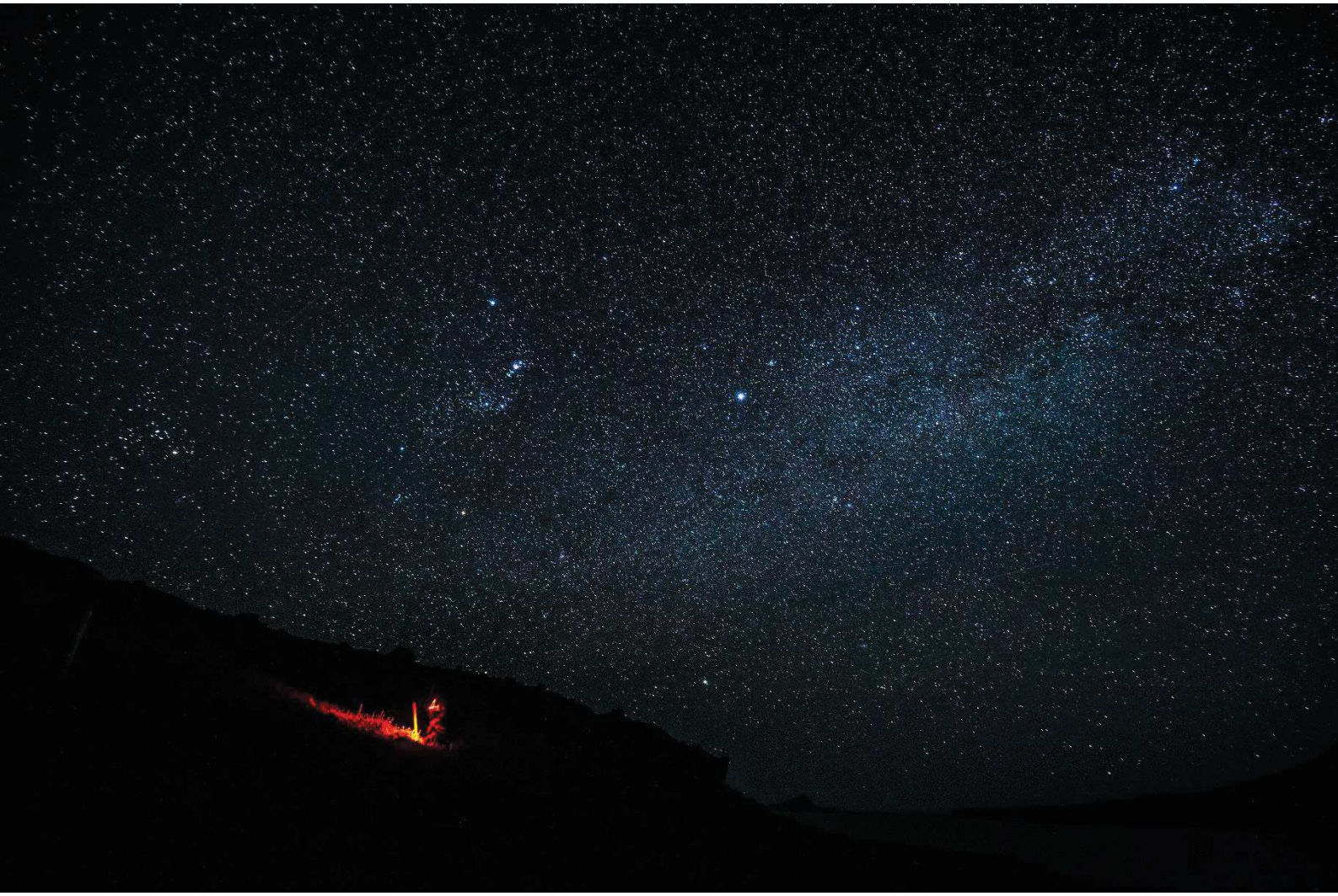
Spectral parameters (i.e., fundamental frequencies and energy spectral distribution) are as important as temporal parameters and syntax. They were extracted automatically on linear amplitude spectrum (Figure 10). Many previous works highlighted the major role of frequencies in individual signature, coding of information on body condition and body size (Charlton et al., 2020). Moreover, frequency shifts according to motivational states of the caller have been described in oscines and mammals, but not in non-oscines. It was thus a challenge to explore this new lead in bioacoustics.

Table 2. Acoustic parameters measured to describe calls of male blue petrels *H. caerulea* and Antarctic prions *P. desolata* in both physical domains (time and frequency) and at different syntactic levels.

No.	Description	Class	Syntactic level
1	Number of phrases in a call	Syntax	Call
2	Number of syllables in a phrase	Syntax	Phrase
3	A syllable duration	Temporal	Syllable
4	B syllable duration	Temporal	Syllable
5	Duration of the first syllable C	Temporal	Syllable
6	D syllable duration	Temporal	Syllable
7	Inter-syllable A-B duration	Temporal	Syllable
8	Inter-syllable B-C_1 duration	Temporal	Syllable
9	Inter-syllable C_{cie}-D duration	Temporal	Syllable
10	Syllable tempo (number of syllables per second for each phrase)	Temporal	Phrase
11	Phrase tempo (number of phrases per second for each call)	Temporal	Call
12	Phrase rhythm (ratio between syllable and silence durations)	Temporal	Phrase
13	Ratio between syllable and phrase durations	Temporal	Phrase
14	Phrase duration	Temporal	Phrase
15	Fundamental frequency of A syllable	Spectral	Syllable
16	Upper quartile (frequency at the upper limit of the 25% of A energy)	Spectral	Syllable
17	Medium quartile (frequency at the upper limit of the 50% of A energy)	Spectral	Syllable
18	Lower quartile (frequency at the upper limit of the 75% of A energy)	Spectral	Syllable
19	Fundamental frequency of B syllable	Spectral	Syllable
20	B upper quartile	Spectral	Syllable
21	B medium quartile	Spectral	Syllable
22	B lower quartile	Spectral	Syllable
23	Fundamental frequency of C_1 syllable	Spectral	Syllable
24	C_1 upper quartile	Spectral	Syllable
25	C_1 medium quartile	Spectral	Syllable
26	C_1 lower quartile	Spectral	Syllable
27	Fundamental frequency of D syllable	Spectral	Syllable
28	D upper quartile	Spectral	Syllable
29	D medium quartile	Spectral	Syllable
30	D lower quartile	Spectral	Syllable
31	Mean fundamental frequency of the phrase	Spectral	Phrase
32	Phrase upper quartile	Spectral	Phrase
33	Phrase medium quartile	Spectral	Phrase
34	Phrase lower quartile	Spectral	Phrase

CHAPTER I

STATIC INFORMATIVE CONTENT IN MALE CALLS



(photo credits : Guilhem Battistella)

As stated by its definition, a signal provides information from an emitter to a receiver. Hence, knowing which information is coded by male calls is the first step before assessing whether male calls are actually signals implied in female mate choice. In this chapter, I aimed to highlight the pieces of static information in male calls of both blue petrels and Antarctic prions. I tested whether particular acoustic parameters of calls are related to physical characteristics that may be quality indicators of the caller.

ARTICLE 1

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

Charlène Gémard[a,b*], Thierry Aubin[b], Francesco Bonadonna[a]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

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Abstract

Acoustic communication in burrowing petrels has been poorly studied. However, as for many other bird species, acoustic communication seems to play an essential role in social interactions during the breeding season of these seabirds. Bachelor males call from their burrow, likely to attract females, but also when vocally challenged by other males. Calling in the breeding colony exposes petrels to high predation risks and thus it should provide an important benefit. The present study focuses on the informative content of males' calls in the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata*, two monogamous petrel species producing a single egg per year. We tested the hypotheses that acoustic parameters of a male's calls 1) reflect phenotypic characteristics, and 2) bear an individual vocal signature. To do so, we first tested on both species the relationships between seven morphometric measurements and 11 acoustic parameters using multivariate analyses. Second, we performed a between-class analysis and calculated the potential of individuality coding (i.e. the ratio between intra- and inter-individual variabilities) for acoustic parameters in both spectral and temporal domains. Results show acoustic parameters (especially energy quartiles, call duration, and syllable or phrase rate) reflect the caller's body size, bill morphology and wing morphology in both species. Considering the seeming pertinence of wing morphology, we suggest wing area may be a more relevant trait to consider than wing length when studying soaring birds. The results support the idea that energy quartiles, phrase rate and call duration also code for individual identity. Information carried by males' calls might play a role in social interactions, such as burrow defence (e.g., male-male competition, neighbour-stranger discrimination) and/or female mate choice.

Keywords: vocal communications, sexual selection, identity, phenotypic features, seabirds, petrels

Introduction

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

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

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

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

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

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

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

As previously mentioned, calling in the colony increases the predation risks (Mougeot & Bretagnolle, 2000) and should thus provide important benefits to balance these costs. Following the suggestions of the wide literature on other bird species, we can hypothesize that calls play a role in mate choice and/or male competition for mate and burrow. However, informative content of most burrowing-petrel species' calls has been neglected so far. Nevertheless, previous studies have shown that heavy males call with a higher rhythm than light males in blue petrels (Genevois & Bretagnolle, 1994) and that large heavy males produce low-pitched calls in snow petrels (Barbraud et al., 2000), suggesting several ways of body size signalling. Here, we investigated the informative content of calls in two burrowing petrels: the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata* (Procellariidae, Gmelin, 1789). These two petrel species, with similar breeding and feeding ecology (Warham, 1990, 1996), are highly vocal and suffer from a high predation pressure by the brown skua (Francois Mougeot et al., 1998). We tested the hypotheses that acoustic parameters in both temporal and spectral domains of petrel calls: 1) reflect morphological characteristics, and 2) bear an individual vocal signature.

Material and methods

Studied species

Blue petrels (*H. caerulea*) and Antarctic prions (*P. desolata*) are monogamous medium-sized (about 190 and 160 g, respectively) seabirds belonging to the Procellariidae. They spend most of their life at sea but they breed in dense colonies on coastal grass slops. These long-lived seabirds do not reach sexual maturity for five years and a couple of years is needed for establishing stable pair-bonds. They show a high partner fidelity, low extra-pair paternities, and divorces are rare. After pairing, pairs produce

a single egg per year. From incubation (50 d in blue petrels, 45 in Antarctic prions) to fledging (50 and 53 d, respectively), they exhibit bi-parental cares. Partners regularly alternate fasting period in the burrow and feeding trips at sea (Brooke, 2004; Warham, 1990, 1996).

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

Study location

Fieldwork was performed in a small sub-Antarctic island (Ile Verte, 49°51′S, 70°05′E) of the Kerguelen Archipelago, in the southern Indian Ocean, where blue petrels and the Antarctic prions gather in stable colonies during the breeding season. We conducted the study during the 2017 and 2018 birds' incubation period (25 November 2017 to 12 December 2017 and 27 November 2018 to 20 December 2018 for blue petrels; 23 December 2017 to 16 January 2018 and 25 December 2018 to 13 January 2019 for Antarctic prions).

Playback procedure and recording of provoked calls

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

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

The recording equipment was composed of an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20–20 000 Hz ± 2.5 dB) connected to a Marantz PMD 660 digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). The microphone was positioned on the ground, at the burrow entrance, and one randomly selected synthesized call was broadcast at a natural sound pressure level (± 67 dB, measured on 111 calls from 54 males with a sound level meter) using a TASCAM DR-

07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). Calls emitted in reply by the burrow owner were recorded during the playback and two minutes after the end of the playback stimulus. If the focal individual did not reply, the playback was repeated every 30 s, up to three times.

Morphometric measurements

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

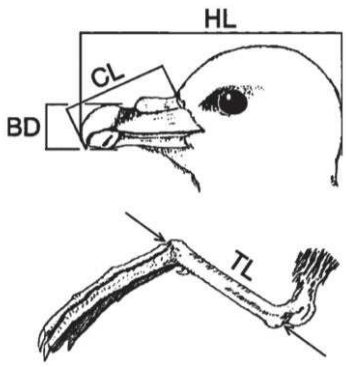

Figure 1. Tarsus and head measurements from Cramp and Simmons (1977), taken on blue petrels and Antarctic prions: head length (HL), bill depth (BD), bill length (CL) and tarsus length (TL).

Head and tarsus measurements (CL, BD, HL and TL) were taken using a calliper with an accuracy of ± 0.1 mm. Wing length was measured with a stainless-steel rule with an accuracy of ± 1.0 mm. To limit measurement biases, a single person (CG) took each measurement three times and calculated the mean. We also took standardized pictures of both sides of the right wing for each tested individual, using a digital camera (Olympus TG-610). Wing area was then measured by a single person (CG) by counting the number of calibrated pixels using ImageJ image analysis software version 1.52a (National Inst. of Health, USA). Correlation scores between morphometric measurements and summary are given in Supplementary material Figure A1, Table A1, respectively.

We chose morphometric measurements likely to be indicators of body size and/or to have an effect on call production based on the literature, and/or may be important in the biology of the species. Head size has been used as an indicator of body size in swallows (Patel et al., 2010; Winkler & Allen, 1996) and nestling growth in blue tits (Plummer et al., 2013). Similarly, tarsus and wing lengths are good indicators of body size in passerines (Gosler et al., 1998; Senar & Pascual, 1997), although it has not been documented if these indicators are suitable in seabirds. Bill is considered as the end of the vocal tract and its morphology (length and depth) may influence sound production. Bill is also the small petrels' feeding means (Warham, 1996), as they filter small crustaceans at the surface of the water, and may thus influence feeding efficiency (Klages & Cooper, 1992). Wing area seems a relevant morphological trait because petrels are a soaring species and travel great distances at sea to feed (Cherel et al., 2002).

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

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

Acoustic analysis

Calls recorded were first down sampled at 11.025 kHz to increase the precision of frequency measurements and high-pass filtered (Cutting frequency: 0.10 kHz, FFT filter) to remove the background noise. We described calls at a phrase level by measuring 11 acoustic parameters in the temporal and frequency domains (see Table 1 for abbreviations and description), on oscillograms and spectra of the signal-processing software Avisoft–SASLab Pro ver. 5.2.11, respectively (Specht, 2017).

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

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

Temporal variables were automatically extracted on the amplitude envelopes using the 'Pulse Train Analysis' function, with a resolution of 0.09 ms (hysteresis: + 30 dB; start/ end threshold: − 30 dB). Settings were not manipulated during measurements, except the threshold, which was manually adjusted to detect all syllables. Mean fundamental frequencies and variables describing energy spectral distribution were automatically extracted on linear amplitude spectra with a resolution of 22 Hz (FFT length: 512, Blackman window) (Figure 2). Automatic extractions are based on clear criteria preliminarily set, insuring objectivity in element demarcation and thus replicable measurements (Fischer et al. 2013). Syllables and phrases were counted on sonograms (Figure 2). Correlation scores between acoustic-parameter measures and summary are given in Supplementary material Figure A2, Table A2, respectively.

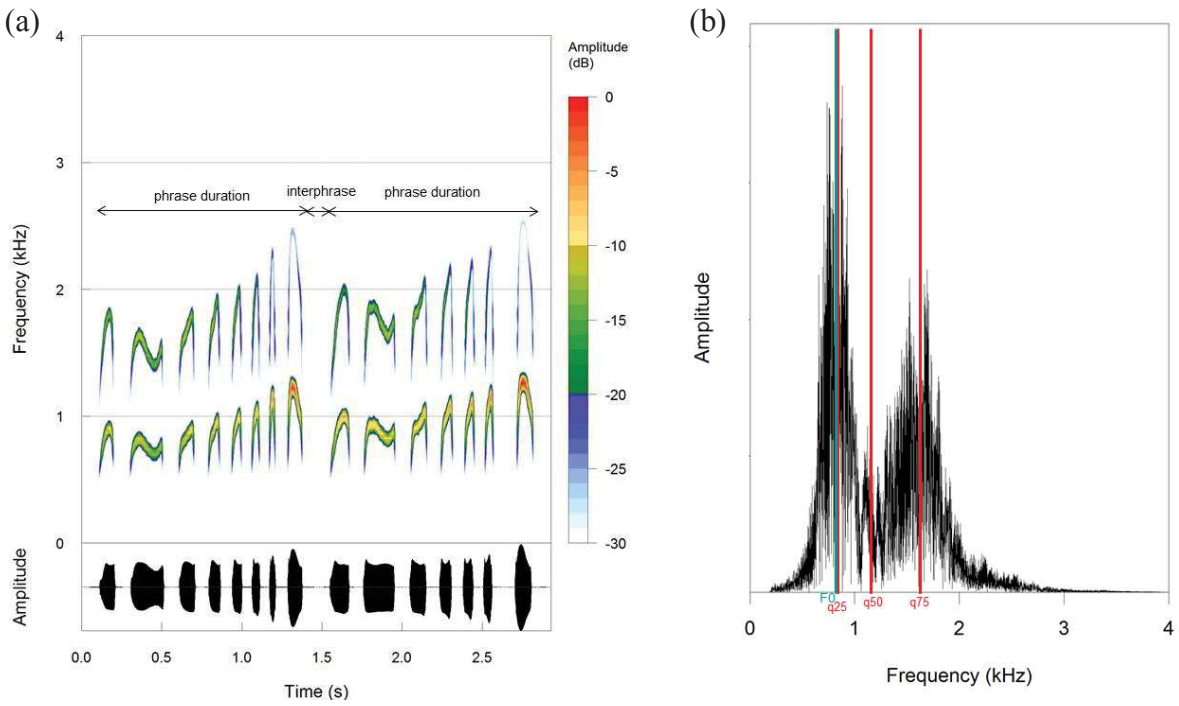

Figure 2. (a) Sonogram (top) and oscillogram (bottom) of a male blue petrel call constituted of two phrases. (b) Linear amplitude spectrum of a call phrase. Red lines indicate energy quartiles and blue line indicates the mean frequency of the phrase.

Statistical analysis

We implemented all analyses results under the R software environment version 3.4.4 (R Core Team) with the ade4 package (Dray & Dufour, 2015).

Relating acoustic parameters and morphological traits

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

We investigated covariance among morphometric measurements and acoustic parameters with a co-inertia analysis (CIA), an ordination method designed to reveal the co-structures among two data tables (Dolédec & Chessel, 1994; Dray et al., 2003). A summary table of acoustic and morphometric

data are given in Supplementary material Figure A1, Table A1, respectively. We first summarized the morphometric measurement table with the two first axes of a normed principal component analysis (PCA1), which explained together 55.5% for blue petrel (32.2 and 23.3% for PC11 and PC12, respectively) and 60.6% of total inertia for Antarctic prion (34.6 and 26.0% for PC11 and PC12, respectively). We ordinated the acoustic-parameters table with a between-class analysis (PCA2), a PCA which accounts for the clustering of object (here phrases) by a grouping factor (here individuals), similarly as in a redundancy analysis (Dolédec & Chessel, 1987). We retained the two first axes of the PCA2 in both species (28.2% and 24.7% of variance explained by PC21 and PC22, respectively, in blue petrel; 34.6% and 24.9% in Antarctic prion). We built the CIA as an ordination of PCA1 and PCA2. Overall similarity between the two ordination tables was assessed by the RV coefficient, a correlation coefficient between two sets of variables recorded from the same sample (0: no similarity, 1: equal tables).

Individual signature

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

We calculated the potential of individuality coding (PIC) of each call acoustic parameter. PIC is defined as the ratio between intra-individual variation (CV_w) and inter-individual variation (CV_b) of a given acoustic parameter. For each parameter and each individual, we calculated the coefficient of intra-individual variation CV_w corrected for small samples (Scherrer, 1984): $CV_w = 100\left(\frac{std}{\bar{X}}\right)\left(1 + \frac{1}{4n}\right)$ with $\bar{X}$ the mean of the parameter measured, and n is the number of measures. We calculated the inter-individual variation coefficient as $CV_b = 100\left(\frac{std}{\bar{X}}\right)$ where *std* and $\bar{X}$ are the standard deviation and the mean calculated with all measures of a given parameters, respectively, from all individuals. PIC values have been calculated as $PIC = \frac{CV_w}{CV_b}$. If PIC > 1, intra-individual variability is smaller than inter-

individual variability for a given parameter, suggesting that this parameter may potentially carry individual information. PIC values are considered high (i.e. likely to carry individual information), when they are superior to two (Lengagne et al., 1997; Robisson et al., 1993).

Results

Relation between acoustic parameters and morphological traits

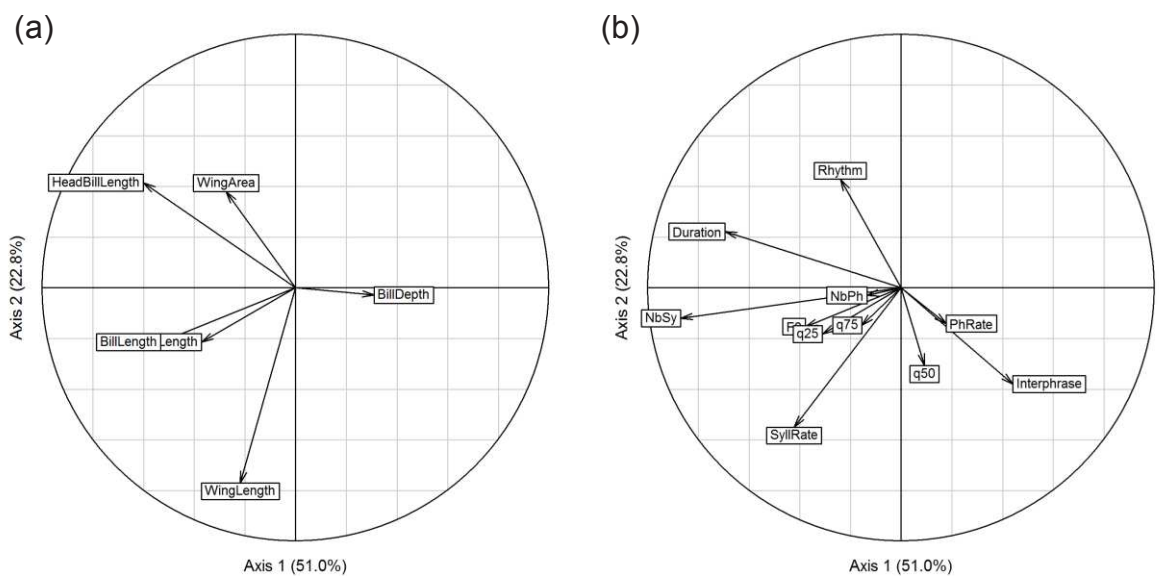

Figure 3. In blue petrels, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.

In blue petrels, the RV coefficient of the CIA between morphometric measurements and acoustic parameters is 0.34. The first two axes of the CIA explained 51.0% and 22.8% of total variance, respectively. The first CIA axis shows the duration and the syllable number of the phrase are mainly related to head and bill length (HL, CL). More precisely, males with a small head (HL) and a short bill (CL) produce short calls with few syllables. The second CIA axis shows rhythm and syllable rate are related to both wing measurements (WL, WA). More precisely, males with short, large wings produce slow (i.e. low phrase rate) calls with long syllables (i.e. high rhythm) and short interphrase silences. Frequency parameters are weakly related to the chosen morphometric measurements (Figure 3).

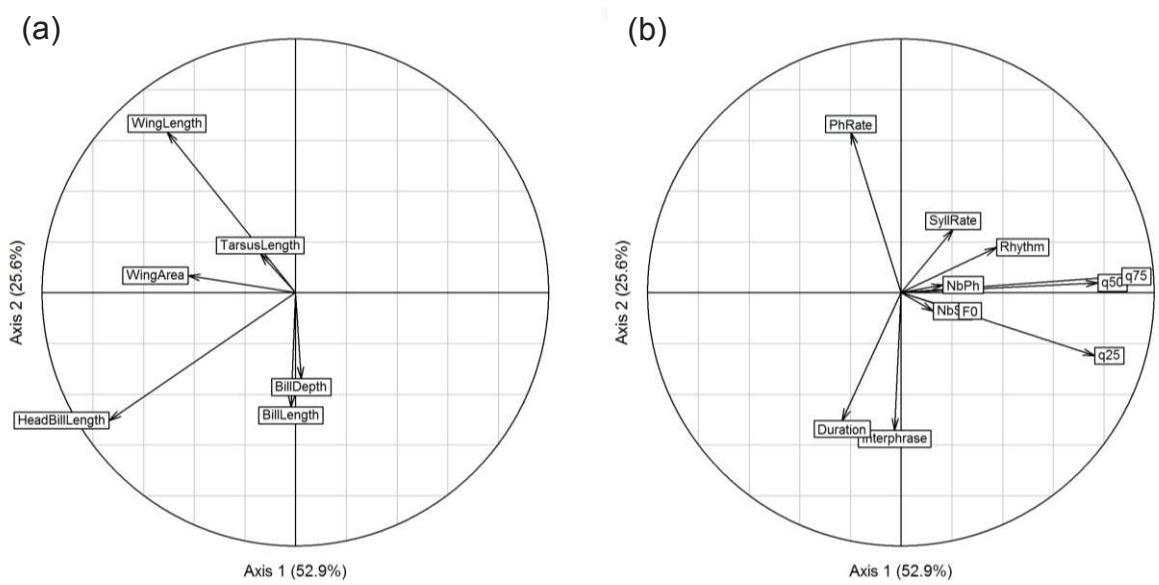

Figure 4. In Antarctic prions, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.

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

Tables of CIA scores for both species are given in Supplementary material Table A3.

Individual signature

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

The total inertia explained by the differences between males in blue petrels and Antarctic prions was 74% and 65%, respectively, showing that the chosen acoustic parameters allow a significant vocal discrimination of individuals ($p < 10^{-5}$ in both species). Composite plots of BCA analyses are given in Supplementary material Figure A3.

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

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

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

Discussion

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

Relationship between acoustic parameters and morphological traits

In both species, results obtained by CIA show a clear relationship between acoustic parameters of males' calls and some morphological traits which may constraint call productions (bill morphology,

body size indicators), and/or may be relevant considering the feeding ecology (bill morphology, wing morphology) of these species.

Specifically, frequency parameters (i.e., fundamental frequency and energy quartiles) are related to bill morphology, especially head-bill length, in both species even though the relationship is weak in blue petrels. Males with a short head and bill produce low-pitched calls in blue petrels whereas they produce high-pitched calls in Antarctic prions. Relationship between bill morphology and frequency is unclear in birds and both opposite patterns have been observed in many species (Christensen et al., 2006; Laiolo & Rolando, 2003; Palacios & Tubaro, 2000). Other studies have found no relationships between frequencies and bill morphology (García & Tubaro, 2018). We can hypothesize that cues that may inform females on this male characteristic might be important as bill morphology influences feeding efficiency in these filter-feeding species (Klages & Cooper, 1992).

Head-bill length is also a body size indicator, suggesting frequencies are related to body size. This frequency–body size relationship has been illustrated in many species at the light of the source-filter theory (Taylor & Reby, 2010). This theory states that vocal signals result from a two-stage production: the source signal is generated by membrane vibrations in the vocal organ (larynx in mammals or syrinx in birds), and subsequently filtered by the vocal tract and the mouth/nostrils (Fant, 1960). Consequently, the anatomy of the 'source', particularly the length and mass of vibrating membranes, shapes the fundamental frequency. Muscular interactions change the airflow in the 'source' and thus influence temporal parameters such as rhythm, duration and amplitude. The 'filter' influences the formants, i.e. the resonant frequencies (Taylor & Reby, 2010; Titze & Martin, 1998). Although this theory is valid in mammals, the relationships between frequencies and body size remains unclear in birds (Galeotti et al., 1997; Mager et al., 2007; Favaro et al., 2017; Kriesell et al., 2018; but see Patel et al., 2010).

Our results show some temporal parameters are related to body size in both species, suggesting big males produce more challenging songs than small males. More precisely, in blue petrels, males with a long head, wings and tarsus produce long, fast calls with many syllables. In Antarctic prions, males with long wings produce short, fast calls. In many species, females are more attracted by males performing challenging songs/calls (i.e. with a high rate and/or a large frequency bandwidth), likely because they

reflect male characteristics linked to qualities such as endurance (Ballentine et al., 2004), survival (Byers et al., 2016), age and size (Ballentine, 2009).

Results show a strong relationship between acoustic parameters and wing morphology, especially wing length in both species, and wing area even though this relationship is weaker in blue petrels. We thus suggest that for soaring seabirds, which travel great distances at sea to feed, wing morphology is a relevant parameter to be considered (Cherel et al., 2002). We can hypothesize that cues that may inform females on this male characteristic might be important as wing morphology is correlated with foraging behaviour (Hertel & Ballance, 1999) and reproductive costs (Mauck & Grubb, 1995). In other Procellariidae, a reduction of parents' flying abilities (e.g. clipping feather tips, removing flight feathers, adding extra weight) affects the incubation routine and results in a decrease of their body condition and/or a deterioration of chick condition (Navarro & González-Solís, 2007; Saether et al., 1993; Weimerskirch et al., 1995)

Blue petrels and Antarctic prions form lifelong monogamous bonds. Pair bonding takes up to two years and partners equally share parental care during the incubation period (Chaurand & Weimerskirch, 1994a; Warham, 1990, 1996). Sexual maturity is reached tardily (around seven years), they show low fecundity (one single egg per year without a replacement clutch), and extra-pair paternity is extremely rare (Jouventin & Mougin, 1981; Warham, 1996). Consequently, choosing the 'wrong' mate affects fitness more than in species that change mates at each breeding. Females should rely on attractive and reliable cues to evaluate the quality of a potential partner (Darwin, 1871; Smith, 1991). As in many bird species, males' calls are likely to be sexual signals that attract and/or stimulate a potential mate (Bretagnolle, 1990). Especially as they are highly vocal, despite the predation cost, and as living in burrows prevents visual communication on long-range. We hypothesize, thus, that the information contained in male calls about the caller body size may have a significant role in sexual selection. In blue petrels, bigger males at the beginning of the breeding season have a higher breeding success (Chastel et al., 1995). Moreover, calls contain information about wing morphology, which may be linked to reproductive success in these soaring birds (Navarro & González-Solís, 2007; Saether et al., 1993; Weimerskirch et al., 1995).

Individual signature

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

In many seabirds, vocal identity is crucial in social interactions, such as mate reunion or kin recognition (e.g. Spheniscidae: Robisson et al., 1993; Jouventin et al., 1999; Aubin & Jouventin, 2002; Procellariidae: Barbraud et al., 2000; Curé et al., 2011; Stercorariidae: Charrier et al., 2001; Laridae: Mathevon et al., 2003). However, in burrowing petrels, finding relatives and nest sites seems not based on vocal signals. As they return from their foraging trip at sea, petrels rely on olfactory signals to find their burrow (Bonadonna et al., 2001, 2004) and take the place of their mate incubating in the burrow, without emitting any call (FB and CG personal observation). Therefore, vocal signature does not seem to be involved in mate reunion. Vocal signatures do not systematically imply recognition (Townsend et al., 2010). So far, there is no clear evidence that burrowing petrels vocally recognize conspecifics as shown in other seabird families (e.g. Spheniscidae: Robisson et al., 1993, Jouventin et al., 1999, Aubin & Jouventin, 2002; Procellariidae: Barbraud et al., 2000; Curé et al., 2011; Stercorariidae: Charrier et al., 2001; Laridae: Mathevon et al., 2003). Nonetheless, vocal signature could be used in neighbour/stranger discrimination processes. Indeed, blue petrel and Antarctic prion males call from their burrow in crowded colonies (respectively up to 0.7 and 1.4 burrows m^{-2} according to Croxall & Prince (1980). The significant costs of calling behaviour (Mougeot & Bretagnolle, 2000) suggests that males should call only when necessary, for instance in the presence of a stranger male not belonging to the neighbouring community, to avoid higher predation risks and useless energy expenditures. This

'dear-enemy phenomenon' (Fisher, 1954) has been documented in many territorial songbirds where males are less aggressive with neighbours than with strangers when defending their breeding territory (Temeles, 1994). One hypothesis is that territory owners adjust their aggressive behaviour according to the familiarity and/or threat degrees and thus minimizes fighting costs (Temeles, 1994).

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

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

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Permits – This study was performed according to 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.

Data availability statement – Data available from the Dryad Digital Repository: <http:// dx.doi.org/10.5061/dryad.1rn8pk0pk>

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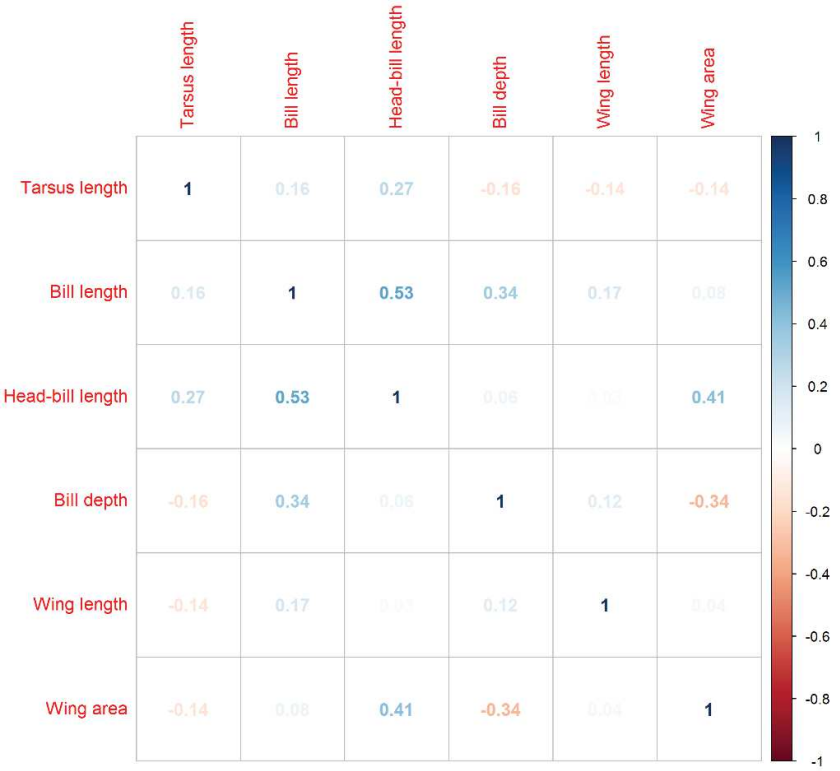
Appendices

Figure A1. Correlograms showing correlation scores between morphometric measurements in (a) blue petrels and (b) Antarctic prions.

(a)



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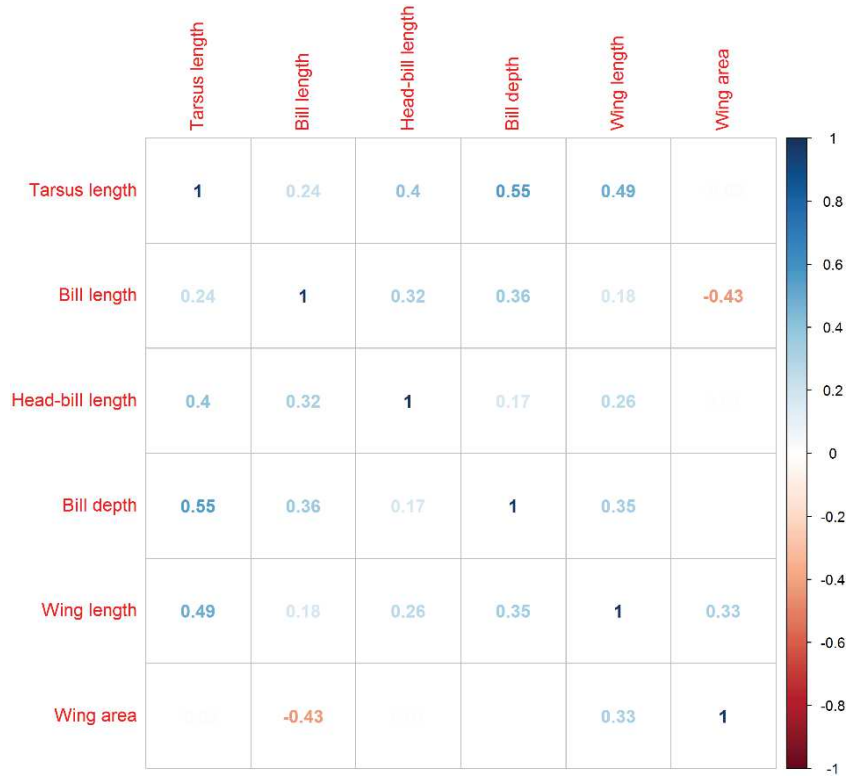
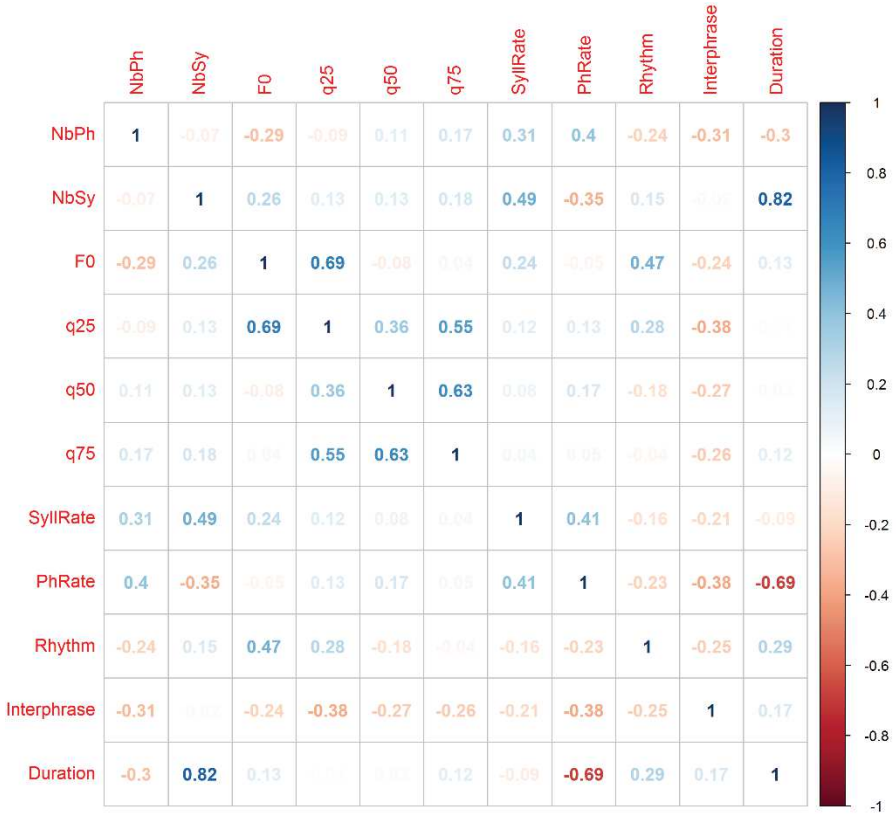


Table A1. Summary of morphometric measurements of males of blue petrels and Antarctic prions.

Morphometric measurements	Blue petrel			Antarctic prion		
	mean	sd	N	mean	sd	N
Tarsus length (mm)	33.30	0.94	25	33.29	1.15	17
Bill length (mm)	25.89	0.89	25	26.92	0.93	17
Head-bill length (mm)	66.33	1.88	25	61.71	0.87	17
Bill depth (mm)	9.46	0.55	25	8.53	0.35	17
Wing length (mm)	218.25	4.02	25	191.80	4.80	17
Wing area (cm^2)	197.54	18.95	25	181.41	18.50	17

Figure A2. Correlograms showing correlation scores between acoustic parameters in (a) blue petrels and (b) Antarctic prions.

(a)



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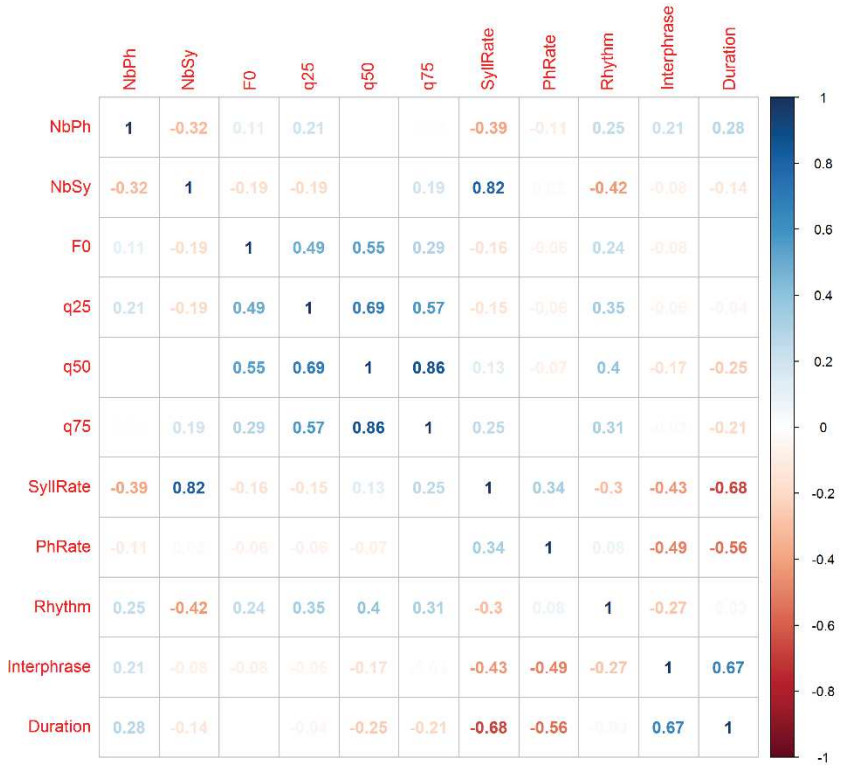


Table A2. Summary of acoustic parameters measured on male calls of blue petrels and Antarctic prions. Abbreviations of acoustic parameters as given in Table 1.

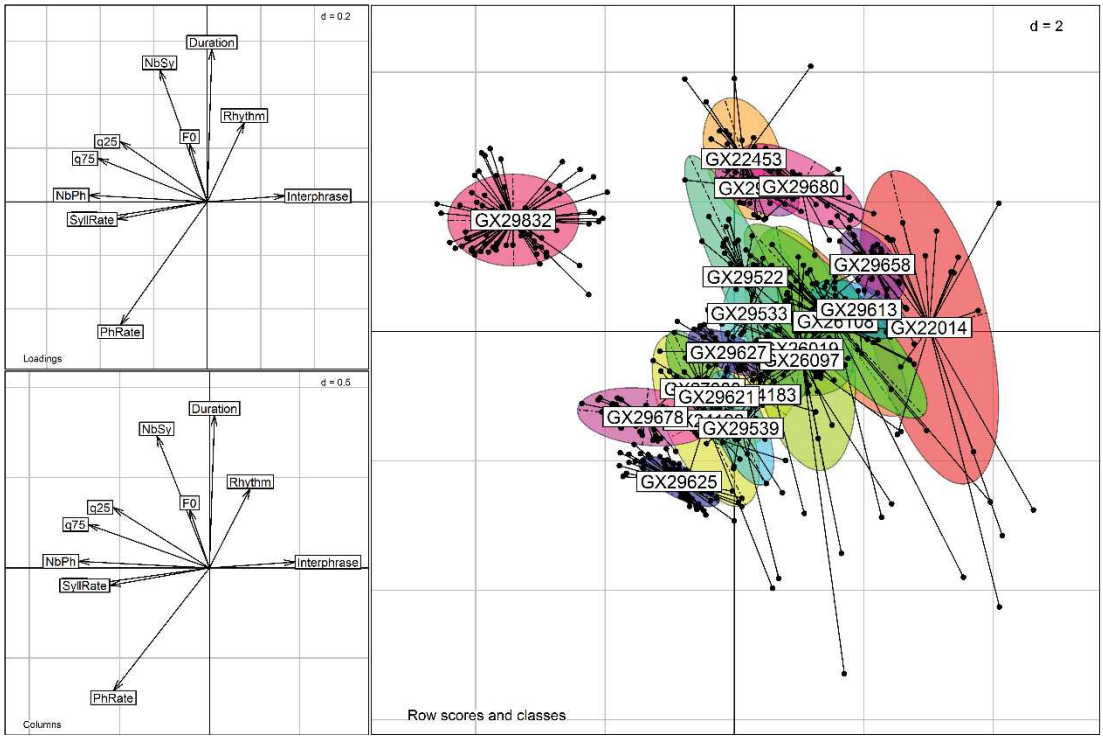
Acoustic parameters	Blue petrel			Antarctic prion		
	mean	sd	N	mean	sd	N
NbPh	21.26	13.42	285	10.62	4.85	148
NbSy	7.41	1.69	285	4.49	0.59	148
F0 (Hz)	458.96	53.91	285	672.11	100.24	148
q25 (Hz)	434.71	43.36	285	562.01	73.02	148
q50 (Hz)	574.74	102.62	285	707.72	108.32	148
q75 (Hz)	818.91	181.93	285	898.14	184.66	148
SyllRate	2.57	0.34	285	3.37	0.58	148
PhRate	0.38	0.06	285	0.75	0.11	148
Rhythm	1.19	0.12	285	1.71	0.27	148
Interphrase (s)	0.24	0.05	285	0.18	0.03	148
Duration (s)	2.89	0.57	285	1.35	0.13	148

Table A3. The first two principal components (PC) resulting from CIA on acoustic parameters of and morphometric measurements measured of blue petrel and Antarctic prion males. Values above 0.5 are in bold. Abbreviations of acoustic parameters as given in Table 1.

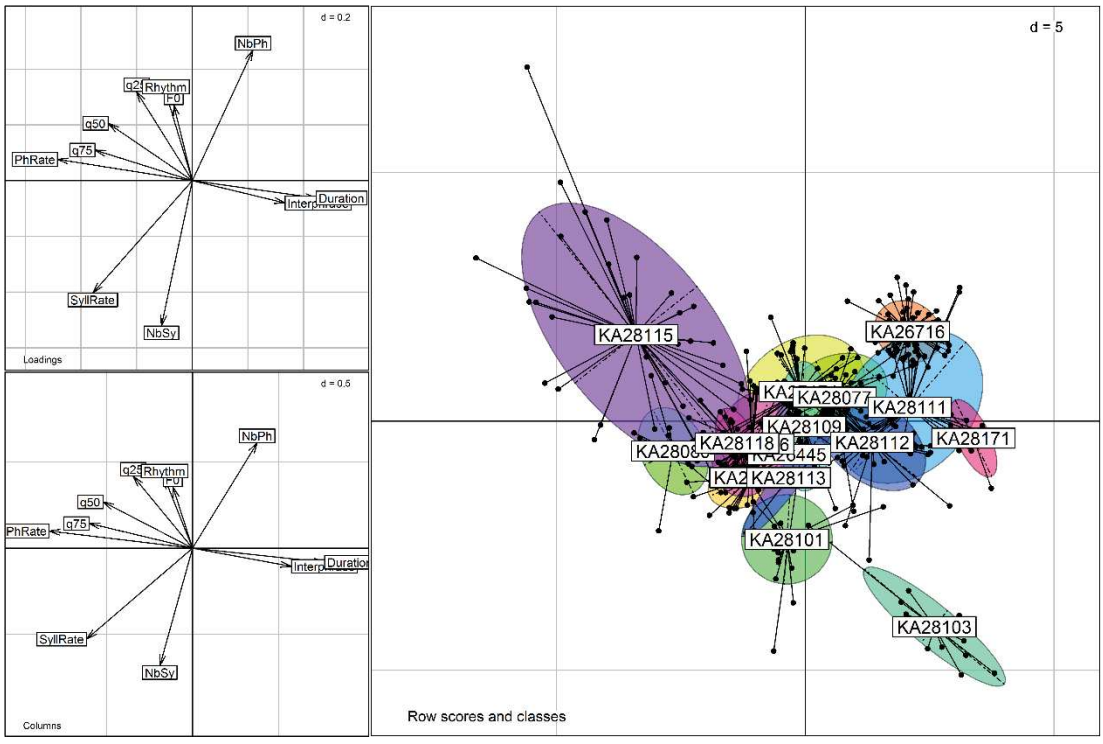
	Blue petrel		**Antarctic prion**	
	PC1 (51.0%)	**PC2 (22.8%)**	**PC1 (52.9%)**	**PC2 (25.6%)**
Acoustic parameters				
NbPh	- 0.10	- 0.03	0.11	0.03
NbSy	**- 0.62**	- 0.13	0.08	- 0.07
F0	- 0.27	- 0.16	0.15	- 0.07
q25	- 0.22	- 0.19	**0.50**	- 0.23
q50	0.07	- 0.33	**0.51**	0.04
q75	- 0.11	- 0.16	**0.57**	0.06
SyllRate	- 0.30	**- 0.58**	0.13	0.24
PhRate	0.13	- 0.15	- 0.13	**0.60**
Rhythm	- 0.17	0.46	0.25	0.17
Interphrase	0.31	- 0.40	- 0.02	**- 0.51**
Duration	- 0.49	0.24	- 0.15	- 0.48
Morphometric measurements				
Tarsus	- 0.37	- 0.21	- 0.14	0.15
Bill length	**- 0.53**	- 0.21	- 0.02	- 0.45
Head-bill length	**- 0.60**	0.41	**- 0.74**	**- 0.50**
Bill depth	0.31	- 0.03	0.02	- 0.34
Wing length	- 0.22	**- 0.77**	**- 0.51**	**0.63**
Wing area	- 0.27	0.38	- 0.42	0.07

Figure A3. Individual vocal discrimination of males based on 11 acoustic parameters, using a Between-Class Analysis (Dolédec & Chessel, 1987), in (a) blue petrels and (b) Antarctic prions. Each ellipse represents a male labelled by its ring number.

(a)



(b)



CHAPTER II

VOCAL PLASTICITY AND MOTIVATION

(photo credits: Francesco Bonadonna)

In vocal signals, particular acoustic parameters related to the emitter condition provide static information to receivers. In blue petrels and Antarctic prions, I assessed relationships between temporal and spectral parameters, the individual identity, the bill and wing morphology, and the body size in a first chapter. Here, I aimed to explore whether male calls also carry a second type of information, the dynamic information, which depends on particular environmental stimuli. I simulated natural vocal interactions in which males are stimulated or challenged by a conspecific, either male or female, to cause a motivational change.

ARTICLE 2

Contextual variations in calls of two non-oscine birds: the blue petrel and the Antarctic prion

Charlène Gémard[ac*], Víctor Planas-Bielsa[b], Francesco Bonadonna[a], Thierry Aubin[c]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Département de Biologie Polaire, Centre Scientifique de Monaco, 8 Quai Antoine 1ère, 98000 Principality of Monaco

[c] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

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Abstract

Bird vocalizations are critical cues in social interactions as they convey temporary information varying with the social context, e.g., the signaller motivation when facing a rival or a potential mate. To date, literature mainly focuses on learning birds. Burrowing petrels (Procellariidae) are non-learning birds with a limited vocal repertoire. Bachelor males communicate with conspecifics with a single 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 call structure 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 signaller'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 two petrel species: the blue petrel (*Halobaena caerulea*) and the Antarctic prion (*Pachyptila desolata*). Despite the obvious call stereotypy, we observed temporal variations and frequency shifts when males react to a female or a male, which may translate the sexual or aggressive motivation of the signaller. Furthermore, the similarity of variations in male-directed calls of both breeder and bachelor males suggests the aggressive motivation. So far, vocal plasticity in non-learning birds have been greatly underestimated. Here, we highlighted the expression of different motivations through vocal variations and the ability to produce frequency variations in species with genetically coded vocalizations.

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

Introduction

In animal communication, the information carried by signals is of two types: stable such as signaller attributes and identity (e.g., species, group membership, individual identity, phenotypic characteristics: Searcy & 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 behaviours such as fighting or mating: Morton, 1977; Bradbury & Vehrencamp, 2011; Briefer, 2020). The transmission of transient information through vocal signals has been well documented since Darwin (1871) hypothesized that vocal signals are indicators of the signaller'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 behaviour: Zahavi, 1982). More-recent studies suggest that information about emotions and motivations of the signaller 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 & 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 (Podos, 1997; Sossinka & Böhner, 1980). 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 & Böhner, 1980). When facing a rival or an intruder, signallers usually vocalize in a way that increases their perceived competitive potential and willingness (Searcy & Beecher, 2009; Todt & Naguib, 2000; Vehrencamp, 2000). According to Motivational-Structural Hypothesis (Morton, 1977), contestants produce longer vocal signals, characterized by lower frequencies and a 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 (Funghi et al., 2014; Linhart et al., 2013; Searcy & Beecher, 2009)

Much of the available literature about acoustic variations related to the social context focuses on learning birds, especially passerines (Catchpole & 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 corncrakes (*Crex crex*), males produce calls with syntactic variations encoding the aggressive motivation (Rek, 2013; Rek & Osiejuk, 2013). Although temporal variations have been highlighted in non-songbirds, frequency variations in their calls have not been investigated until very recently (Jedlikowski et al., 2021). 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, 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., *in press*; 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 & Bretagnolle, 2000). After pairing, adults scarcely call spontaneously as partner and nest recognitions are mainly olfactory (Bonadonna & Nevitt, 2004; Mardon et al., 2010). Both breeder and bachelor males call after being vocally challenged by same-sex conspecifics (Bretagnolle & Lequette, 1990; Curé et al., 2011; Taoka & Okumura, 1989). 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 variations. 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, faster, and lower-pitched than spontaneous calls based on previous studies in other learning and 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' vocal response.

Material and methods

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.

Experimental signals

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 (i.e., syllable order and types). 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 petrels, and 3.43 ± 0.85 s in Antarctic prions), 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).

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 & 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 playback series, 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 for bachelor males. Each male – bachelor or breeder – was tested only once. To avoid testing males twice, the nest entrance was labelled by a coloured marker.

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. Tested individuals might return to a spontaneous vocal behaviour before the end of the experiment. To limit bias related to a behavioural

change, we restricted our analyses to the last spontaneous calls before playback and the first directed calls after playback. In total, we obtained 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).

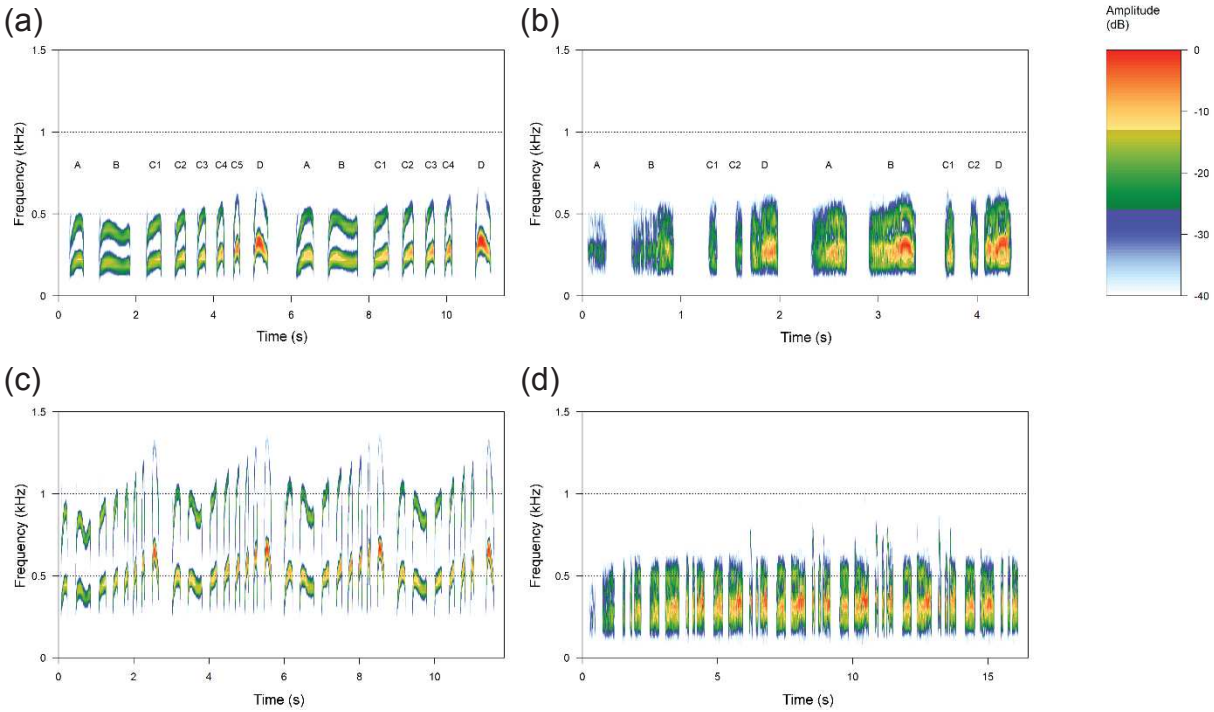

Figure 1. Spectrograms of calls from a bachelor male of blue petrel *H. caerulea* and Antarctic prion *P. desolata* (Blackman window, FFT length: 512): (a) spontaneous blue petrel call; (b) spontaneous Antarctic prion call; (c) male-directed blue petrel call; (d) male-directed Antarctic prion call.

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 & 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 & Miller, 1982 for a review) on syllables and on phrases (classification, description, and abbreviations are provided in Table 1).

Table 1. Summary and abbreviations of the 34 syntactic, temporal and spectral parameters 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% of A energy)
	A.Q50	A medium quartile (frequency at the upper limit of the 50% of A energy)
	A.Q75	A lower quartile (frequency at the upper limit of the 75% of A energy)
	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

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 analyse 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.

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 blue petrels and Antarctic prions.

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 a standard deviation for each entry 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 syntactic variables. We then graphically compared the accuracy of the three NN with each other, and with the full NN as well.

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 (Figures A1, A2). We thus analysed 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 checked its factorability by calculating the KMO index (Table A1; Kaiser & Rice, 1974; Budaev, 2010). 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 Tables A2, A3. 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).

Results

Motivation Hypothesis

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).

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)

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

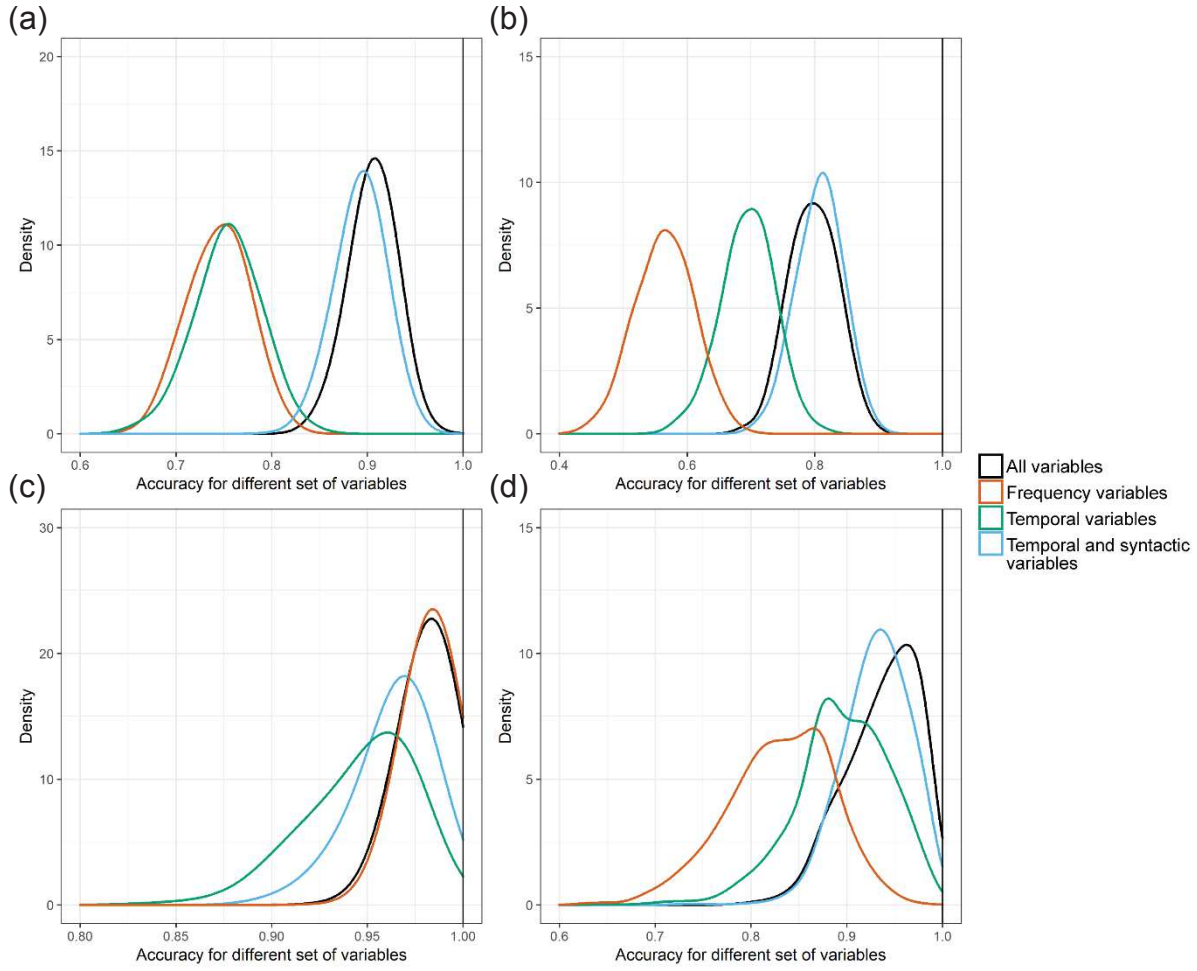

Figure 2. Accuracy of NN trained to discriminate the three call types of bachelor males based on their acoustic parameters in (a) blue petrel *H. caerulea* and (b) Antarctic prion *P. desolata.* Accuracy of NN trained to discriminate male-directed calls of bachelors and breeders in (c) blue petrels and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

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 at syllable and phrase levels, in both blue petrels and Antarctic prions (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). Results of PCA_T showing variable contributions to each principal component in both species are given in Table A2. Detailed results of binomial GLMM comparing call types in both species are presented in Table A3.

Table 3. Variations of acoustic parameters between the three different call types of bachelor males in blue petrels and Antarctic prions. Acoustic parameters given here are the most correlated with the principal components (see Table A2 for the contribution of each 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, A.Q75, C.Q75	NS	↗ ↘	↗ ↘
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, 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
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 Syll.Tempo	NS	↗ ↘	NS
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.

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).

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).

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).

Breeding-Status Hypothesis

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 (Table A4). Details of variable contribution to each principal component in both species are given in Table A4. Detailed results of binomial GLMM used to compare bachelors' and breeders' male-directed calls are presented in Table A5 in both species.

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)

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).

Table 5. Variations of acoustic parameters between 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 (see Table A4 for the contribution of each 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.

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 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).

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 signaller.

	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 - Shifts on syllables	- Higher pitched - Narrower bandwidth	- Narrower bandwidth
Temporal variables	- Longer phrases - Lower tempo	- Longer phrases - Lower tempo	- Shorter syllables - Higher rhythm
Syntax	- More phrases per call	- More phrases per call	- More syllables per phrase - Less phrases per call
Antarctic prions			
Frequency variables	- Higher pitched	- Higher pitched	- Higher pitched
Temporal variables	- Higher tempo	- Lower tempo - Longer syllables - Shorter silences	- Longer syllables A
Syntax	- More phrases per call	- More phrases per call	- Less phrases per call

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).

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 context-dependent frequency shifts at the fine scale of syllables within phrases between the different call types. In blue petrels and Antarctic prions, the presence of conspecifics thus influences the vocal performance of callers, resulting in acoustic variations in both temporal and spectral domains.

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., *in press*; 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 (Sakata et al., 2008; Sossinka & Böhner, 1980). 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 & 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. Another hypothesis is that short syllables (syllables C in the two species studied here) encode more information than long syllables and repeating these syllables ensure the information redundancy, as shown in display songs of African penguins (Favaro et al., 2020).

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 calls. When reacting to a potential mate, males usually enhance the acoustic parameters related to their qualities (Podos, 1997; Sossinka & Böhner, 1980). 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., *in press*). 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.

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 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 & 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 & Beecher, 2009). Alternatively, non-learning birds may have evolved a different signalling 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 learning (e.g., DuBois et al., 2009; Szipl et al., 2017) and non-learning birds (Jedlikowski et al., 2021) 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.

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 in size but breeders coming back from their feeding

trips at sea are heavier than bachelors (Chaurand & Weimerskirch, 1994; Figure A3). 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 & Weimerskirch, 1994). Another hypothesis is that, in species vulnerable to predation (Mougeot & 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 caller's breeding status 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 only, contrary to our hypothesis.

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 signaller motivation in non-songbirds. It opens new leads in the assessment of vocal plasticity in non-oscine species.

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Conflicts of interest - The authors declare that they have no conflict of interests.

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Ethics approval - 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.

Data availability - Analyses reported in this article can be reproduced using the data from the Dryad Digital Repository: < https://doi.org/10.5061/dryad.8sf7m0cmj >

Authors' contributions **-** All authors made substantial contributions to conception of experiment, analysis and interpretation of data, and critical review of the manuscript. CG, FB, and TA contributed to the study conception and design. CG and FB performed material preparation and data collection. CG and VPB analysed the data. The first draft of the manuscript was written by CG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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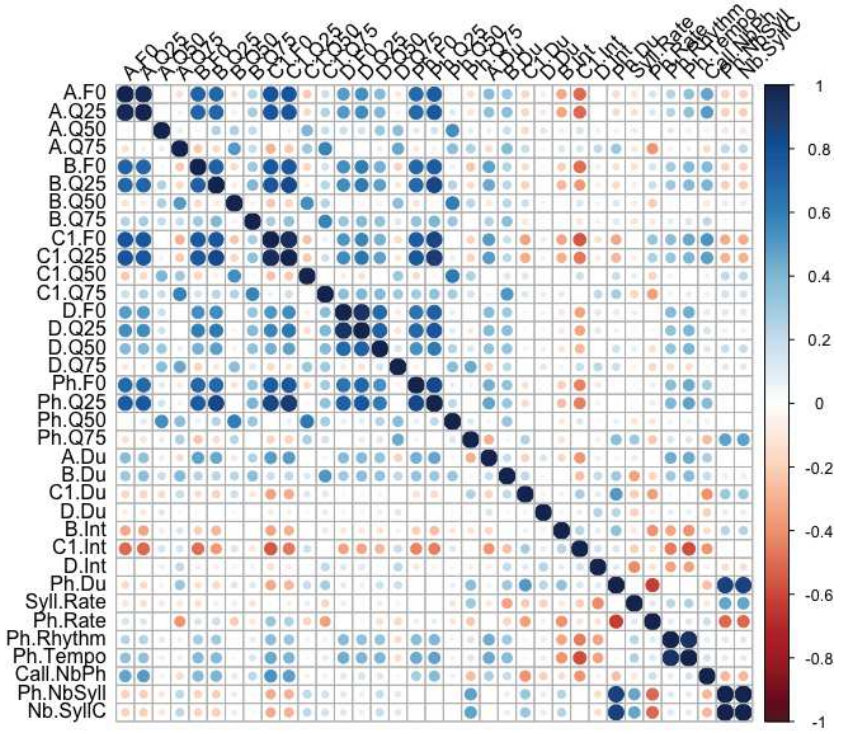
Appendices

Figure A1. Correlograms showing relationships between acoustic parameters of three types of bachelor males calls (Motivation Hypothesis) in (a) blue petrels *H. caerulea* and (b) Antarctic prions *P. desolata*. Parameter abbreviations given in Table 1.

(a)



(b)

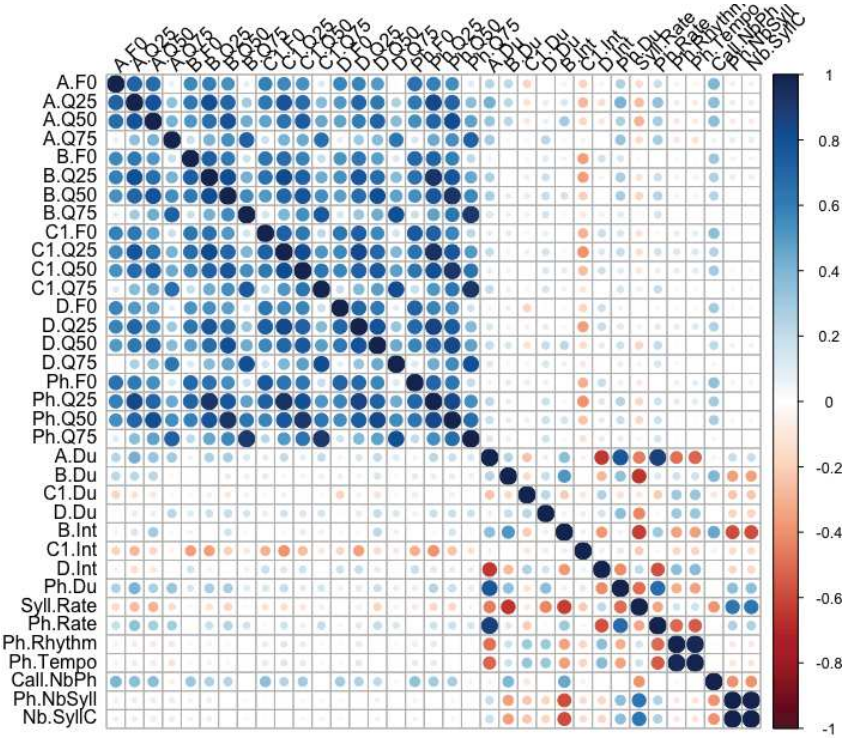
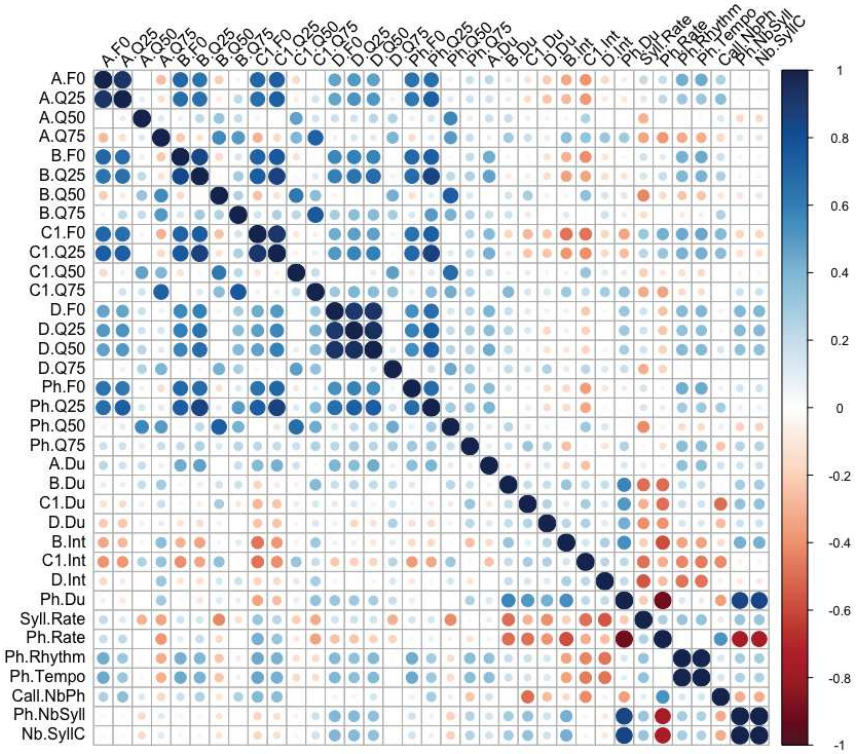


Figure A2. Correlograms showing relationships between acoustic parameters of male-directed calls of bachelor and breeder males (Breeding-Status Hypothesis) in (a) blue petrels *H. caerulea* and (b) Antarctic prions *P. desolata*. Parameter abbreviations given in Table 1.

(a)



(b)

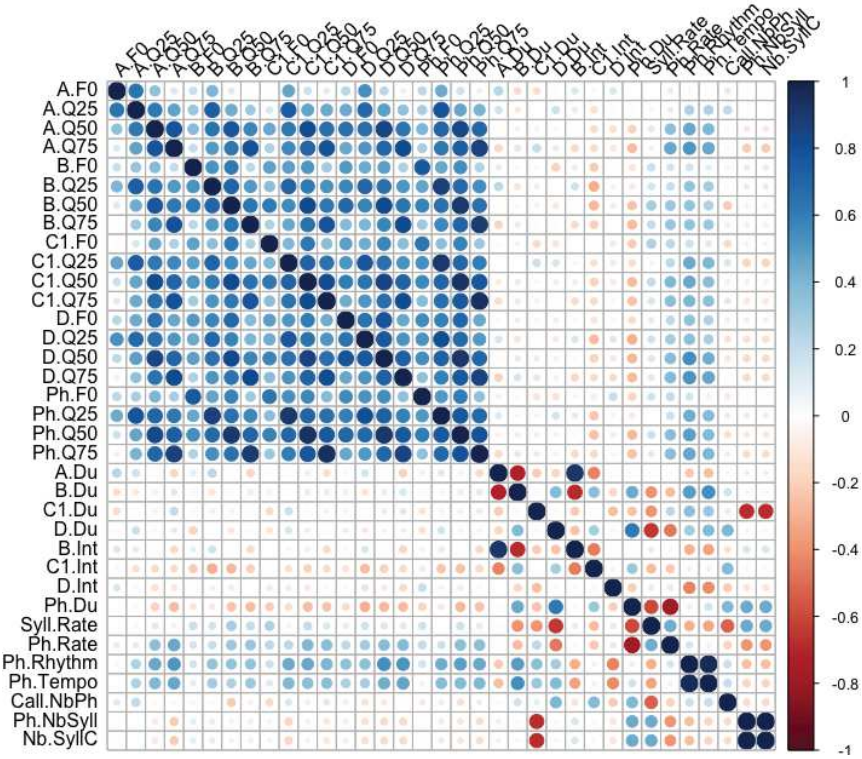


Table A1. Results of the Kaiser-Meyer-Olkin (KMO) Index

Species	Hypothesis	Variable category	MSA value
Blue petrels	Breeding-status	Spectral	0.84
		Temporal	0.52
	Motivation	Spectral	0.87
		Temporal	0.48
Antarctic prions	Breeding-status	Spectral	0.88
		Temporal	0.57
	Motivation	Spectral	0.90
		Temporal	0.59

Table A2. Coordinates of the six principal components (PC) of each frequency and temporal variables describing the three call types (Motivation Hypothesis) of bachelor males in blue petrels *H. caerulea* (N = 561) and Antarctic prions *P. desolata* (N = 357). Values in bold indicate the main variable in each principal component (value > 0.6). Variable abbreviations given in Table 1.

	Blue petrels						**Antarctic Prions**					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Frequency variables												
A.F0	**0.84**	-0.15	0.09	-0.36	-0.04	0.08	**-0.65**	0.48	0.30	-0.11	0.38	0.07
A.Q25	**0.84**	-0.07	0.08	-0.38	-0.01	0.09	**-0.83**	0.23	0.31	0.17	0.10	0.23
A.Q50	0.15	0.57	0.40	0.39	0.01	-0.38	**-0.82**	0.04	0.45	-0.19	0.08	0.02
A.Q75	-0.12	**0.70**	-0.39	-0.30	0.16	0.23	-0.54	**-0.61**	0.07	0.19	0.05	-0.17
B.F0	**0.83**	-0.16	0.13	-0.05	0.09	0.03	**-0.70**	0.37	-0.05	0.34	-0.02	-0.35
B.Q25	**0.86**	0.02	0.23	-0.01	0.08	-0.12	**-0.89**	0.14	0.06	0.27	-0.13	-0.03
B.Q50	-0.12	**0.73**	0.20	-0.15	0.09	0.43	**-0.88**	-0.07	0.24	-0.06	-0.23	-0.21
B.Q75	0.46	**0.37**	-0.27	0.00	0.43	-0.40	-0.59	**-0.70**	-0.06	-0.02	0.13	-0.13
C1.F0	**0.88**	-0.24	0.18	-0.16	-0.06	-0.06	**-0.72**	0.41	-0.33	0.11	0.12	0.10
C1.Q25	**0.92**	-0.15	0.14	-0.14	0.00	-0.08	**-0.90**	0.12	-0.12	0.20	-0.08	0.22
C1.Q50	-0.18	**0.66**	0.48	0.07	-0.04	0.20	**-0.90**	-0.06	-0.03	-0.14	-0.02	0.02
C1.Q75	0.35	**0.57**	-0.56	-0.12	0.27	-0.10	**-0.63**	**-0.66**	-0.11	-0.03	0.11	0.14
D.F0	**0.76**	0.13	-0.24	0.42	-0.10	0.26	**-0.65**	0.42	-0.31	-0.37	0.10	-0.10
D.Q25	**0.82**	0.10	-0.25	0.38	-0.01	0.21	**-0.85**	0.24	-0.21	-0.03	-0.19	0.17
D.Q50	**0.65**	0.33	-0.18	0.40	-0.21	0.01	**-0.84**	0.03	0.00	-0.36	-0.31	0.03
D.Q75	-0.09	**0.67**	-0.04	-0.27	-0.33	-0.35	-0.54	**-0.71**	-0.14	-0.03	0.06	0.08
Ph.F0	**0.86**	0.00	-0.05	-0.02	-0.19	-0.01	**-0.73**	0.44	-0.22	-0.06	0.24	-0.21
Ph.Q25	**0.95**	0.10	0.05	-0.03	-0.09	0.04	**-0.94**	0.10	-0.05	0.22	-0.07	0.11
Ph.Q50	0.15	**0.76**	0.43	-0.01	0.22	0.02	**-0.94**	-0.12	0.10	-0.14	-0.10	-0.11
Ph.Q75	-0.13	0.45	-0.20	-0.14	-0.73	-0.08	**-0.65**	**-0.70**	-0.09	0.00	0.14	0.02
Temporal variables												
A.Du	0.53	-0.31	0.27	-0.37	0.16	-0.48	**0.89**	0.06	-0.31	0.17	0.00	0.01
B.Du	0.20	**-0.69**	0.29	0.28	0.29	0.19	0.36	**0.69**	0.43	0.23	-0.17	0.03
C1.Du	-0.27	-0.57	-0.28	0.56	-0.27	-0.10	-0.36	0.32	-0.33	-0.17	**0.71**	0.34
D.Du	-0.06	-0.32	0.37	-0.54	**-0.62**	0.14	-0.01	**0.73**	-0.37	-0.29	-0.06	-0.31
B.Int	-0.55	-0.20	-0.25	-0.42	0.32	-0.01	0.58	0.19	**0.66**	0.05	0.28	-0.08
C1.Int	-0.71	0.10	-0.08	0.13	-0.42	-0.30	0.14	0.02	0.21	**-0.79**	-0.37	0.41
D.Int	-0.45	-0.23	**0.61**	0.04	0.03	0.39	**-0.69**	0.06	0.01	-0.42	0.04	-0.40
Ph.Du	-0.29	**-0.76**	-0.37	-0.17	-0.09	0.08	0.73	0.30	-0.48	-0.07	-0.21	-0.04
Syll.Tempo	0.36	0.31	**-0.68**	-0.22	-0.09	0.38	-0.58	**-0.66**	-0.22	0.25	-0.23	0.05
Ph.Tempo	0.37	**0.63**	0.34	0.18	-0.20	0.06	**0.84**	-0.07	-0.32	0.09	0.00	0.12
Ph.Rhythm	**0.84**	-0.33	-0.11	0.05	-0.20	-0.03	**-0.69**	0.56	-0.06	0.29	-0.19	0.18
Ratio.Du	**0.89**	-0.34	-0.07	0.07	-0.12	0.05	**-0.72**	0.56	-0.05	0.28	-0.17	0.15

Table A3. Comparison between three call types of bachelor males (spontaneous, male-directed, female-directed: Motivation Hypothesis) in blue petrels and Antarctic prions using binomial GLMMs. p-values under 0.05 are in bold.

	Blue petrels				**Antarctic prions**			
	estimate	**std. error**	***z* value**	***p*-value**	**estimate**	**std. error**	***z* value**	***p*-value**
Male-directed calls vs spontaneous*								
Frequency variables								
Intercept	-1.10	0.51	-2.15	**0.03**	-13.97	4.54	-3.08	**0.002**
PC1	0.73	0.13	5.69	**< 0.001**	-1.82	0.46	-3.93	**< 0.001**
PC2	-0.59	0.19	-3.12	**0.002**	-1.77	0.59	-2.99	**0.003**
PC3	0.51	0.20	2.53	**0.01**	0.35	0.51	0.69	0.49
PC4	-0.36	0.25	-1.47	0.14	-1.46	0.77	-1.88	0.06
PC5	1.51	0.29	5.18	**< 0.001**	0.15	0.55	0.26	0.79
PC6	0.35	0.24	1.47	0.14	-	-	-	-
Temporal variables								
Intercept	-1.16	0.70	-1.67	0.10	-2.08	0.49	-4.28	**< 0.001**
PC1	0.31	0.19	1.63	0.10	-1.28	0.22	-5.79	**< 0.001**
PC2	-0.75	0.32	-2.33	**0.02**	0.52	0.17	3.16	**0.002**
PC3	0.52	0.29	1.81	0.07	0.44	0.44	0.99	0.32
PC4	-0.44	0.40	-1.10	0.27	0.04	0.23	0.17	0.86
PC5	0.92	0.36	2.56	**0.01**	-0.24	0.21	-1.13	0.26
PC6	-2.02	0.46	-4.39	**< 0.001**	0.41	0.28	1.45	0.15
syntax								
Intercept	-23.48	6.48	-3.62	**< 0.001**	-79.67	28.43	-2.80	**0.005**
Call.NbPh	3.48	0.94	3.71	**< 0.001**	9.00	3.17	2.84	**0.004**
Ph.NbSyll	-	-	-	-	3.57	2.56	1.39	0.16
Female-directed calls vs spontaneous*								
Frequency variables								
Intercept	-1.47	0.41	-3.58	**< 0.001**	-0.48	0.33	-1.47	0.14
PC1	0.15	0.09	1.58	0.11	-0.32	0.09	-3.45	**0.001**
PC2	0.21	0.13	1.58	0.12	-0.39	0.18	-2.17	**0.03**
PC3	0.19	0.19	0.97	0.33	-0.11	0.26	-0.41	0.69
PC4	-0.66	0.17	-3.79	**< 0.001**	-0.02	0.22	-0.10	0.92
PC5	-1.62	0.34	-4.80	**< 0.001**	0.81	0.28	2.92	**0.004**
PC6	-0.32	0.23	-1.38	0.17	0.47	0.27	1.74	0.08
Temporal variables								
Intercept	-1.26	0.48	-2.61	**0.01**	-0.88	0.29	-3.09	**0.002**
PC1	0.19	0.13	1.46	0.14	0.67	0.14	4.67	**< 0.001**

PC2	-0.78	0.20	-3.99	**< 0.001**	0.22	0.13	1.71	0.09
PC3	-0.12	0.21	-0.59	0.56	0.11	0.16	0.70	0.48
PC4	0.12	0.25	0.45	0.65	0.71	0.17	4.21	**< 0.001**
PC5	-0.05	0.24	-0.19	0.85	-0.06	0.30	-0.20	0.84
PC6	-0.55	0.31	-1.78	0.07	0.31	0.25	1.22	0.22
Syntax								
Intercept	-21.49	4.61	-4.67	**< 0.001**	-10.53	2.63	-4.01	**< 0.001**
Call.NbPh	3.60	0.75	4.82	**< 0.001**	1.04	0.258	4.05	**< 0.001**
Ph.NbSyll	0.18	0.29	0.60	0.55	0.82	0.35	2.33	**0.02**
Female-directed vs male-directed calls*								
Frequency variables								
Intercept	6.31	2.84	2.23	**0.03**	-12.97	2.80	-4.63	**< 0.001**
PC1	4.24	1.16	3.65	**< 0.001**	0.01	0.57	0.01	0.99
PC2	-7.07	1.98	-3.57	**< 0.001**	0.32	1.14	0.28	0.78
PC3	6.00	2.11	2.85	**0.004**	-1.26	2.38	-0.53	0.60
PC4	5.63	2.67	2.11	**0.04**	0.03	2.17	0.01	0.99
Pc5	20.47	5.31	3.86	**< 0.001**	-0.04	2.12	-0.02	0.98
Temporal variables								
Intercept	-12.66	2.39	-5.29	**< 0.001**	-43.45	18.39	-2.36	**0.02**
PC1	0.02	0.83	0.02	0.98	-36.21	17.38	-2.08	**0.04**
PC2	0.20	0.89	0.22	0.83	-2.04	2.96	-0.69	0.49
PC3	0.67	1.32	0.51	0.61	14.65	11.26	1.30	0.19
PC4	-0.45	1.45	-0.31	0.76	-	-	-	-
Syntax								
Intercept	-32.40	11.44	-2.83	**0.005**	-30.33	7.46	-4.07	**< 0.001**
Call.NbPh	2.89	0.91	3.18	**0.001**	2.44	0.65	3.75	**< 0.001**
Ph.NbSyll	-0.34	1.05	-0.32	0.75	-	-	-	-

*: comparative reference

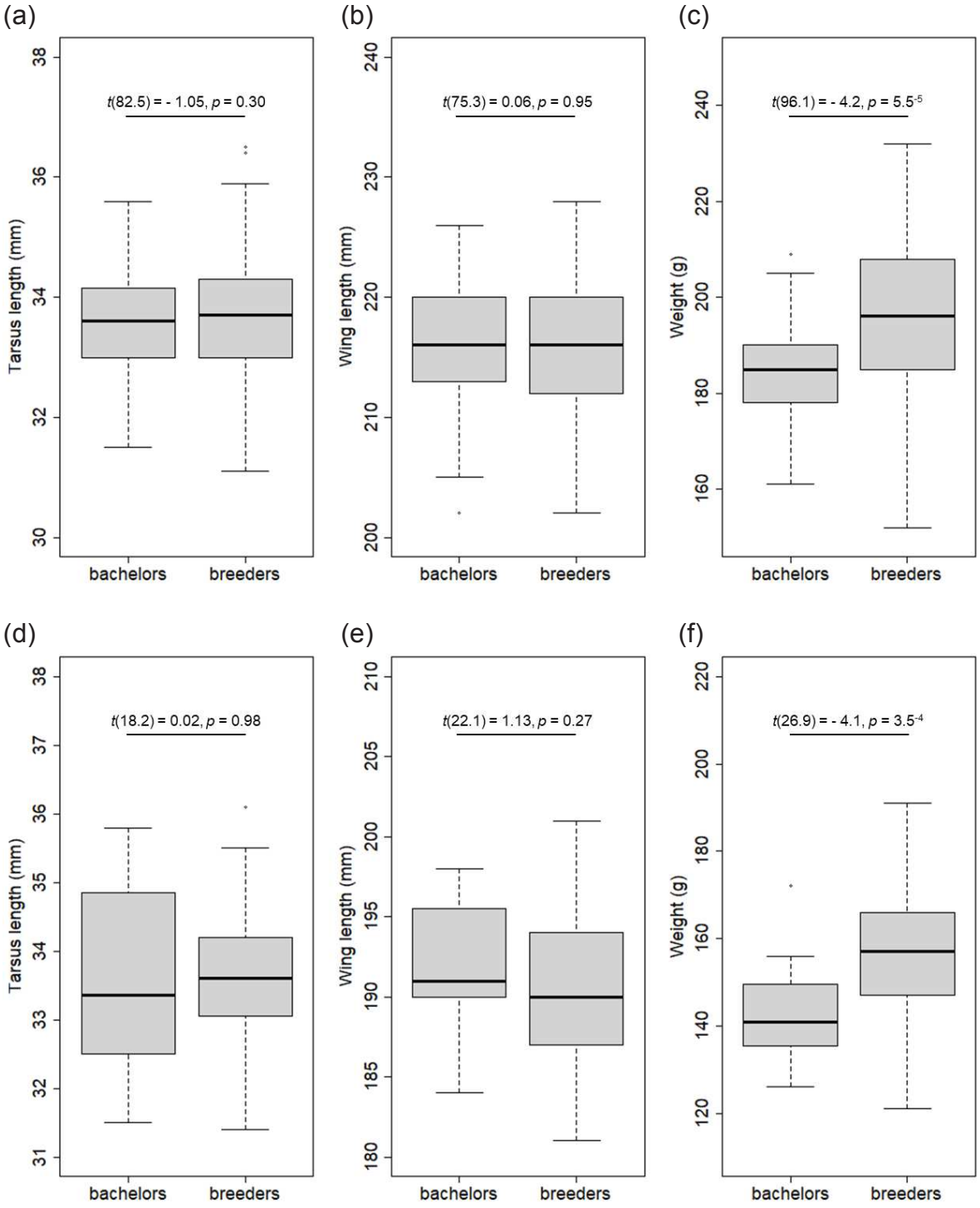
Table A4. Coordinates on the six principal components of each frequency and temporal variables describing male-directed calls of bachelor and breeder males (Breeding-Status Hypothesis) in blue petrels and Antarctic prions. Values in bold indicate the main variable in each PC (values > 0.6).

	Blue petrels						**Antarctic prions**					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Frequency variables												
A.F0	**-0.77**	0.33	-0.17	0.16	-0.08	0.30	0.33	**0.64**	-0.46	0.04	0.20	0.39
A.Q25	**-0.80**	0.16	-0.14	0.20	-0.20	0.29	**0.65**	0.44	-0.49	0.00	-0.07	-0.12
A.Q50	-0.18	-0.47	-0.42	-0.48	-0.05	-0.20	**0.87**	-0.02	-0.09	0.34	-0.02	0.04
A.Q75	0.01	**-0.80**	0.34	0.20	-0.05	0.14	**0.79**	-0.41	-0.25	0.07	0.00	0.10
B.F0	**-0.83**	0.25	-0.13	0.00	-0.01	-0.05	0.56	0.37	0.48	-0.34	-0.26	0.17
B.Q25	**-0.89**	0.07	-0.17	-0.01	-0.05	-0.20	**0.80**	0.29	-0.15	-0.10	-0.32	-0.23
B.Q50	0.03	**-0.78**	-0.27	0.00	-0.09	0.15	**0.86**	-0.05	0.29	0.11	-0.23	-0.04
B.Q75	-0.40	-0.57	0.37	0.27	-0.24	-0.34	**0.73**	-0.51	-0.13	-0.19	-0.12	0.13
C1.F0	**-0.79**	0.32	-0.19	0.21	-0.05	-0.19	0.56	0.07	**0.62**	0.08	0.37	-0.24
C1.Q25	**-0.88**	0.20	-0.15	0.19	-0.13	-0.13	**0.82**	0.29	-0.20	-0.22	0.18	-0.19
C1.Q50	-0.03	**-0.72**	-0.46	-0.13	0.05	-0.01	**0.91**	-0.13	0.15	0.03	0.14	-0.06
C1.Q75	-0.29	**-0.69**	0.52	0.21	-0.13	0.00	**0.82**	-0.38	-0.14	-0.19	0.14	0.00
D.F0	**-0.77**	-0.06	0.32	-0.44	0.14	0.13	**0.73**	0.20	0.23	0.37	-0.18	0.13
D.Q25	**-0.83**	-0.11	0.35	-0.34	0.10	0.10	**0.80**	0.36	-0.13	0.11	0.17	0.00
D.Q50	**-0.83**	-0.15	0.26	-0.39	0.09	0.09	**0.91**	-0.02	0.14	0.30	0.01	0.02
D.Q75	-0.11	**-0.60**	-0.26	0.30	0.23	**0.33**	**0.79**	-0.44	-0.09	-0.05	0.05	0.12
Ph.F0	**-0.78**	0.18	-0.09	0.05	0.18	0.06	**0.62**	0.31	0.51	-0.30	0.12	0.22
Ph.Q25	**-0.94**	-0.12	0.01	0.11	-0.12	-0.06	**0.88**	0.23	-0.26	-0.13	-0.05	-0.20
Ph.Q50	-0.24	**-0.80**	-0.34	-0.11	-0.13	-0.07	**0.95**	-0.11	0.17	0.07	-0.03	0.00
Ph.Q75	-0.34	-0.25	-0.01	0.29	**0.78**	-0.22	**0.83**	-0.46	-0.17	-0.14	0.03	0.04
Temporal variables												
A.Du	-0.16	-0.43	0.00	**0.74**	-0.27	0.14	**0.61**	0.41	**-0.63**	0.02	-0.01	0.18
B.Du	0.58	-0.39	-0.07	0.00	**0.66**	-0.14	**-0.85**	-0.08	0.25	-0.25	-0.08	-0.17
C1.Du	0.48	-0.37	-0.27	-0.41	-0.24	**0.49**	-0.29	-0.46	-0.29	**0.71**	0.20	-0.22
D.Du	0.48	-0.34	-0.30	0.18	-0.40	**-0.50**	**-0.68**	0.42	-0.09	0.14	-0.30	0.22
B.Int	0.65	0.04	**0.61**	0.03	0.02	-0.21	**0.65**	0.42	-0.57	0.01	0.02	0.07
C1.Int	0.59	0.30	-0.37	-0.28	-0.21	-0.15	-0.45	0.19	0.55	0.20	0.39	0.49
D.Int	0.57	0.36	-0.11	0.45	0.14	0.39	0.34	0.13	0.47	0.25	**-0.73**	0.02
Ph.Du	**0.75**	-0.52	0.29	-0.02	-0.07	0.08	-0.55	**0.76**	-0.10	-0.16	0.07	-0.04
Syll.Tempo	**-0.69**	-0.17	0.54	-0.22	-0.22	0.06	**0.64**	-0.39	0.28	-0.50	0.11	0.02
Ph.Tempo	**-0.79**	0.40	-0.31	0.06	0.13	-0.09	0.37	**-0.79**	-0.03	0.09	-0.12	0.33
Ph.Rhythm	-0.36	**-0.89**	-0.15	-0.06	0.11	-0.01	**-0.65**	-0.45	-0.51	-0.18	-0.14	0.15
Ratio.Du	-0.39	**-0.88**	-0.15	-0.03	0.12	-0.02	**-0.70**	-0.38	-0.48	-0.22	-0.18	0.10

Table A5. Comparison between male-directed calls of bachelor and breeder males (Breeding-Status Hypothesis) in blue petrels and Antarctic prions using binomial GLMs. p-values under 0.05 are in bold.

	Blue petrels				**Antarctic prions**			
	estimate	**std. error**	***z* value**	***p*-value**	**estimate**	**std. error**	***z* value**	***p*-value**
Frequency variables								
Intercept	-4.09	0.82	-5.01	**< 0.001**	-0.30	0.20	-1.48	0.14
PC1	-0.05	0.15	0.32	0.75	0.33	0.09	3.60	**< 0.001**
PC2	0.92	0.28	3.28	**0.001**	0.11	0.14	-0.81	0.42
PC3	-0.76	0.32	2.38	**0.02**	0.62	0.23	2.75	**0.01**
PC4	1.13	0.43	2.63	**0.01**	0.73	0.31	2.35	**0.02**
PC5	6.30	0.93	6.75	**< 0.001**	-0.22	0.28	-0.80	0.42
PC6	-1.65	0.70	-2.37	**0.02**	-1.16	0.34	-3.42	**0.001**
Temporal variables								
Intercept	-1.11	0.15	-7.38	**< 0.001**	-0.43	0.18	-2.42	**0.02**
PC1	-0.08	0.08	-0.92	0.36	0.06	0.10	0.605	0.55
PC2	-0.77	0.10	-7.35	**< 0.001**	0.03	0.12	0.25	0.80
PC3	-0.93	0.17	-5.489	**< 0.001**	-0.44	0.15	-3.00	**0.003**
PC4	-0.85	0.15	-5.55	**< 0.001**	-0.32	0.17	-1.86	0.06
PC5	-0.38	0.15	-2.46	**0.01**	-0.35	0.20	-1.77	0.08
PC6	0.41	0.16	2.56	**0.01**	0.92	0.29	3.29	**0.001**
Syntax								
Intercept	-0.82	0.69	-1.19	0.24	-0.43	2.10	-0.20	0.84
Call.NbPh	-0.13	0.02	-7.00	**< 0.001**	-0.16	0.04	-4.47	**< 0.001**
Ph.NbSyll	0.28	0.09	3.32	**< 0.001**	0.39	0.41	0.96	0.34

Figure A3. Morphological comparisons using unpaired Student's T-tests between bachelor and breeder males of the Verte population, Kerguelen archipelago: (a) tarsus length, (b) wing length, and (c) mass in blue petrels *H. caerulea* (N = 207 males); (d) tarsus length, (e) wing length, and (f) mass in Antarctic prions *P. desolata* (N = 95 males).



In blue petrels and Antarctic prions, males vocally react towards male calls and female flight calls by producing male-directed or female-directed calls, respectively. Directed calls are characterized by temporal variations and spectral modulations, providing information about the aggressive and sexual motivations of the caller. To go further, I here tested whether males vocally react in a similar manner to all females or whether the vocal investment depends on the distance between the emitter and the potential receivers. I therefore assessed the variations of the acoustic parameters related to male sexual motivation, highlighted in the previous chapter.

ARTICLE 3

Getting the timing right: Doppler Effect in female flight calls as a distance cue for male calling in two burrowing petrels

Charlène Gémard [a,b*], Francesco Bonadonna [a], Thierry Aubin [b]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

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Abstract

Blue petrels (*Halobaena caerulea*) and Antarctic prions (*Pachyptila desolata*) are burrow-nester seabirds clustering in dense colonies in sub-Antarctic areas during the breeding season. In the colony, at night, bachelor males call in individual burrows while females call flying over the colony. Burrowing habits prevents the use of visual signals and, likely to attract potential mates, males vocalize from their burrow all night long in absence of a sure audience. However, after hearing a female flight call, they intensely vocally react and produce female-directed calls characterized by acoustic modulations related to their sexual motivation. Here, we experimentally tested whether males (i) detect the frequency shifts and/or tempo variations related to the Doppler Effect in female flight calls, and (ii) use the Doppler Effect as a cue of female proximity to adjust their vocal investment accordingly. In both species, males reacted differently according to different Doppler Effects applied to female calls played back. It suggests that males detect frequency shifts and/or tempo variations, and that they use it as a distance cue. More notably, we found a positive relationship between the proximity of the flying female and males' vocal investment. Males called more intensely at approaching and close females than flying-away females. We discuss different hypotheses to explain this behaviour.

Keywords: Doppler Effect, vocal communication, sexual signal, seabirds, burrowing petrels

Introduction

Vocal signals, such as calls and songs, are commonly used in many crucial social interactions such as offspring-parent interactions, group coordination, predator avoidance (Bradbury & Vehrencamp, 2011). Vocal signals are also involved in mate attraction, rival competition, and territory defence (Catchpole & Slater, 2008). Vocal signals are thus likely to affect the fitness and to be under severe evolutionary pressures. They may have evolved because they reliably provide information from signaller to receivers (e.g., signaller identity: Searcy & Nowicki, 2005; motivation and emotion: Marten et al., 1977; Briefer, 2012; qualities: Ballentine et al., 2004; Byers et al., 2016) and because they have an effective effect on the receiver behaviour (Rendall et al., 2009). Although many studies focused on the informative content of vocal signals and their effect, the first step of any communication is that receivers actually detect and correctly discriminate the signals (Endler & Basolo, 1998).

Between their emission by the signaller and their reception by a receiver, vocal signals propagate in the atmosphere where they are degraded and attenuated (Wiley & Richards, 1978, 1982) with the risk that the receiver does not perceive nor discriminate the message. Vocal signals are also sensitive to interfering abiotic and biotic sounds that may blur or mask the signal ("noises", Brumm & Zollinger, 2013). For instance, the abiotic noises generated by climatic processes (e.g., wind, rain, moving water) generate strong interferences, especially in close habitats. Vocalizations of conspecifics and heterospecifics also interfere and impair the extraction of information. The resulting reduction of the communicative potential of vocal signals may consequently affect the fitness of the signaller (Brumm & Zollinger, 2013).

To avoid masking interferences, several strategies have been highlighted in birds. In noisy environments such as urban areas or animal aggregations, birds increase the amplitude (Lombard Effect: see Brumm & Zollinger, 2013 for a review), the minimum frequencies (Luther & Derryberry, 2012), or the redundancy (Catchpole & Slater, 2008) of their vocalizations according to the ambient noise. Another strategy to boost the signal-to-noise ratio is to reduce the noise. Some species vocalize when environmental conditions are the most appropriate for sound propagation (e.g. dawn choruses of birds: Kacelnik & Krebs, 1983, but see Catchpole & Slater, 2008 for a critic) or when the ambient noise is low

(e.g., tawny owls *Strix aluco* during rainy periods: Lengagne & Slater, 2002). Finally, in bird communities, song divergence based on the displacement of spectral and/or temporal acoustic parameters limits heterospecific interferences (Grant & Grant, 2010; Planqué & Slabbekoorn, 2008)

Due to attenuation, degradation, and interferences, vocal signals do not propagate indefinitely and may be detected at a maximum certain distance, namely the active space (Marten et al., 1977; Larsen, 2020). The shorter the distance to the sound source, the better chance of reliably perceive the signal (Wiley & Richards, 1978, 1982). The signal natural degradation/attenuation is not always a burden: receivers may use it as acoustic cues of the distance from the signaller. In birds, males vocally react according to the signal degradation: the reaction is more intense to undegraded songs mimicking a close rival than to degraded song mimicking a distant rival (McGregor & Krebs 1984; Mathevon et al 2008; but see Fotheringham & Ratcliffe, 1995). More specifically, amplitude decrease, high-frequency attenuation, and reverberation of the signal - either combined or independently - are auditory cues used by songbirds to estimate distance (see Naguib & Wiley, 2001 for a review).

In situations where the sender and/or the receiver is moving, they may use other distance cues such as binaural cues, intensity changes, reverberation, and Doppler Effect (Rosenblum et al., 2000). Doppler Effect is a change in the frequency and wavelength of the perceived acoustic sound. It occurs when the distance between the signaller and the receiver varies because the signaller and/or receiver is moving (Doppler, 1842). A well-known example is the siren sound that seems higher-pitched with a faster tempo when the vehicle approaches you, then lower-pitched with a lower tempo when it leaves. Except for species using echolocation and humans, very few studies investigated the role of the Doppler Effect. In birds, first evidences suggest that homing pigeons might detect frequency shifts (Quine & Kreithen, 1981). One may hypothesize that the Doppler Effect may be a cue of the signaller position, but to our knowledge, it has never been tested.

To address this question, we studied blue petrels *Halobaena caerulea* and Antarctic prions *Pachyptila desolata*, two burrow-nester seabirds living in sub-Antarctic islands. These areas are known for their extreme climatic conditions, such as high humidity and strong winds throughout the year. During the breeding season, burrowing petrels gather in dense colonies where birds vocalize only at night. Both unpaired males and females vocalize males from their burrow, and females when flying

above the colony. Despite environmental constraints and conspecifics interferences, acoustic is one of the main channels for long-range signalling (Warham, 1990; Bretagnolle, 1996). Spontaneous calls of males are sexual signals implied in female mate choice (Bretagnolle, 1996; Gémard et al., 2021; Warham, 1990). Spectral and temporal modulations, which characterized female-directed calls, translate the sexual motivation of the caller (Gémard et al., *in press*). Female flight calls may also be sexual signals to stimulate males, as males vocally react after hearing them.

We may hypothesize that males maximise their chance of being detected by adjusting their vocal investment according to the female proximity. Because of the burrow, flight calls are the only cue signalling the female presence to males. Female movement and male immobility induce a Doppler Effect in female flight calls, which may be a distance cue for a male receiver. Using playback experiments in the field with blue petrels and Antarctic prions, we tested whether males detect Doppler Effect in female flight calls and adjust their vocal response accordingly. Based on the game theory (Smith, 1984), we expected males to vocally invest more when females are the most likely to detect them, i.e. when close.

Material and methods

Study site

Fieldwork was performed in a colony of blue petrels and Antarctic prions in a small island of the Kerguelen archipelago, Southern Indian Ocean (Ile Verte, 49°51′ S, 70°05′ E). Experiments were carried out on 18 male blue petrels and 11 male Antarctic prions, during their respective 2018's breeding season (from November 25 to December 12, 2018 on blue petrels; from December 23, 2018 to January 16, 2019 on Antarctic prions).

Synthesis of Doppler signals

To avoid pseudoreplication, for each species, we built four playbacks series, each series consisting in three female's calls: a call without Doppler Effect simulating a not-moving close female, a call with a Doppler Effect simulating an approaching female, a call with a Doppler effect simulating a female flying away. To do so, we recorded flight calls of four females in the same petrel and prion colonies in 2017 (four female blue petrels and four female Antarctic prions) using a directional Sennheiser K6-ME66 microphone (frequency response: 40-20 000 Hz ± 2.5 dB; all uncertainties in mean ± SD

otherwise stated) connected to a Marantz PMD 660 digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). Microphone was stationary when recording flying females to preserve the perception of a Doppler Effect, similarly to the males' perception of females' flight calls.

To simulate a female with different flight paths, we extracted two phrases with limited Doppler Effect (i.e., phrases emitted when the female was flying just above the microphone or very closely) from the complete flight calls of each recorded female. The playback calls simulating a close female consisted in the extracted two phrases. Playback calls simulating an approaching or a flying-away female were synthetized from these two phrases using the "Doppler Effect" function in the digital audio editor GoldWave v6.51 (GoldWave Inc, 2020). For each species, we artificially applied a Doppler Effect by increasing or decreasing the frequency of the call with limited Doppler Effect stimulating a close female (playbacks sonograms in Figure A1). The frequency shift was calculated using the formula: $f' = \left(\frac{v \pm v_0}{v \pm v_s}\right) f$ with v the wave propagation speed, v_0 the observer speed, v_s the sound-source speed, f the sound frequency and f' the frequency perceived by the observer. Here, we considered a static observer so v_0 = 0. We also considered v = 331 m/s which corresponds to the wave-propagation speed at 0°C, and v_s = 14 m/s (unpublished data based on maximum flight speed measured on eight petrels equipped with GPS in the same colony in 2014). For both species, blue petrels and Antarctic prions, we synthesised 12 Doppler signals from four females (signal total duration: 4.0 ± 1.2 s; 4.7 ± 1.0 s, respectively).

Playback experiment

We carried out our playback experiment during dark nights (Mougeot & Bretagnolle, 2000) and the hours of maximal vocal activity in the colony (22:00-02:00). To limit background noises, we carried out playback sessions during quiet nights (wind speed < 4 km.h^{-1} and no rain).

The playback sessions (one per tested male) consisted in broadcasting the three calls of a playback series. Prior to each playback session, we randomly located in the colony a bachelor vocalizing from its burrow. The recording equipment was then positioned on the ground, at the burrow entrance. It consisted in an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20-20 000 Hz ± 2.5 dB) connected to a Marantz PMD 660 digital recorder. We waited a few minutes before starting the

experiment to ensure that the tested individual had a natural and spontaneous vocal activity, and that it did not react to the recorder presence. We then recorded spontaneous calls for four minutes, before we randomly selected one of the four playback series. Considering that the sound pressure level of a male in its burrow was 66.3 ± 9.6 dB for Blue petrels and: 68.1 ± 11.0 for Antarctic prions (Gémard et al., in press), and that females may call at the same amplitude than males because there is no sexual dimorphism in both studied species, natural amplitude of female flight calls was estimated to be similar to male calls. Thus, we broadcast playbacks at about 65 dB using a TASCAM DR-07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits) positioned at one meter high, close to the burrow entrance. We then mimicked a natural situation where an attracted female flies very close to the burrow (less than two meters, Gémard et al., in press). To avoid an order effect, the three playback calls of the selected series (without Doppler Effect or simulating an approaching female or a flying-away female) were broadcasted in a raw with a random order and a four-minute interval of silence between them (Figure 1). According to our observations during previous experiments, a four-minute interval includes one minute of vocalization in reaction of the playback, one minute for the tested male to get back to its natural vocal rate, and two minutes of natural spontaneous vocal rate. Female-directed calls emitted by the burrow owner were recorded from the start of the playback for 18 minutes (that includes the whole playback and the replay of the burrow owner; Figure 1). Each male was recorded only once. To avoid testing males twice, coloured markers labelled burrow entrance of already-tested males. In total, we stimulated 18 blue petrel males and 11 Antarctic prion males.

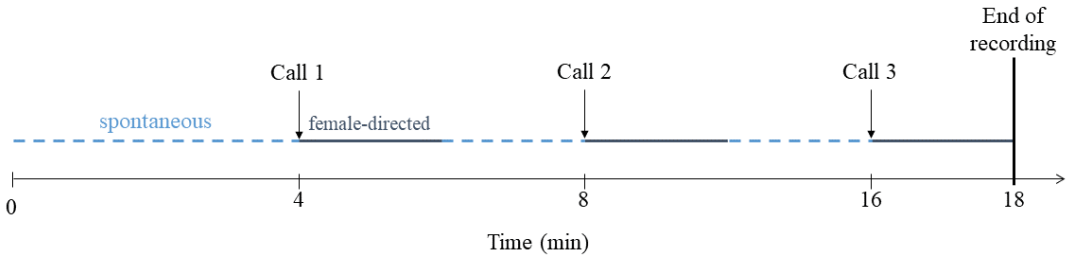

Figure 1. Playback experimental design. The three playback calls were randomly broadcast with a four-minute interval. Spontaneous (dashed blue lines) and female-directed (solid black lines) calls of the tested bachelor males were recorded.

Acoustic analyses

Acoustic analyses on the recorded calls were performed using the signal processing software Avisoft–SASLab Pro v 5.2.11 (Specht, 2017). We preliminarily down sampled the records from 44.1 to 11.025 kHz to increase the precision of the frequency measurements. We also high-passed filtered (cutting frequency: 0.10 kHz, Fast Fourier Transform (FFT) filter) the records to remove the low-frequency background noise.

Burrowing petrels produce stereotyped calls consisting in four syllable types, referred from "A" to "D" (see Bretagnolle ,1996 and Gémard et al., *in press* for sonograms). In our analyses, we considered only complete calls (i.e. produced with the four syllable types). Recorded calls were measured in both temporal and spectral domains. The parameters chosen were those related to sexual motivation in our studied species (Gémard et al., *in press*, summarized in Table 1). In blue petrels, we selected the duration of B syllable, phrase tempo, fundamental frequency and the two first energy quartiles of A (q25, q50), and the number of phrases per call, which all increase with sexual motivation; and the third energy quartile of B (q75), which decrease with sexual motivation. In Antarctic prions, we selected the duration of A syllable, phrase tempo, fundamental frequency and energy quartiles of the phrase (q25, q50, q75), and the number of phrases per call, which all increase with sexual motivation. We measured these parameters using automatic extraction tools based on similar pre-sets to ensure replicable measurements: temporal variables on the amplitude envelopes using the "Pulse Train Analysis" of Avisoft-SASLab Pro with a resolution of 11.6 ms; spectral variables on linear amplitude spectra with a resolution of 22 Hz.

Table 1. Acoustic parameters related to sexual motivation in two burrowing petrels

	Sexual motivation		Sexual motivation
Blue petrels		**Antarctic prions**	
B duration	↗	A duration	↗
Phrase tempo	↗	Phrase tempo	↗
A F0	↗	Phrase mean F0	↗
A q25	↗	Phrase q25	↗
B q75	↘	Phrase q50	↗
Phrases per call	↗	Phrase q75	↗
		Phrases per call	↗

↗ indicates positive relationship whereas ↘ indicates negative relationships

Statistical analyses

We aimed to test whether the three vocal responses to playback calls can be discriminated based on acoustic parameters. We performed a Within-Class Analysis (WCA) using the ade4 package under the R software environment version 3.4.4 (Dolédec & Chessel, 1987; R Core Team, 2018). WCA is a particular case of Principal Component Analysis used to reduce the multidimensionality of the data while taking into account a factor, here the identity of the tested male. This method thus maximises the within-individual inertia rather than the between-individual inertia (Thioulouse et al., 2018). We kept the two first axes of the WCA, labelled RS1 and RS2, which explained more than 60% of the total inertia in both species (WCA results in Figure A2).

For both species, we used a linear model to model the vocal reaction (WCA axes) as a function of the covariate "Doppler Effect" (categorical with three levels). The three playback types in a random order stimulated all males. We thus added the "playback order" as a covariate (categorical with five levels in blue petrels, three in Antarctic prions) in our models. We plotted residuals versus fitted values to verify model assumptions.

Results

We tested 18 male blue petrels and 11 male Antarctic prions of which 11 blue petrels and 6 Antarctic prions vocally replied to playbacks. The others did not react to any of the three playback types.

In blue petrels, WCA results show that both axes $RS1_{bp}$ and $RS2_{bp}$ positively correlate with acoustic parameters indicating the caller's sexual motivation. More precisely, the first axis $RS1_{bp}$ (53.8% of total inertia) positively correlates with the phrase tempo, the fundamental frequency F0 and the first energy quartile q25 of syllable A. The second axis $RS2_{bp}$ (19.8% of total inertia) positively correlates with the number of phrases per call (Figure 2). Model results show a positive trend between male sexual motivation and approaching females (Table 2). Male sexual motivation ($RS2_{bp}$) is significantly higher when the female is approaching than when it is close (estimate = - 0.76 ± 0.26; t value = - 2.97; p = 0.004), or possibly flying away (estimate = -0.50 ± 0.26; t value = -1.92; p = 0.06). This suggests that males were sexually more motivated towards an approaching female than towards a female flying away or close.

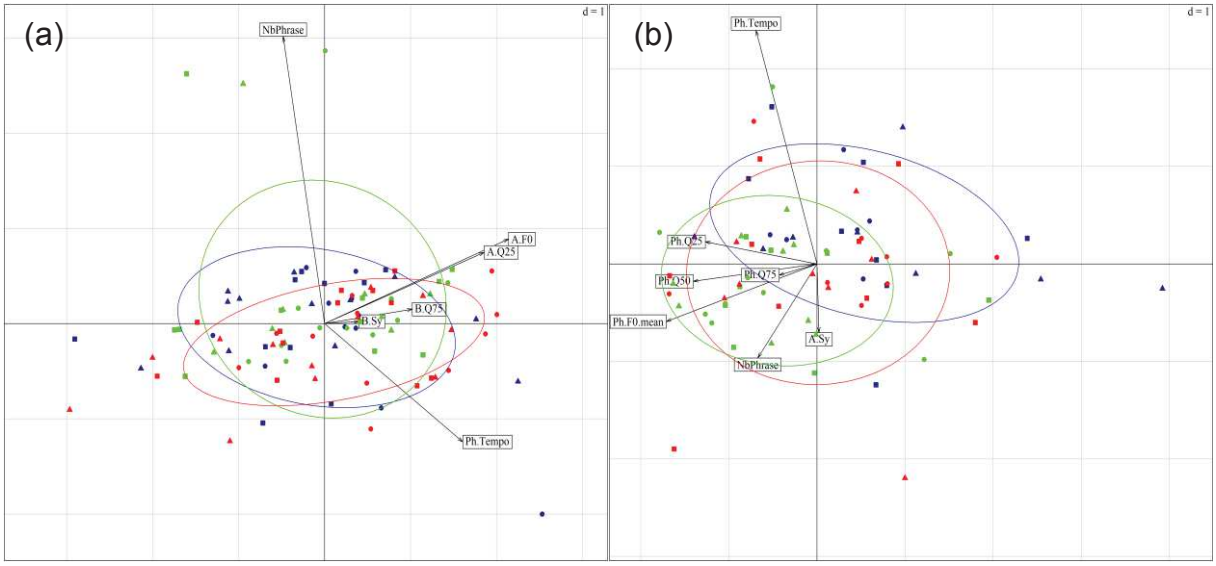

Figure 2. Biplot of the WCA for acoustic parameters related to sexual motivation in female-directed calls of males in two burrowing petrels: (a) blue petrels, and (b) Antarctic prions. Colours represent the female flight path from the male perspective (green: approaching; red: close; dark blue: flying away).

In Antarctic prions, both WCA axes $RS1_{ap}$ and $RS2_{ap}$ negatively correlate with acoustic parameters indicating the caller's sexual motivation. More precisely, the first axis $RS1_{ap}$ (44.8% of total inertia) negatively correlates with the phrase frequencies (F0, q25, q50, q75) and the number of phrases per call. The second axis $RS2_{ap}$ (18.0% of total inertia) positively correlates with the phrase tempo (Figure 2). Model results show a negative significant relationship between WCA axes and female approaching or close (Table 2). Male sexual motivation ($RS1_{ap}$ and $RS2_{ap}$) does not significantly vary when the female is close or approaching (estimate = 0.43 ± 0.27; *t* value = - 1.6; $p = 0.11$; and estimate = 0.12 ± 0.27; *t* value = 0.44; $p = 0.66$; respectively). This suggests that males were sexually more motivated towards an approaching or close female than towards a female flying away.

In both species, the playback order had no significant effect on the vocal response of the tested males (Table 2).

Table 2. Effect of female proximity on male vocal investment.

	RS1				RS2			
	Estimate	SE	*t* value	*p* value	Estimate	SE	*t* value	*p* value
Blue petrels								
Intercept	-0.061	0.248	-0.247	0.805	-0.070	0.237	-0.295	0.768
Approaching female	0.038	0.270	0.140	0.889	**0.496**	**0.258**	**1.921**	**0.058**
Close female	0.161	0.262	0.616	0.540	-0.269	0.251	-1.072	0.287
Playback Order 2	-0.028	0.305	-0.092	0.927	0.092	0.291	0.314	0.754
Playback Order 3	-0.100	0.780	-0.128	0.898	0.339	0.746	0.454	0.651
Playback Order 4	0.023	0.655	0.036	0.971	-0.426	0.627	-0.680	0.498
Playback Order 5	0.003	0.260	0.013	0.989	-0.007	0.248	-0.027	0.978
Playback Order 6	-0.038	0.566	-0.068	0.946	-0.044	0.541	-0.081	0.936
Antarctic prions								
Intercept	0.479	0.241	1.986	0.051	0.447	0.247	1.805	0.076
Approaching female	**-0.913**	**0.279**	**-3.268**	**0.002**	**-0.711**	**0.287**	**-2.480**	**0.016**
Close female	-0.481	0.284	-1.695	0.095	**-0.588**	**0.291**	**-2.023**	**0.047**
Playback Order 2	0.067	0.340	0.197	0.844	0.037	0.349	0.106	0.916
Playback Order 3	0.046	0.304	0.153	0.879	0.034	0.312	0.109	0.914
Playback Order 4	-0.014	0.297	-0.045	0.964	-0.004	0.305	-0.013	0.990

Intercept is the playback calls with a Doppler Effect simulating a female flying away, broadcast with the playback order no. 1

Discussion

For the first time, we experimentally tested whether birds detect Doppler Effect in conspecifics flight calls, and whether they use it as a distance cue to adjust their vocal behaviour accordingly. Results of our field playback experiment showed that males of two burrowing-petrel species, blue petrels and Antarctic prions, reacted differently to signals with different Doppler Effect broadcast to them. More notably, males of both species responded more intensely to an approaching than a flying away female. Antarctic prion males also responded more intensely to a close female than to a females flying away.

Our results show that males reacted to all three playback types but with subtle vocal variations. In our experimental design, we specifically controlled for the intrinsic vocal characteristics of the female, and especially for possible acoustic cues of distance such as intensity and other distance-dependent degradations (Naguib & Wiley, 2001). All signals tested come from female calls recorded at close range and emitted at the same intensity. Thus, the Doppler Effect, i.e. the modifications of intensity and tempo, appears to be the only factor that modulates the vocal response of males. This result is consistent with a

first paper in homing pigeon, in which authors suggested that pigeons might be able to detect subtle frequency shifts. However, in this paper, acoustic parameters like amplitude were not experimentally controlled and tempo variations were not tested (Quine & Kreithen, 1981).

More notably, results show that males of both species responded more intensely to close or getting close females, than to females flying away. In birds, and more generally in non-echolocating species, this is an exciting finding of the use of the Doppler Effect as an auditory cue, and the first indication of vocal adjustment based on this cue. One may wonder why it would be advantageous for males to invest vocally more when the female is close or approaching. A possible explanation is that female flight calls are not all equally detectable. In theory, frequencies and amplitude of an approaching caller seem higher and thus easier to detect (Dooling, 1982; Klump, 2000; Park & Dooling, 1991). This explanation seems poorly plausible as males reacted to all three playback types and we specifically controlled amplitude in our experimental design. Another explanation is that males may be more stimulated by females calling with high frequencies and/or high tempo. Preferences for these acoustic parameters have been tested in blue petrel females (Gémard et al., in press) and indeed females are more attracted by high-pitched male calls than low-pitched ones, but they show no preference for calls with a high or low syllable rate. Nonetheless, females and males may be attracted by different acoustic parameters and the attractiveness of female calls for males have not been tested so far.

A last explanation for the more intense vocal response of males toward close females is that the informative potential of vocal signals decreases with distance. A female flying above the burrow has more chances than a distant female to locate the caller and to reliably extract the call information. Conversely, males are also more likely to perceive the message carried by female flight calls if the female is close. Reliable information extraction allow a reliable assessment of a potential mate and would benefit to both male and female, especially in long-lived monogamous species with bi-parental responsibilities, such as burrowing petrels, because mate choice is likely to be mutual (Trivers, 1972). Consequently, both males and females should favour signals efficiently perceptible. In burrowing petrels, males may thus react more strongly to close females (or getting close) because they are the most likely to detect and perceive each other (Smith, 1984).

According to the game theory (Smith, 1984), males should vocally react only to closest females, and not to all female flight calls as shown in our results. It may be the consequence of a strong intra-male competition. Female-directed calls addressed to distant females may be enough to deter other males to compete vocally for mates. Female-directed calls addressed to females actually able to extract reliably the informative content of male calls may be a real demonstration of the caller motivation. Males may be opportunistic, maximising their chances to be visited by a female but they may demonstrate a certain strategy by adjusting their vocal behaviour to the probability of being reliably detected and perceived.

Our results are consistent with previous studies showing that birds estimate the distance to a potential mate and adjust their vocal investment accordingly. In zebra finches, males sing louder when females are further away, likely to ensure signal transmission (Brumm & Zollinger, 2013). Proximity-dependant vocal investment is not restricted to mate choice and may occur in many social behaviours, including territorial defence in songbirds (e.g., great tits *Parus major*, meadowlarks *Sturnella neglecta*, Carolina wrens *Thryothorus ludovicianus*: reviewed in Naguib & Wiley, 2001), risk avoidance (e.g. yellow-bellied marmots *Marmota flaviventris:* Blumstein et al., 2004), and antiphonal calling (e.g. common marmoset *Callithrix jacchus*: Choi et al., 2015).

Previous experiments have provided numerous illustrations of sound degradation as distance cues, but there remains a need for investigations on moving vocal cues. Despite the huge number of species emitting calls in flight, the available examples seem restricted to echolocating species (e.g. horseshoe bats, killer whales) and humans. Here, we report the results of an experimental design to show that males perceive Doppler Effect in females' flight calls and modulate their vocal response accordingly. We found encouraging results on the use of Doppler Effect as an acoustic cue to estimate the distance to a conspecific. Males vocally invest more when the female is close or approaching, maybe because calls of close and approaching females are more reliably detectable or more attractive. An alternative hypothesis is that close or approaching females are most likely to locate callers and perceive their message. These hypotheses are not mutually exclusive. We strongly hope that this study opens new leads in the understanding of display-flight calls. Soaring species, such as most seabirds, are particularly relevant models to investigate the implication of moving vocal cues in mate choice.

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Conflict of interest – The author declare no conflicts of interest associated with this study.

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Permits – This study was performed according to 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.

Data availability – Data generated for this study will be available in a data repository at the time of submission.

Authors' contributions – All authors made substantial contributions to conception of experiment, analysis and interpretation of data, and critical review of the manuscript. CG, FB and TA contributed to the study conception and design. CG performed material preparation and data collection on the field. CG statistically analysed the data. The first draft of the manuscript was written by CG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Appendices

Figure A1. Sonograms of playback types with an artificial Doppler Effect in blue petrels (top) and Antarctic prions (bottom): (a) approaching blue petrel female, (b) close blue petrel female, (c) flying-away blue petrel female, (d) approaching Antarctic prion female, (e) close Antarctic prion female, (f) flying-away Antarctic prion female.

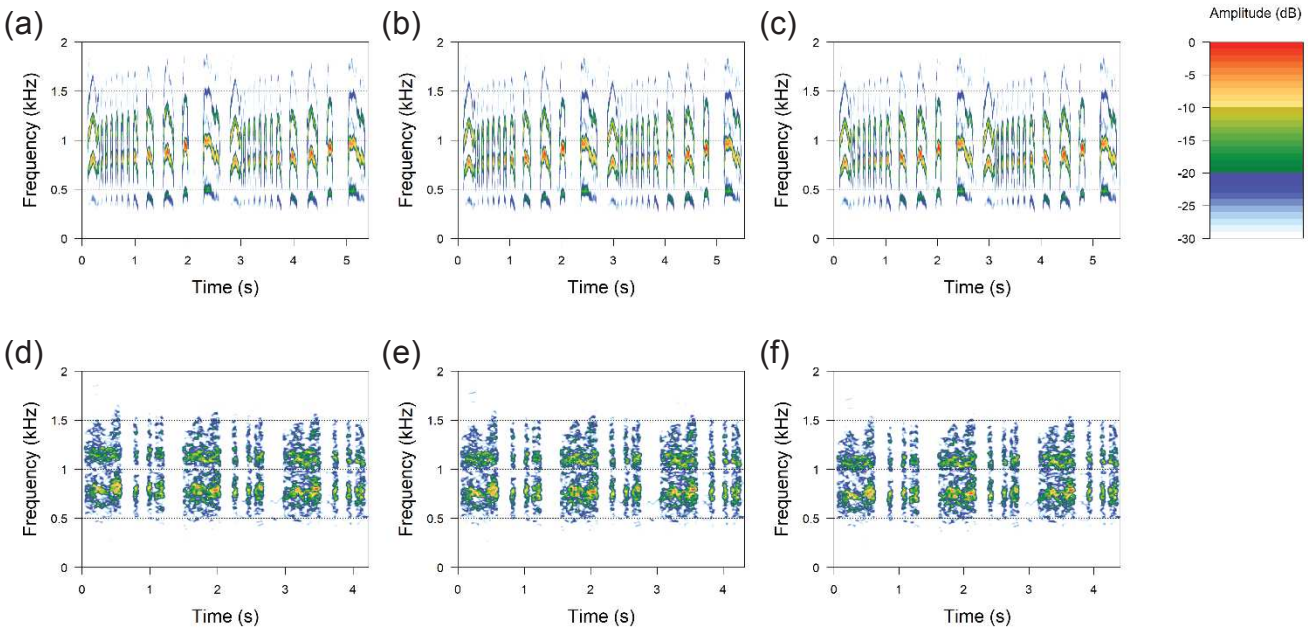
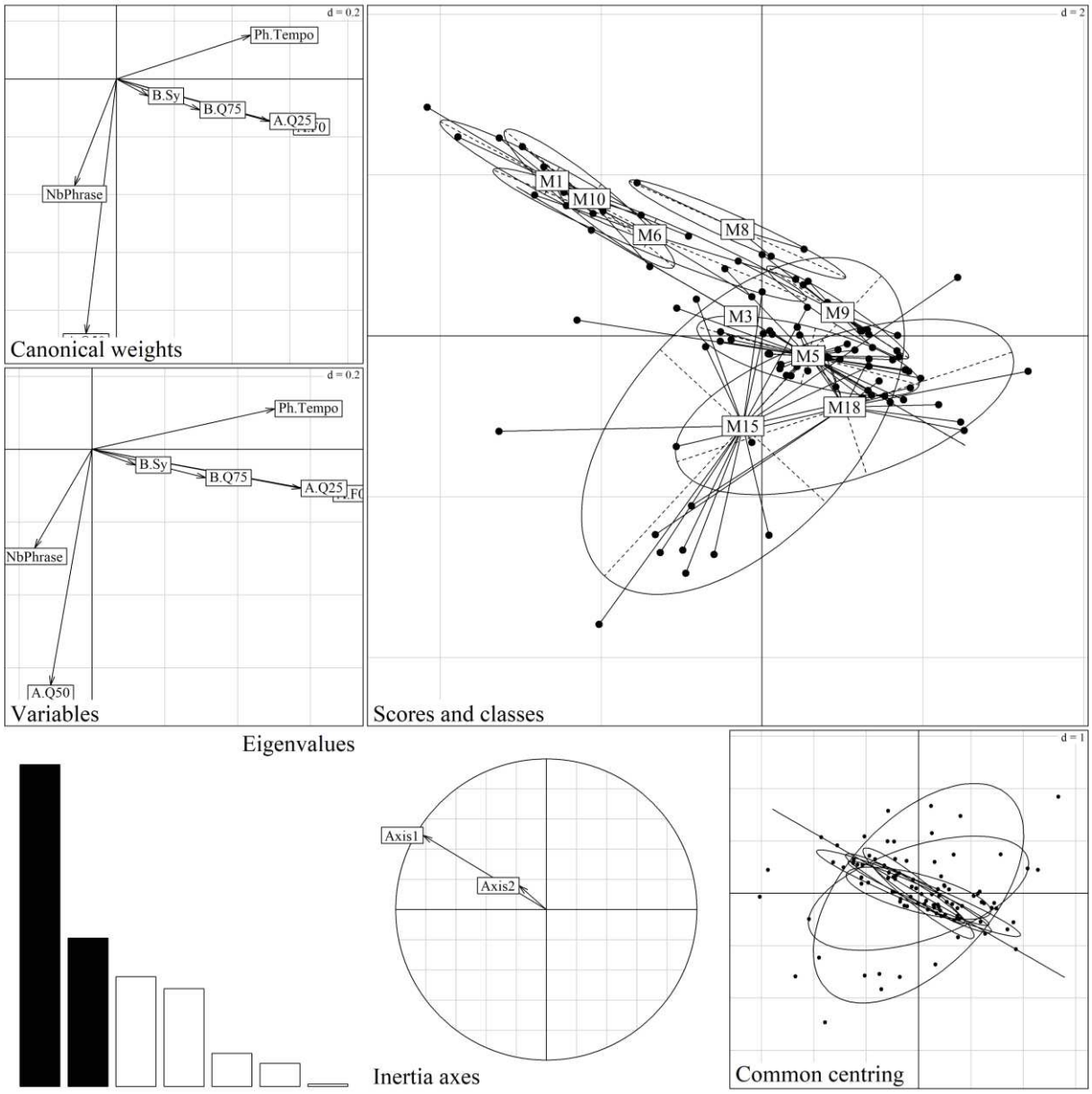
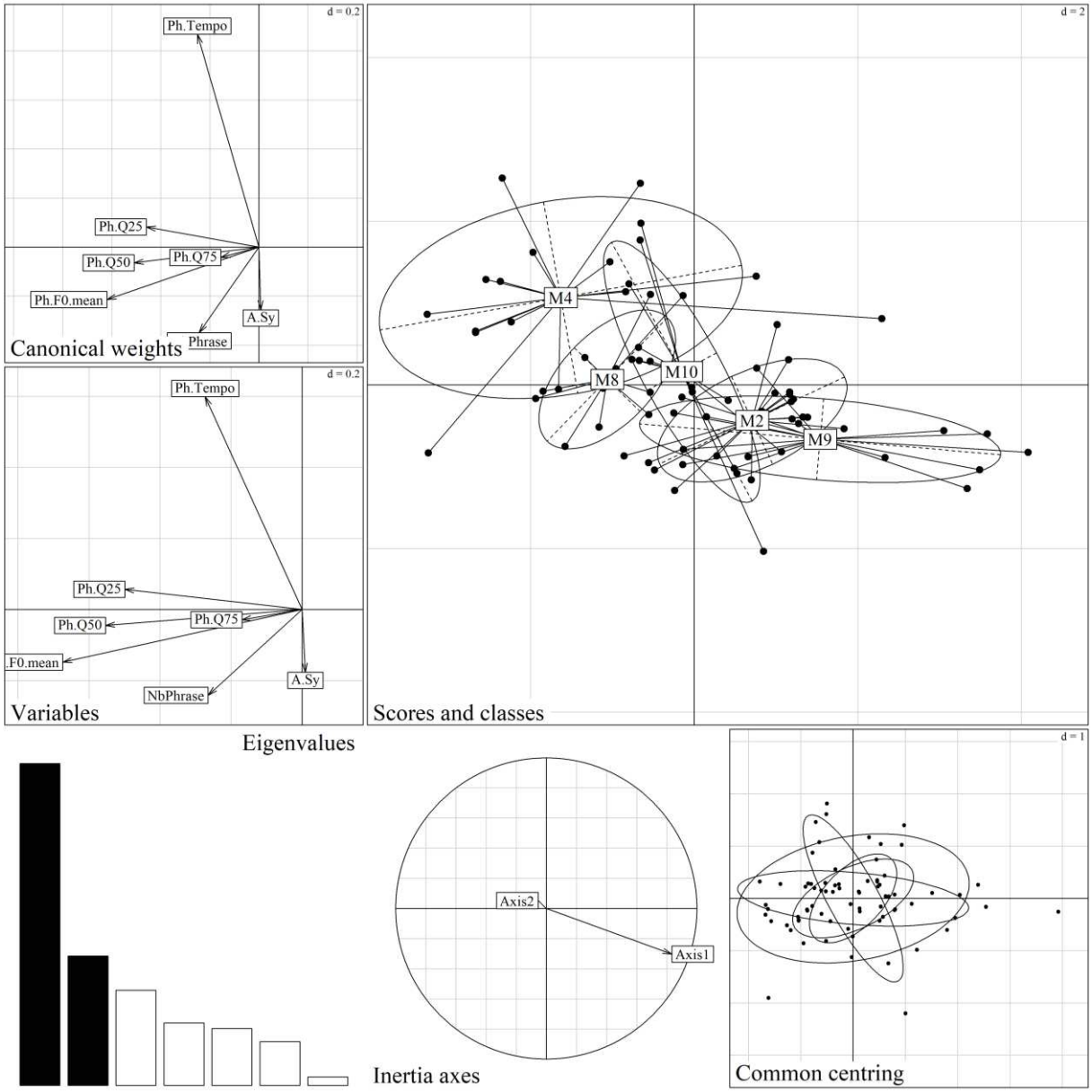


Figure A2. Within-Class Analysis (WCA) plots in (a) blue petrels and (b) Antarctic prions: : species loadings, species scores, eigenvalues screeplot, projection of principal axes on within-class axes, sites scores, projections of sites and groups (i.e. playback types) on within-class axes.

(a)



(b)


d = 0.2
Ph.Tempo
Ph.Q25
Ph.Q50
Ph.Q75
Ph.F0.mean
A.Sy
Phrase
Canonical weights
d = 2
M4
M8
M10
M2
M9
d = 0.2
Ph.Tempo
Ph.Q25
Ph.Q50
Ph.Q75
.F0.mean
A.Sy
NbPhrase
Variables
Scores and classes
Eigenvalues
Axis2
Axis1
Inertia axes
d = 1
Common centring

CHAPTER III

INFLUENCE OF MALE CALLS IN FEMALE MATE CHOICE

Signals provide information underlying the emitter's qualities, and can thus alter the behaviour of the receivers. In the two preceding chapters, I investigated both static and dynamic information provided by male calls in blue petrels and Antarctic prions. I showed that acoustic parameters of male calls are related to physical characteristics and motivation of the caller. In this chapter, I assessed whether the informative content of male calls influences female mate choice by experimentally testing the attractiveness of acoustic parameters previously highlighted.

ARTICLE 4

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

Charlène Gémard[a,b*], Thierry Aubin[b], Eliette L. Reboud[a], Francesco Bonadonna[a]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

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Abstract

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

Keywords: vocal communication, sexual signal, attractiveness, mate choice, seabird, blue petrel

Introduction

In animal species, mating is not random and the probability of mating with a given individual of the opposite sex increases with some behavior patterns (Halliday, 1983). According to theoretical and empirical studies, in many species, both males and females should profit from being choosy when selecting their mating partner (Andersson, 1994; Bakker and Pomiankowski, 1995; Courtiol et al., 2016). They rely on attractive signals that inform them about the signaler's qualities (Smith 1991). Although sexual signals are often multimodal, the implication of vocal signals in mate choice has been well documented in many taxa (reviewed in Bradbury & Verhencamp, 1998). Male vocalizations, apart from their role in male-male competition, attract potential mates in insects (Walker, 1957), fish (Amorim et al., 2006), frogs (Ryan, 1980), bats (Knornschild et al., 2017), songbirds (Mountjoy & Lemon, 1991), and non-songbirds (Gibson, 1989; Martín-Vivaldi et al., 1999).

Mate choice using vocalizations is influenced by (i) the selection of certain acoustic parameters in the absence of the signaler and (ii) that these acoustic parameters correlate with mating success in natural conditions (Searcy & Andersson, 1986). Well-known examples of attractive acoustic parameters in birds and mammals are a low fundamental frequency (F0 or pitch), a high vocalizing rate, long vocalizations, and vocalizations consisting in many elements (reviewed in Nowicki & Searcy, 2005). These parameters reflect some overall qualities, such as morphological characteristics (e.g., body size: Ballentine et al., 2004; Ballentine, 2009; Byers et al., 2016; Favaro et al., 2017; Kriesell et al., 2018; bill morphology: Christensen et al., 2006), endurance, and fighting abilities (McComb, 1991). These parameters are also related to breeding success in natural conditions (Chastel et al., 1995; Salton et al., 2015). For instance, in red deer (*Cervus elaphus*), females are preferentially attracted by high roaring rate and low-pitched roars, emitted by large males, which have a better reproductive success than small males (Reby et al., 2010). In several songbird species, females are more attracted by males singing with a high song rate, which have a better territory quality, body condition, or feeding rate, and thus a higher reproductive success (reviewed in Marler & Slabbekoorn, 2004).

Most of our knowledge on vocal signal implication in mate choice focuses on songbirds. Comparatively, non-songbirds, such as seabirds, have been poorly documented, although mate choice

is crucial in these species due to their particular breeding ecology (reviewed in Bried & Jouventin, 2001; Schreiber & Burger, 2001). Seabirds have distinct feeding and nesting areas: they feed at sea, while they breed on land. This implies obligatory bi-parental care and cooperation between mates during the whole breeding cycle. Burrowing petrels (Procellariiformes) are colonial seabirds breeding in self-dug burrows on coastal grass slopes (Warham, 1990), to which they show a high fidelity year after year (Bried & Jouventin, 2001). These monogamous species also show lifelong fidelity to their mate, and divorces and extra-pair copulations are rare (Jouventin & Mougin, 1981; Warham, 1990, 1996; Quillfeldt et al., 2012). Moreover, parental investment is high despite the small clutch size (one egg per year with no possibility of replacement clutch) and reproductive success is based on parents' cooperation and synchrony (Warham, 1990, 1996). Consequently, with respect to species that can change partner at each breeding, correcting possibly wrong choices, choosing the wrong partner will affect the lifelong fitness more drastically in petrels than in other species.

Mate choice in burrowing petrels appears to rely on male calls, emitted at night from burrows while females fly calling over the colony. After hearing a male call, females can land close to the sound source, then enter the caller's burrow. On the contrary, empty burrows do not attract females (James, 1985). Females visit several males for a couple of years before pairing (Bretagnolle, 1996), suggesting that the mate choice by females is active, and that male calls attract and/or stimulate potential mates (Bretagnolle, 1990; Warham, 1990). More precisely, female mate choice may be influenced by information carried by male calls, such as the caller's morphological characteristics (Genevois & Bretagnolle, 1994; Gémard et al., 2019), linked to male overall qualities and reproductive success. For instance, big blue petrel males with a long, thin bill produce high-pitched calls consisting of many syllables. Because bill morphology may determine the filtering surface in filter-feeding species like petrels, these males might have a better filter-feeding efficiency (Klages & Cooper, 1992). Blue petrel males with long and thin wings (i.e., high aspect ratio: Pennycuick, 1982) produce fast calls (high syllable rate). Considering the soaring flight mode of petrels, these males may be able to travel over longer distances to feed (Pennycuick, 1982). Consequently, they may have a better feeding rate (Chastel et al., 1995; Weimerskirch et al., 1995). Nevertheless, calling in the colony may be considered intriguing as this behavior exposes petrels to predators, especially the brown skua (*Stercorarius antarcticus*) which

uses the calls of petrels (mostly blue petrels *Halobaena caerulea* and prions *Pachyptila* spp.) to locate and catch them (Mougeot & Bretagnolle, 2000b).

Considering the high predation cost associated with their production, vocal signals should play a major role in mate choice. Despite the seeming implication of male calls in mate choice, vocal communication in burrowing petrels has been poorly studied so far, likely due to constraints associated with fieldwork in remote locations and their particular breeding ecology (nocturnal and burrowing habits). A recent study suggests that acoustic parameters of male calls reflect qualities and mating success but the hypothesis that females actually show a preference for these parameters has never been tested. Here, we experimentally tested by playback experiments with modified calls: (i) the role of male calls in mate attraction and (ii) the role of certain acoustic parameters of male calls in mate choice. Among burrowing petrels, the blue petrel is a good candidate to assess this question because it is highly vocal and suffers from a high predation pressure (more than 70% of the brown skua diet: Montcorps et al., 1998; Mougeot et al., 1998). Based on our previous study on the informative content of blue petrels' calls (Gémard et al., 2019), we hypothesized that females should be attracted by males producing long calls with many syllables and a high syllable rate. According to the handicap theory (Zahavi, 1975, 1977), females may also be attracted by males that take large risks of predation, for instance by calling at a high call rate and/or producing long calls as shown in other species (Johnstone, 1995; Zuk & Kolluru, 1998).

Material and methods

Study area

We conducted the fieldwork on a small island of the Kerguelen Archipelago (Ile Verte: 49° 51′ S, 70° 05′ E), southern Indian Ocean. In blue petrels *H. caerulea*, bachelor males and females are vocally active and actively prospecting for a mate in the colony, at night, throughout the breeding season (Warham, 1996), although the daily activity in the colony is dependent of the moon phase and clouds cover (Mougeot & Bretagnolle, 2000a). We conducted the fieldwork during the birds' incubation period, from November 27 to December 27, 2018.

Studied species

In blue petrels, callers are mainly bachelor males and females, although breeders call when they are vocally challenged by a conspecific, likely to defend their burrow (Warham, 1996). Their calls consist of distinct and repeated sections called "phrases". Phrases are themselves composed of indivisible units organized in a particular order, called "syllables" (Bretagnolle, 1996; Catchpole & Slater, 2008). There are four types of syllable (mentioned as A, B, C, D, in their order of appearance), distinguishable by the shape of their frequency modulations. Each syllable is produced once per phrase, except syllable C which is repeated between two and twelve times per phrase depending on the individuals (see Bretagnolle, 1996; Gémard et al., 2019 for spectrograms).

Playback procedure

To assess whether particular acoustic parameters play a role in female mate choice, we used a two-choice playback experiment to compare the attractiveness of chosen acoustic parameters, one by one. The experimental design consists in broadcasting two stimuli from inside two artificial burrows simultaneously. The two stimuli (i.e., the stimuli dyad) are two modified versions of a same call, whose tested acoustic parameter has been either decreased ("low version" of the call) or increased ("high version"). We chose five acoustic parameters to test, related to morphological characteristics and possibly to reproductive success in blue petrels according to a previous study (Gémard et al., 2019): call rate (number of calls per minute), call duration (in seconds), frequency spectrum (in Hertz), number of syllables per phrase, and syllable rate (number of syllables per second).

To build the playbacks, we first chose two representative male calls (hereafter call1 and call2) of the studied population in 2017. Call1 and call2 were chosen among recorded calls to have syntax, temporal parameters and frequencies close to the mean values of the population, based on measurements of 38 acoustic parameters (Table A1). For both call1 and call2, we modified the five acoustic parameters (call rate, call duration, frequency spectrum, number of syllables per phrase, syllable rate) one by one, by either decreasing or increasing them, while letting the other parameters unchanged (Table 1; Figure 1). We made the modifications of acoustic parameters of call1 and call2 using the signal processing software Avisoft-SASLab Pro v 5.2.11 (Specht, 2017). More precisely, in the temporal domain, we

modified the number of syllables by manually removing or adding the last C syllables and we modified the call duration by adding or removing phrases among the call. We modified the syllable rate by cutting or inserting inter-syllable silences. In the spectral domain, we modified the frequency spectrum by shifting up or down the frequency spectrum of ± 50 Hz using the Avisoft tool "frequency shift" (Figure 1). To avoid extreme values and bias related to supra stimulus, we increased/decreased the acoustic parameters in the natural range previously observed in the studied colony (Table 1; Table A1). Considering five acoustic parameters, this gave us five dyads of stimuli consisting in a low-parameter-call and a high-parameter-call, for both call1 and call2.

Table 1. Dyads of experimental signals modified to test the attractiveness of five different acoustic parameters

Acoustic parameter	**Low**	**High**
Call rate	1 call/3 min	1 call/3 s
Call duration	2 phrases	8 phrases
Frequency spectrum	Frequencies decreased by -50 dB*	Frequencies increased by +50 dB*
Number of syllables per phrase	2 syllables C	6 syllables C
Syllable rate	Duration of inter-syllable silences doubled*	Duration of inter-syllable silences halved*

*Modifications of frequency spectrum and syllable rate are proportional to the original values of these parameters

For each of the five acoustic parameters, a trial consists in broadcasting a stimuli dyad in a same burrow twosome during two consecutive nights (Figure 2). The stimuli dyad is composed of the same call in two versions: one with a given acoustic parameters increased ("high" version) and the other with the same acoustic parameter decreased ("low" version). During the first night of the trial, the low version was broadcast in a burrow, and the high version in the other burrow of the twosome. During the second night of the trial, the same stimuli dyad was broadcast in the same burrow twosome but we shifted the "low" and "high" versions. The playbacks for a given acoustic parameter thus were done on two successive nights. For example, if we consider the given parameter "frequency spectrum" and the burrow twosome A, the high-pitched version of the call was broadcast in the burrow Aa and the low-pitched version in the burrow Ab during the first night. During the second night, the low-pitched version was broadcast in Aa and the high-pitched version in Ab (Figure 2). Basically, each night, we performed a binary choice experiment where flying females had the choice between the two versions of the same call. With this design, the possible burrow effect is taken into account while habituation during the two

nights of a trial is unlikely to occur. We first carried out the two-choice experiments in the twosome "A" (made of burrows Aa and Ab) with stimuli dyads created from the original call1. We then repeated it in the burrow twosome "B" (made of burrows Ba and Bb) with stimuli dyads from call2. The binary choice tests in the burrow twosome B were performed, depending on the parameter, 6 to 26 days after the burrow twosome A. The order or presentation of stimuli dyads was randomized and thus differed between the two burrow twosomes. In total, we carried out 10 trials (two per chosen acoustic parameters) during 20 nights using four burrows organized in two twosomes.

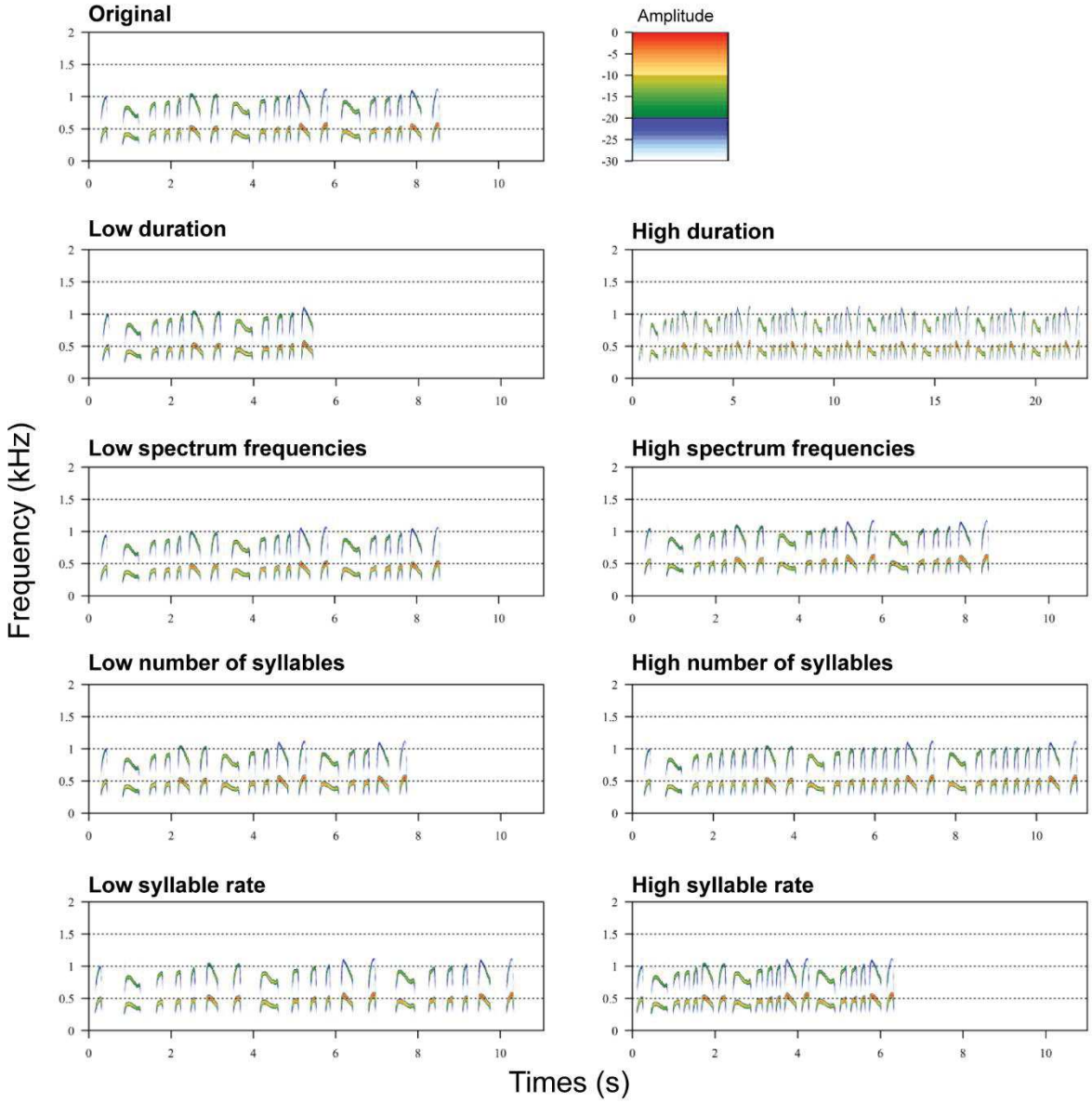

Figure 1. Spectrograms of the stimuli dyad to broadcast, created from an original representative male call of the studied population of blue petrels (call1). On the left, the chosen acoustic parameters have been decreased; on the right increased.

Stimuli were emitted from the burrow chambers using a Sony NWE393B connected to a JBL Flip 4 speaker (frequency response: 70-20000 Hz ± 5 dB). The volume occupied by the speaker is close to the volume occupied by a blue petrel (about 0.7 L). Playbacks were broadcast during the most intense vocal activity (10:00 pm to 3:00 am, unpublished data) at a natural amplitude (mean ± SD: 66 ± 9 dB, measured at the entrance of burrows with an A-weighted decibel-meter Lutron SL-4001 on 115 spontaneous calls from 24 bachelor males in the studied population) and a natural call rate (a call every 40 s, unpublished data from 21 bachelor males in the studied population), except when we specifically tested the call rate attractiveness.

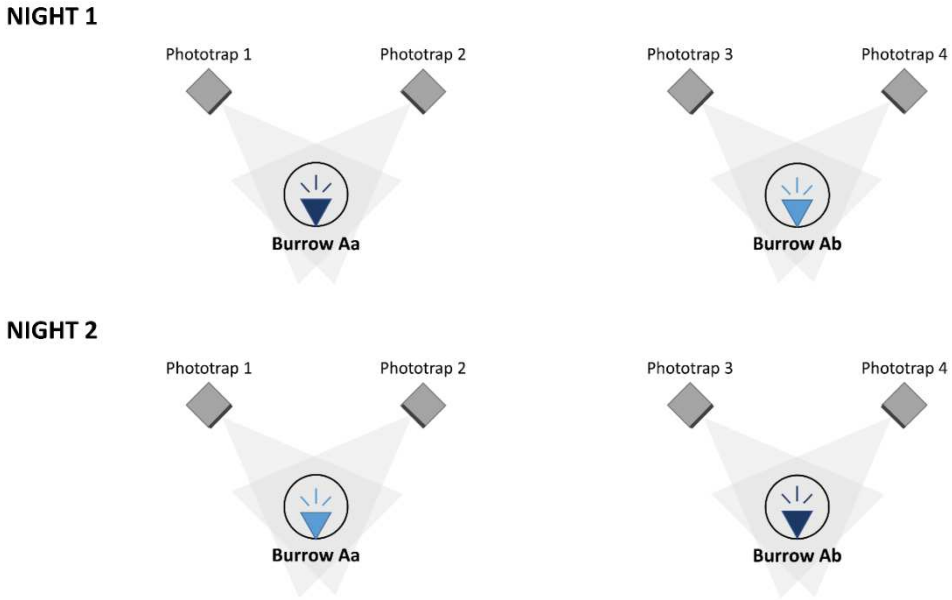

Figure 2. Experimental design of the two-choice playback experiment. Both burrows of a twosome (circles) are equipped with two phototraps (gray squares) with overlapped visual ranges (gray triangles). A trial consists in testing a given acoustic parameter during two consecutive night. During the first night, a low-version (light blue triangle) and a high-version (dark blue triangle) of a male call (i.e., the stimuli dyad) are broadcast in burrows. During the following night, call versions to broadcast are shifted.

Two-choice playback experiments were carried out in four unoccupied artificial burrows (i.e., two twosomes) because they offer the advantage of limiting biases of sound propagation caused by volume differences. Artificial burrows were installed during the previous breeding season in the colony (2017). They consisted in a chamber made of a clay pot diameter 30 cm upside down, a 66-centimeter tunnel made of two end-to-end half fired-clay wine rack, and a 30-centimeter PVC pipe diameter 125 mm above the chamber to easily reach the birds and/or the egg. They were buried at a depth of 40 cm

and covered by the existing vegetation. A wooden board and a stone recovered the hole above the chamber, as the other monitored burrows of the colony (Figure A1 for pictures). During the 2018 breeding season, 75% of artificial burrows installed in 2017 were occupied by breeding petrels. The two burrows of a twosome were at least 5 m apart and had different orientation to avoid the influence of sound propagation from a burrow to the other burrow.

To record female behaviors at proximity of the tested burrows, we equipped each burrow with two infrared phototraps (Bushnell Nature View Essential HD Camera) (Figure 2, Figure A2). We placed phototraps 50 cm above the ground on wooden sticks at equidistance of the burrow entrance. We oriented phototraps toward the burrow entrance. We used phototraps in video mode with both automatic detection (i.e., 1-min record after movement detection) and "Field Scan" option (i.e., automatic 1-min record every 5 min). Videos were analyzed by a blind-to-the-experiment student with VLC media player 2.1.5 Rincewind. In several burrowing-petrel species, bachelor females use a two-step approach: first flying and landing close to the sound source, then listening to calls until they reach the source by walking (Storey, 1984). Here, for each night and each burrow, we counted the number of females flying close to the burrow and the number of females on the ground. We calculated the total time each female spent on the ground. To limit the risk of considering breeders shifting and transient individuals, we only considered individuals flying at a maximum distance of 5 m from the burrow entrance, and individuals showing exploration behaviors on the ground, e.g., calling, walking, moving head in the direction of the burrow (Figure A3). Although there is no sexual dimorphism in blue petrels, bachelor males competing for burrow are scarce at this advanced stage of the breeding season (Warham, 1990). Recorded prospecting individuals were thus considered females.

Data analyses

All analysis results were implemented under the R software environment version 3.4.4 (R Core Team, 2018). Raw data are available in Tables A2, A3.

We statistically compared the attractiveness of the "low version" and the "high version" of each of the five acoustic parameters using three distinct models. The dependent variables — one per model — were the number of females flying close to the burrow, the number of females on the ground close to the burrow, and the time females spent on the ground. To model the number of females flying as a

function of the independent variables, a Negative Binomial General Linear Model (NB GLM) with a log link function was used as our count data was overdispersed and zero inflated. To model the number of females on the ground, a Poisson GLM with a log link function was used because Poisson distribution is typically used for count data. To model the time females spent on the ground, a linear model from the *lme4* R package (Bates et al., 2015) was used. The "total time" variable was previously log-transformed to normalize its distribution. In the three models, independent variables consisted in three categorical variables: burrow twosome (A or B), and the interaction between acoustic parameter and condition (low or high). Model assumptions were verified by checking the dispersion parameter for the two first models (respectively 1.02 and 4.12) and by plotting residuals versus fitted values for all three models (Figures A4, A5, and A6). For each of the three models, we created a contrast matrix based on Tukey contrasts with a Bonferroni-Holm correction method for multiple testing.

Results

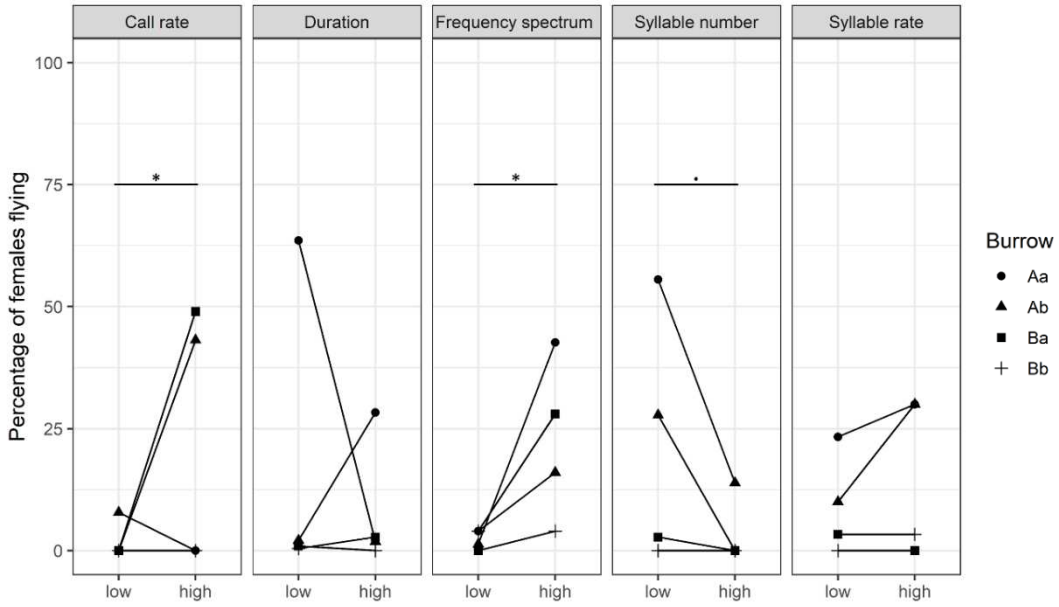

Figure 3. Number of blue petrel females flying at a maximum distance of 5 m from the burrow where modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow twosome where we broadcast a stimuli dyad. *$p < 0.05$, ·$0.05 < p < 0.01$.

Results showed significant differences between the maximum and the minimum in two acoustic parameters. More specifically, a high call rate attracted more flying females than a low call rate (estimate (SE) = 2.12 (0.90), $z = 2.35$, $p = 0.02$; Figure 3). High-pitched calls attracted more flying females than

low-pitched calls (estimate (SE) = 1.94 (0.89), z = 2.18, p = 0.03; Figure 3). Based on the model parameters, calls with phrases made of few syllables might also be more attractive than calls with phrases of many syllables, although the relationship is not significant (estimate (SE) = -1.94 (1.03), z = -1.88, p = 0.06; Figure 3). The call duration did not influence the average number of flying females per night (estimate (SE) = -0.25 (0.84), z = -0.30, p = 0.77; Figure 3). Burrow twosome A was significantly more attractive than burrow twosome B (estimate (SE) = -2.06 (0.42), z = -4.9, p < 0.001).

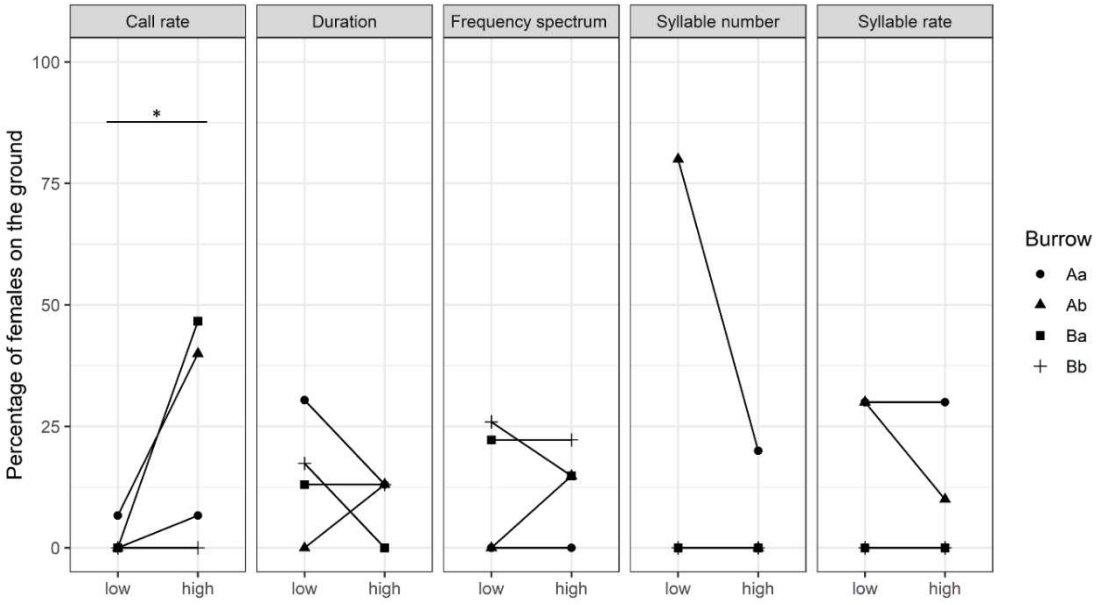

Figure 3. Number of blue petrel females showing exploratory behaviors on the ground at proximity of the burrow where modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow twosome where we broadcast a stimuli dyad. *p < 0.05.

Results show that a high call rate significantly attracted more females on the ground than a low call rate (estimate (SE) = 1.22 (0.51), z = 2.41, p = 0.02: Figure 4). The call duration, frequency spectrum, number of syllables per phrase and syllable rate were not significantly related to the number of females on the ground per night (respectively: estimate (SE) = -0.46 (0.31), z = -1.49, p = 0.14; estimate (SE) = 0.18 (0.35), z =0.52, p = 0.60; estimate (SE) = -1.79 (1.08), z = -1.66, p = 0.10; estimate (SE) = -0.34 (0.41), z = -0.81, p = 0.42; Figure 4). Burrow twosome A was significantly more attractive than burrow twosome B (estimate (SE) = -0.47 (0.18), z = -2.61, p = 0.009).

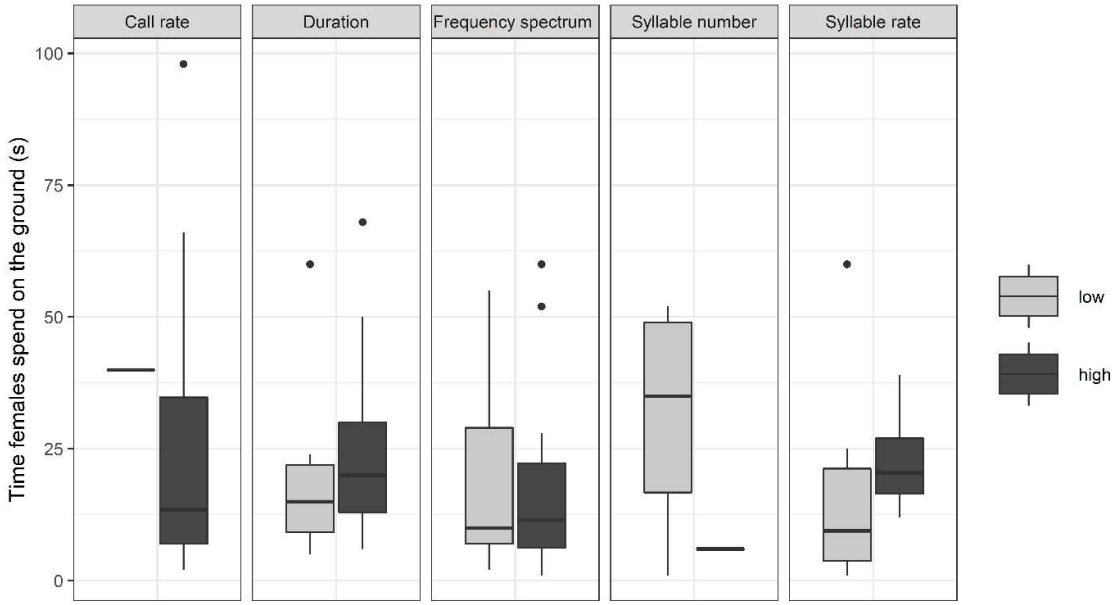

Figure 4. Time spent by blue petrel females showing exploratory behaviors on the ground, at proximity of the burrow where modified calls of male blue petrel were broadcast. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to 1.5*IQR and outliers.

Results show that the time females spend on the ground was not significantly influenced by the five acoustic parameters tested ($F_{10\text{-}81} = 1.27$, $p = 0.26$, $r^2 = 0.03$; Figure 5). The time females spent on the ground was not significantly different between the two burrow twosomes (estimate (SE) = -0.47 (0.30), $z = -1.60$, $p = 0.11$).

Discussion

We aimed to assess the role of male calls in female mate choice, and the attractiveness of certain acoustic parameters of male calls (call rate, call duration, frequency spectrum, number of syllables per phrase, and syllable rate) in blue petrels. Our two-choice playback experiments with modified calls successfully attracted females. The results indicate that more females were attracted by the high-pitched calls, by high-rate versions of the call exemplars tested, and possibly by modified calls with few-syllable phrases. We found no relationships between acoustic parameters and time females spend on the ground exhibiting exploratory behaviors.

Results show that in blue petrels, male calls attracted potential mates even in absence of the caller. Similar results have been found in many taxa, including non-songbirds such as sage grouses and hoopoes (Gibson, 1989; Martín-Vivaldi et al., 1999). Previous studies have assessed that olfactory

signals contain genetic information about the signaler, and that they are likely to influence mate choice (Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Leclaire et al., 2017). We thus hypothesize that both vocal and olfactory signals may influence mate choice but with a different timing: first, male calls may attract flying females, then olfactory signals may play a role when females land and/or when both male and female are in the burrow.

Results suggest that males calling with a high rate attract more flying females and more females on the ground. Similar results have been found in mammals and birds (McComb, 1991; Riebel, 2009). One possible explanation would be that males producing many frequent calls are easier to locate in dense and noisy colonies (up to two burrows per m^2: Brothers, 1984) because the repetition of calls helps the female walking on the ground to locate the source of emission (Storey, 1984). Producing redundant vocal signals is a communication strategy in response of misdetection and/or misclassification in noisy environment ("cocktail-party effect": Cherry, 1957; Aubin & Jouventin, 1998; Jouventin et al., 1999; Lengagne et al., 1999). A high call rate is also indicative of the signaler's sexual motivation in many birds, including burrowing petrels (Catchpole & Slater, 2008; Searcy & Beecher, 2009; Gémard et al. in press). Nonetheless, bachelor petrels face a high predation pressure and a high call rate also increases the risk of being detected by predators (Mougeot & Bretagnolle, 2000b). The handicap principle states that good-quality males take larger risks than other males to produce sexual signals (Zahavi, 1975, 1977). Based on this theory, we could hypothesize for the blue petrels too that females are preferentially attracted by males that produce frequent calls, and thereby are more exposed to predation.

Our results also indicate that females are preferentially attracted by high-pitched calls when they fly over the colony. One possibility is that calls higher in frequency make the emitter easier to locate (Dooling, 1982; Park & Dooling, 1991; Klump, 2000). Low frequencies are usually easier to detect because they are less attenuated by distance and less attenuated and/or degraded by environmental constraints than high frequencies (Marten et al., 1977). Nonetheless, male calls are emitted from burrows in burrowing petrels and low frequencies are attenuated by the ground effect (Morton, 1975; Marten & Marler, 1977). Moreover, some animal species are more sensitive to high frequencies but so far, little is known about how call frequency affects the ability of petrels to localize calls. Another possibility is that high-pitched calls indicate males of good quality, as shown in many taxa, including tortoises (Galeotti

et al., 2004), passerines (Cardoso et al., 2012), and mammals (Reby et al., 2010). In blue petrels, big males with a long, thin bill produce high-pitched calls (Gémard et al., 2019). Because bill morphology may determine the filtering surface and efficiency (Klages & Cooper, 1992), these males might have a better filter-feeding efficiency and consequently a better reproductive success.

Our results suggest that calls made of few-syllable phrases might be attractive to females. They contradict our assumptions that females may be preferentially attracted by long calls with many syllables. For example, in another non-songbirds, the hoopoe *Upupa epops*, songs with many syllables are more attractive than songs with few elements as it is indicative of the singer's body condition (Martín-Vivaldi et al., 1998, 2000). Moreover, males producing long calls with many elements are easier to detect and to locate than males producing short calls with few elements (Brumm & Zollinger, 2013), but this may be true for both potential mates and predators. We thus may hypothesize that females might be more attracted by males producing short calls with few syllables, but at a high call rate, as the result of a trade-off between predation avoidance and conspicuous sexual signaling.

Broadcast signals, regardless of the tested acoustic parameter, had no influence on the time attracted females spend on the ground, at the proximity of the burrow. In burrowing petrels, females vocalize towards the sound source (male in the burrow) when they are on the ground, and then walk following female-directed calls produced by males until they find the burrow entrance (Storey, 1984). In blue petrels, males produce female-directed calls characterized by frequency and temporal modulations that may indicate their sexual motivation (Gémard et al., in press). Olfactory signals may also be involved in sexual signaling because previous studies have shown burrows have a chemical signature (Bonadonna et al., 2001, 2004), and individuals have a body odor containing genetic information (Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Leclaire et al., 2017). Thus, we hypothesize that a necessary exchange of vocal and/or olfactory signals might take place before the female enters the burrow. In our experiments, we used a repetitive playback in an artificial burrow, so that we could not interactively reply in an appropriate way to a female close to the burrow, and no odors were emitted. In the absence of these vocal and olfactory stimuli, and considering the predation risks (Mougeot & Bretagnolle, 2000b), females may fly rapidly away independently of the nature of the modified call emitted.

In summary, we showed for the first time that males' calls with certain acoustic characteristics are attractive to females in a burrowing petrel. More precisely, females flying over the colony are more attracted by males producing high-pitched calls and calling at a high rate. Flying females might also be attracted preferentially by calls consisting in few-syllable phrases rather than many-syllable phrases. These acoustic parameters are related to male bill morphology and may thus be linked to male qualities such as feeding efficiency. Another explanation is that males producing high-pitched calls at a high call rate may be easier to locate. Females are also attracted by short calls with few syllables, which make the caller less conspicuous. It might indicate a trade-off between predation avoidance and conspicuous sexual advertisement to attract potential mates in the hubbub of the colony. The time spent by females exploring on the ground might be influenced by additional signals, such as a vocal response from the male, olfactory signals, or both.

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Conflicts of interest - The authors declare that they have no conflict of interests.

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Ethics approval - 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.

Data availability - The dataset generated and analysed during the current study is available in Appendices.

Authors' contributions - All authors made substantial contributions to conception of experiment, analysis and interpretation of data, and critical review of the manuscript. CG, FB and TA contributed to the study conception and design. CG and FB performed material preparation and data collection. CG and ELR analysed the data. The first draft of the manuscript was written by CG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Appendices

Table A1. Syntactic, temporal, and spectral acoustic parameters as descriptors of male calls in blue petrels (measured on 105 calls from 22 bachelor males). Playback calls 1 and 2 are the chosen representative calls for our study.

	Population		Playback call 1		Playback call 2	
	mean	sd	mean	sd	mean	sd
Number of phrases per call	6.15	6.92	3.00	0.00	4.00	0.00
Number of syllables per phrase	6.53	2.08	6.00	0.00	5.75	0.50
Fundamental frequency of syllable A	481.42	97.18	507.33	32.62	531.75	99.85
Lower energy quartile of syllable A	470.15	86.47	479.67	28.75	473.00	65.84
Medium energy quartile of syllable A	573.66	136.81	511.33	27.39	547.50	32.87
Upper energy quartile of syllable A	802.12	156.55	830.67	109.66	718.00	110.38
Fundamental frequency of syllable B	396.41	111.40	427.00	15.72	429.75	60.04
Lower energy quartile of syllable B	406.31	115.15	410.67	14.01	413.25	48.96
Medium energy quartile of syllable B	581.75	177.59	637.33	157.79	521.50	61.56
Upper energy quartile of syllable B	785.61	209.92	813.00	15.72	811.75	55.23
Fundamental frequency of syllable C1	420.59	114.52	451.67	16.20	469.00	52.20
Lower energy quartile of syllable C1	426.51	112.86	449.67	17.21	472.00	47.91
Medium energy quartile of syllable C1	582.68	176.51	470.67	7.37	500.00	39.67
Upper energy quartile of syllable C1	813.42	198.09	890.33	25.72	879.25	71.71
Fundamental frequency of syllable D	568.65	235.04	496.67	5.69	631.00	316.04
Lower energy quartile of syllable D	527.97	216.95	478.67	6.81	584.67	293.03
Medium energy quartile of syllable D	579.61	242.66	510.00	8.72	621.33	311.10
Upper energy quartile of syllable D	719.89	325.22	811.67	52.65	641.33	321.06
Mean fundamental frequency of the phrase	424.23	87.82	459.67	14.85	486.63	47.81
Lower energy quartile of the phrase	422.98	68.17	432.87	13.34	444.75	32.99
Medium energy quartile of the phrase	555.01	108.91	499.00	14.89	516.68	22.84
Upper energy quartile of the phrase	794.47	119.13	831.67	7.15	773.13	21.22
Phrase rate of a call	0.40	0.15	0.36	0.00	0.43	0.00
Syllable rate of phrase	2.64	0.98	2.31	0.14	2.49	0.12
Phrase rhythm	1.03	0.38	1.06	0.05	1.03	0.04
Phrase tempo	0.50	0.17	0.51	0.01	0.51	0.01
Interphrase silence duration	0.21	0.20	0.17	0.15	0.19	0.12
Duration of syllable A	0.17	0.04	0.18	0.01	0.17	0.02
Duration of syllable B	0.41	0.11	0.44	0.03	0.43	0.03
Duration of syllable C1	0.18	0.05	0.17	0.00	0.19	0.00
Duration of syllable D	0.24	0.06	0.29	0.00	0.18	0.00
Duration of silence between A and B	0.29	0.08	0.33	0.02	0.24	0.03
Duration of silence between B and C1	0.23	0.17	0.23	0.01	0.22	0.01
Duration of silence between Cn and D	0.24	0.07	0.18	0.00	0.28	0.02
Total duration of syllables in a phrase	1.13	0.49	1.34	0.05	1.17	0.08
Total duration of silences in a phrase	1.14	0.53	1.26	0.10	1.14	0.12
Phrase duration	2.27	0.96	2.60	0.15	2.32	0.21
Call duration	11.66	7.26	8.23	0.00	9.26	0.00

Frequencies are given in hertz (Hz); durations in seconds (s)

Figure A1. Use of artificial burrows in the blue-petrel colony: (a) installation of an artificial burrow in 2017; (b) the same burrow in 2018, after a year.

Figure A2. Picture of the experimental setup.

Figure A3. Phototrap video capture showing two blue petrels, one the ground and one flying, at proximity of the focal artificial burrow.

Table A2. Raw data of the number of blue petrel females and predators (skuas) attracted by the five acoustic traits, condition and burrow.

Acoustic parameter	Condition	Burrow twosome	Burrow	Females flying	Females on the ground	Skuas on the ground
Call rate	low	A	Ab	24	4	0
Call rate	low	A	Aa	0	1	0
Call rate	low	B	Ba	0	0	0
Call rate	low	B	Bb	0	0	0
Call rate	high	A	Ab	28	7	0
Call rate	high	A	Aa	0	1	0
Call rate	high	B	Ba	29	9	1
Call rate	high	B	Bb	0	0	0
Duration	low	A	Ab	9	2	2
Duration	low	A	Aa	279	15	0
Duration	low	B	Ba	4	5	6
Duration	low	B	Bb	1	5	0
Duration	high	A	Ab	10	3	0
Duration	high	A	Aa	133	11	2
Duration	high	B	Ba	13	0	0
Duration	high	B	Bb	2	3	2
Energy spectrum	low	A	Ab	1	0	0
Energy spectrum	low	A	Aa	4	0	0
Energy spectrum	low	B	Ba	1	6	0
Energy spectrum	low	B	Bb	4	9	1
Energy spectrum	high	A	Ab	12	5	1
Energy spectrum	high	A	Aa	41	0	0
Energy spectrum	high	B	Ba	22	4	0
Energy spectrum	high	B	Bb	5	9	0
Number of syllables	low	A	Ab	9	6	0
Number of syllables	low	A	Aa	21	0	0
Number of syllables	low	B	Ba	1	0	0
Number of syllables	low	B	Bb	3	0	0
Number of syllables	high	A	Ab	6	0	0
Number of syllables	high	A	Aa	0	1	0
Number of syllables	high	B	Ba	0	0	0
Number of syllables	high	B	Bb	0	0	0
Syllable rate	low	A	Ab	2	5	0
Syllable rate	low	A	Aa	11	9	0
Syllable rate	low	B	Ba	1	0	1
Syllable rate	low	B	Bb	0	0	0
Syllable rate	high	A	Ab	7	3	0
Syllable rate	high	A	Aa	11	7	0
Syllable rate	high	B	Ba	0	0	0
Syllable rate	high	B	Bb	1	0	1

Table A3. Raw data of the total time females spend on the ground depending on the five acoustic traits, condition and burrow. Each line corresponds to one female.

Acoustic parameter	Condition	Burrow twosome	Burrow	Behaviour total duration (s)
Call rate	high	B	Ba	14
Call rate	high	B	Ba	7
Call rate	high	B	Ba	43
Call rate	high	B	Ba	13
Call rate	high	B	Ba	10
Call rate	high	B	Ba	66
Call rate	high	B	Ba	2
Call rate	high	A	Ab	38
Call rate	high	A	Ab	5
Call rate	high	A	Ab	5
Call rate	high	A	Ab	20
Call rate	high	A	Ab	7
Call rate	high	A	Ab	98
Call rate	high	A	Aa	25
Call rate	low	A	Aa	40
Duration	high	B	Bb	13
Duration	high	B	Bb	30
Duration	high	B	Bb	15
Duration	high	A	Ab	20
Duration	high	A	Ab	68
Duration	high	A	Ab	8
Duration	high	A	Aa	20
Duration	high	A	Aa	50
Duration	high	A	Aa	6
Duration	low	B	Ba	16
Duration	low	B	Ba	6
Duration	low	B	Ba	9
Duration	low	B	Bb	24
Duration	low	B	Bb	18
Duration	low	B	Bb	9
Duration	low	B	Bb	10
Duration	low	A	Aa	14
Duration	low	A	Aa	22
Duration	low	A	Aa	60
Duration	low	A	Aa	22
Duration	low	A	Aa	11
Duration	low	A	Aa	5
Duration	low	A	Aa	60
Energy spectrum	high	B	Ba	7
Energy spectrum	high	B	Ba	2

Energy spectrum	high	B	Ba	6
Energy spectrum	high	B	Ba	10
Energy spectrum	high	B	Bb	52
Energy spectrum	high	B	Bb	24
Energy spectrum	high	B	Bb	60
Energy spectrum	high	B	Bb	2
Energy spectrum	high	B	Bb	17
Energy spectrum	high	B	Bb	1
Energy spectrum	high	A	Ab	12
Energy spectrum	high	A	Ab	16
Energy spectrum	high	A	Ab	28
Energy spectrum	high	A	Ab	11
Energy spectrum	low	B	Ba	9
Energy spectrum	low	B	Ba	29
Energy spectrum	low	B	Ba	2
Energy spectrum	low	B	Ba	33
Energy spectrum	low	B	Ba	9
Energy spectrum	low	B	Ba	14
Energy spectrum	low	B	Bb	10
Energy spectrum	low	B	Bb	3
Energy spectrum	low	B	Bb	17
Energy spectrum	low	B	Bb	6
Energy spectrum	low	B	Bb	52
Energy spectrum	low	B	Bb	55
Energy spectrum	low	B	Bb	7
Number of syllables	high	A	Aa	6
Number of syllables	low	A	Ab	52
Number of syllables	low	A	Ab	22
Number of syllables	low	A	Ab	48
Number of syllables	low	A	Ab	1
Syllable rate	high	A	Ab	23
Syllable rate	high	A	Aa	12
Syllable rate	high	A	Aa	18
Syllable rate	high	A	Aa	39
Syllable rate	low	A	Ab	60
Syllable rate	low	A	Ab	25
Syllable rate	low	A	Ab	10
Syllable rate	low	A	Aa	1
Syllable rate	low	A	Aa	2
Syllable rate	low	A	Aa	9

Figure A4. Residuals of the Negative Binomial GLM used to model the number of females flying, depending on the calls' acoustic traits and conditions in blue petrels *H. caerulea.*

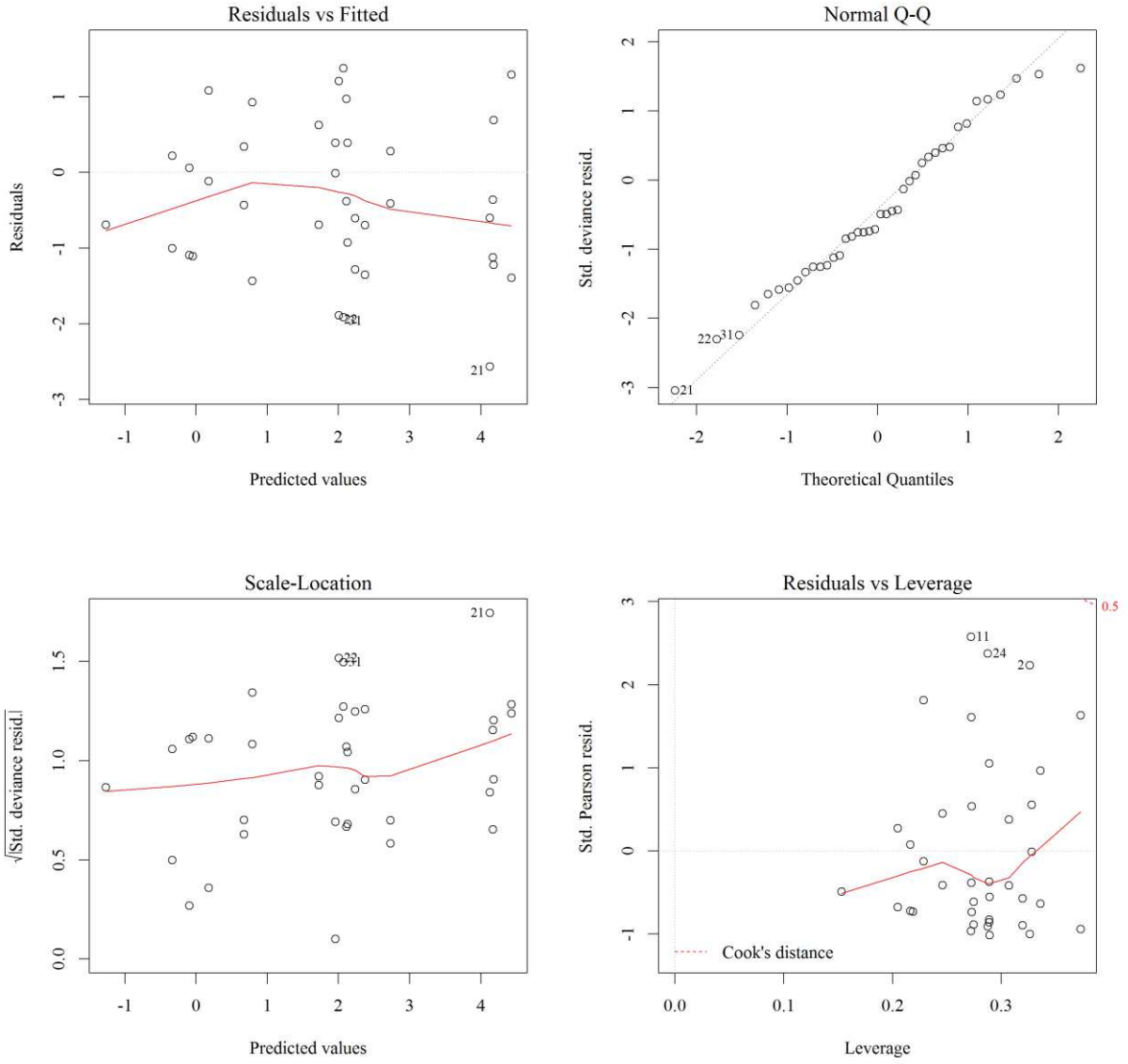


Figure A5. Residuals of the Poisson GLM used to model the number of females on the ground depending on the calls' acoustic traits and conditions in blue petrels *H. caerulea.*

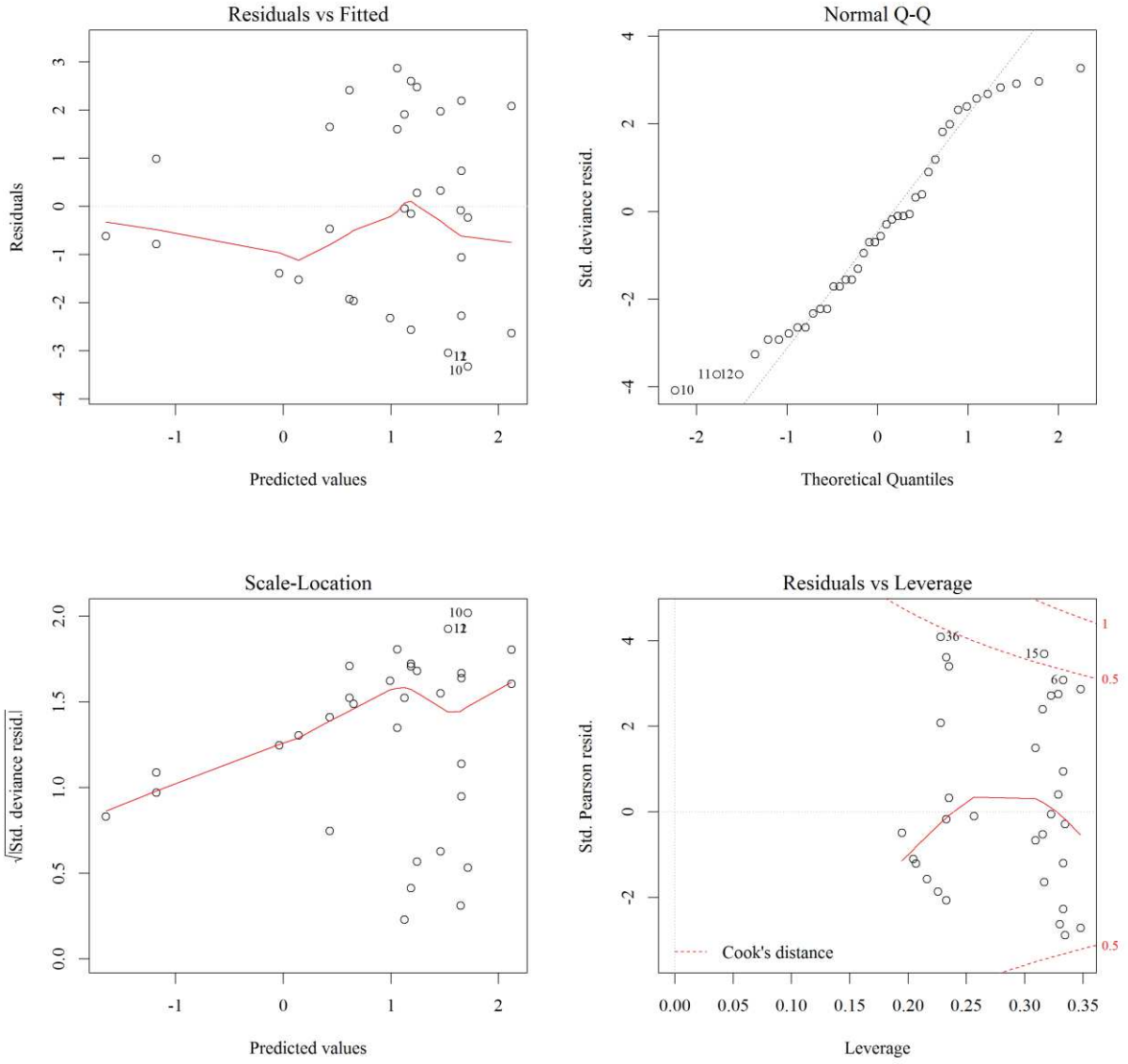
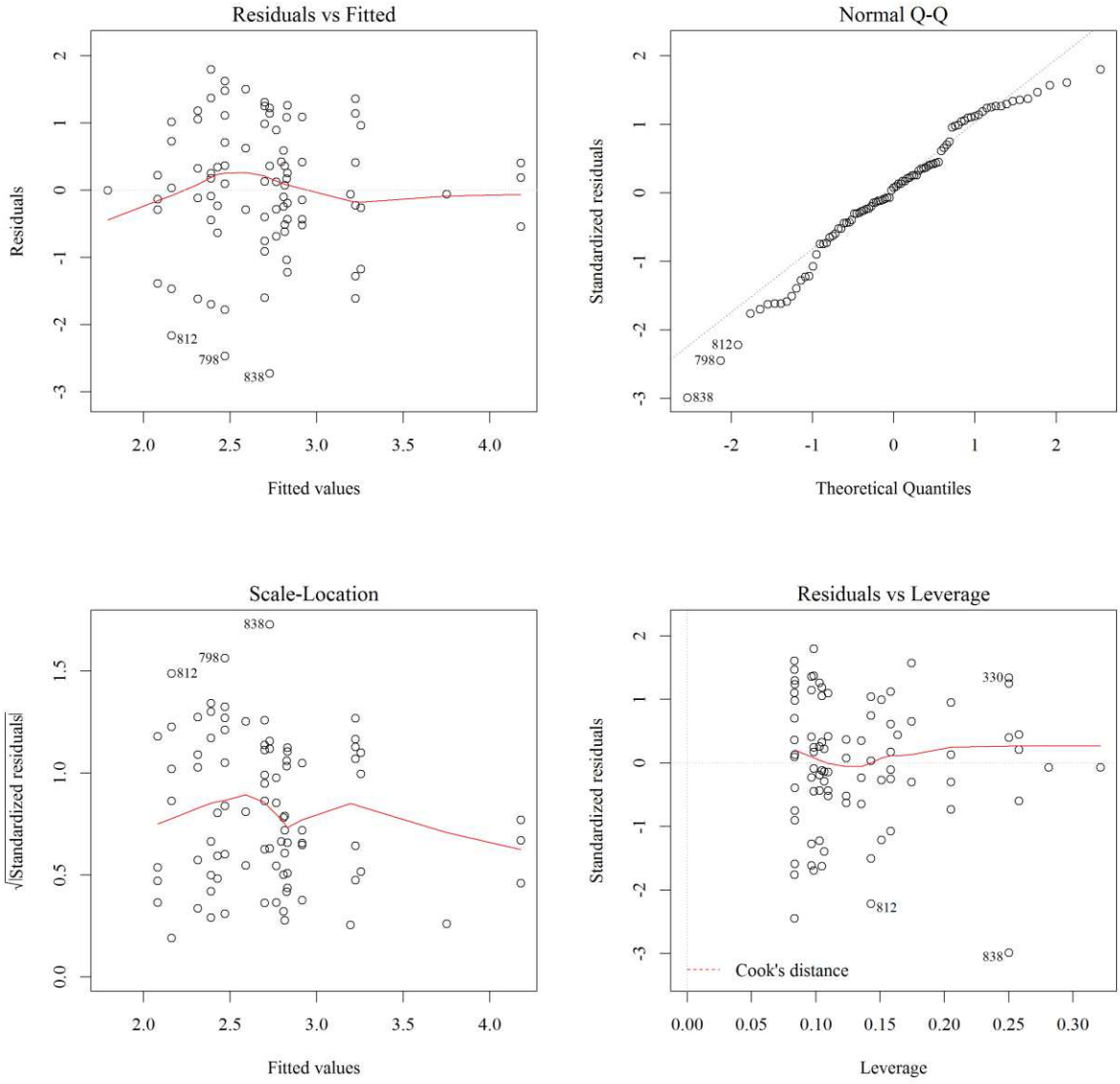


Figure A6. Residuals of the Linear Model used to model the time females spent on the ground depending on calls' acoustic traits and conditions in blue petrels *H. caerulea.*



In blue petrels and Antarctic prions, female mate choice is influenced by particular parameters of males calls related to the caller physical characteristics and motivation. In this chapter, I hypothesized that factors, other than intrinsic acoustic parameters of male calls, may be influential for females. Working in the petrel colony, we noticed that some males aggregate in groups of few individuals, whereas other males do not. I experimentally tested whether these small aggregations within the colony are more attracted to females in Antarctic prions and I discussed several hypotheses.

ARTICLE 5

Females do not prefer aggregated males in breeding colonies of Antarctic prions *Pachyptila desolata*

Charlène Gémard[1,2*], Thierry Aubin[2], Annick Lucas[1], Timothée Zidat[1], Francesco Bonadonna[1]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

In prep.

Abstract

Aggregations where males conspicuously display in close proximity may be the evolutive consequence of female preference for grouped males. Despite associated costs, such as increased risks of pathogen transmission, aggregations facilitate mate meeting, reduce the predation risks, and make males more detectable. Antarctic prions (*Pachyptila desolata*) are colonial and socially monogamous seabirds. During the breeding season, they gather in dense colonies ashore, in which couples and bachelor males occupy burrow for incubation and vocal advertising, respectively. Colony monitoring throughout years showed two patterns within the colony: some males aggregate in small groups of few individuals while others males stay away ("lone callers"). We here tested whether female mate choice may explain this duality. Using a field playback experiment, we compared the attractiveness of grouped and lone callers to females and predators (brown skuas *Stercorarius antarcticus*). Our results showed no female preference for either of the two tested situations. Grouped and lone callers equally attracted predators, but predators spent more time close to lone callers, suggesting a confusion effect when preys are grouped. We hypothesized that males may gather in small groups to reduce predation and/or find the most suitable microhabitats. Female mate choice may rather be influenced by the informative content of male calls, in spite of benefits associated with male groups.

Keywords: vocal communication, breeding aggregations, mate choice, seabirds, petrels

Introduction

In many species, males advertise in close proximity within breeding aggregations, here defined as "non-random distribution of individuals across the landscape, such that they are close together in a pattern that does not necessarily reflect resource distribution". Several types of aggregations can be distinguished, including colonial breeding, clustered territories, and lekking system (see Macedo et al., 2018 for a review). Breeding coloniality is a widely distributed system in animal taxa, consisting in an aggregation of small, tightly-packed breeding territories with limited resources, usually distinct from the feeding area. Clustered territories, also called "loose colonies", are large territories including the breeding site and further resources. Leks are aggregation of males displaying in a small mating territory ("arena"), distinct from breeding and feeding sites. Lekking males usually display using extravagant visual, acoustic, and olfactory displays to attract choosy females, which attend with the primarily purpose of mating (Höglund & Alatalo, 1995). In the strict definition, contribution of males is restricted to mating, but after examination, Höglund & Alatalo (1995) considered the possibility of a lekking system in species with high male investment.

A fruitful approach was to assess the evolution of breeding aggregation at the light of the sexual selection. Aggregations may be the evolutive consequence of female preference for males advertising in groups. In spite of the increased risks of pathogen transmission and competition for resources, breeding aggregations of males provide benefits outweighing these costs (Macedo et al., 2018). Aggregation decreases the risk of predation through dilution effect, confusion effect, alarm calling or mobbing (Macedo et al., 2018). Aggregations also facilitate mate choice because females favour areas of "high display density" where they have access to more potential mates at once, and where the competition between them is high (Alexander, 1975). Finally, males may aggregate to increase female attraction. Vocalizing in synchrony with other males increases the active space of the signal and thus give a detection advantage (signal enhancement hypothesis: Bradbury, 1981, also called "Beacon effect": Buck & Buck, 1966), as shown in insects and anurans (Bates et al., 2010; Rehberg-Besler et al., 2017). Males thus actively overlap conspecifics' vocalizations (Araya-Salas et al., 2017), in spite of the strong competition between callers for the leading role (Hartbauer et al., 2014; Siegert et al., 2011),

and the loss of individual discrimination due to interferences (Brumm & Slabbekoorn, 2005). Vocalizing in groups also reduces silences and preserves a calling rhythm attractive to females (Walker, 1969).

A classic case of colonial and highly vocal species are seabirds, which gather ashore in dense colonies of dozens, hundreds, thousands of individuals, perfectly distinct from the feeding area at sea (Bried & Jouventin, 2001). Among seabirds, burrowing petrels form breeding aggregations consisting in a mix of breeding couples and bachelor males occupying tightly-packed burrows (e.g., up to 0.7 burrows/m² in blue petrels *Halobaena caerulea* and 1.4 burrow/m² in Antarctic prions *Pachyptila desolata*; Croxall & Prince, 1980). All night long, bachelor males vocally advertise from their burrow to attract females overflying the colony (Bretagnolle, 1996; Warham, 1990, 1996), despite the high predation cost associated with vocal production (Mougeot & Bretagnolle, 2000). Bachelor females repeatedly visit the colony at night exclusively to find a suitable partner, as they do not occupy burrow, nor feed at the colony (Warham, 1990, 1996), similarly to a lekking system. Hence, burrowing-petrel colonies may be seen as "a mosaic of small territories vocally defended" by the occupants, renewed year after year at the same place (Warham, 1990). Within colonies of Antarctic prions and blue petrels, we observed two patterns: males vocally advertising in small groups and lone callers. One may wonder whether female mate choice may favour one of these patterns.

Mate choice in burrowing petrels takes a couple of years, likely because of female choosiness. Females visit several males before bonding for life, suggesting an active mate choice by females based on male calls in the first place. To evaluate and discriminate males, females may thus use information carried by male calls including identity, morphology, and motivation of the caller (Gémard et al., 2019; Gémard et al., 2021; Gémard et al., *in press*). Call detectability of the caller may also be a significant factor influencing female attraction. In Antarctic prions, females are preferentially attracted by males vocalizing at a high call rate, maybe because it makes the caller easier to locate or because it is a sign of sexual arousal (Gémard et al., 2021). However, vocal communication in burrowing petrels is costly as signals also attract predators (Mougeot & Bretagnolle, 2000). Males are faithful to their burrow they entire life, implying that when choosing a life mate, female also choose a burrow with particular characteristics and location. Whether females choose males directly or particular sites in the colony is still an open question.

To go further in our understanding of male aggregation and female mate choice in burrowing petrels, we aimed to assess whether aggregated callers preferentially attract females and predators. We conducted a two-choice playback experiment in Antarctic prions *P. desolata* to compare the attractiveness of four-male groups and lone males. We hypothesized that several males calling in partial synchrony attract more females than lone callers because: (i) the formers are more detectable according to the signal enhancement hypothesis (Bates et al., 2010; Rehberg-Besler et al., 2017); and (ii) they give the opportunity to females to compare several males at once (Alexander, 1975). Predators should theoretically be more attracted by lone callers based on predator confusion, but grouped callers may be more detectable.

Material and Methods

Study location and species

Antarctic prions (*Pachyptila desolata*) spend most of their life at sea but they come ashore and gather in dense colonies at the beginning of the breeding season. Throughout this period, bachelor males and females are active at night (Warham, 1990). We conducted fieldwork during the bird's incubation period (December 23th 2019 to January 13th 2020) in an Antarctic prion colony on the Ile Verte (49°51'S, 70°05'E), a small island of the Kerguelen Archipelago, in Southern Indian Ocean.

Playback stimuli

We used a two-choice attractiveness experiment on the field to test whether females are preferentially attracted by several males calling rather than by a lone caller. To do so, we created eight playback stimuli of two types to avoid pseudo replication: four "lone" playbacks consisting of tracks with a lone bachelor male calling, and four "group" playbacks consisting of tracks with four males calling successively. To avoid bias related to unnatural calls or supra-stimuli, we chose representative calls of the population that we used in previous experiments too. Playback stimuli were created with the signal processing software Avisoft–SASLab Pro v 5.2.11 (Specht, 2017) from spontaneous call of four bachelor males recorded in 2018 in the same colony. The call rate in both "lone" and "group" playbacks was about one call or one vocal exchange every 30 seconds to respect the mean natural call rate in the population (24.1 ± 20.2 s, measured on 21 males in the same colony in 2017). In "group" playbacks, the

order of the males calling was different in each playback in order to avoid bias related to female preference for the leading signaller, as shown in bush crickets (Hartbauer et al., 2014).

Playback procedure

To ensure that the female response is related to the broadcast stimulus and not to the burrow from where we broadcast the stimulus, we used artificial burrows as we already did in previous experiments (Gémard et al., 2021). Prior to the beginning of the breeding season, we dug four artificial burrows at the edge of the colony. All artificial burrows were identically made of a chamber, a tunnel, and an access above the chamber for convenience. The chamber consisted of a clay pot diameter 30 cm upside down, and the tunnel consisted of a 90-centimetre plastic gutter. We added a PVC pipe diameter 120 mm above the chamber to reach easily the birds and/or the egg. Burrows were 16-centimeter deep and covered by the existing vegetation. A wooden board and a stone recovered the hole above the chamber, similarly to the other monitored burrows of the colony.

Playback session took place at night during the vocal activity of the colony: from 10:00 pm to 3:00 am (unpublished data). To compare the attractiveness of a lone bachelor male calling and several bachelors calling, we broadcast a “lone playback” in one of the four artificial burrows and a “group playback” in another artificial burrow. The next night, we broadcast the same playbacks in the same two burrows but we switched playbacks with each other. The order of the broadcast stimulus pairs and the burrow pairs to use each night had been randomly determined prior to the experiment. At the end of the experiment, all burrows had been compared with each other, and each one of the four “lone playbacks” had been compared to each one of the four “group playback”. To mimic a male calling from the burrow, playbacks were broadcast from artificial burrows using a loudspeaker JBL Flip 4 (frequency response: 60 Hz- 12000 Hz ± 5 dB) connected to a SONY NWE393B at about 65 dB, the mean natural amplitude in the population (mean ± SD: 68.1 ± 11.0 measured using a sound level meter on 443 calls from 40 males of the same colony in January 2019).

We assessed the attractiveness of each playback type (“lone” / “group”) by counting the number of females flying or walking on the ground, and the time they spent, in a four-meter range around the entrance of the experimental burrow. To do so, each burrow was equipped with a Reconyx HP2X Hyperfire 2 camera trap placed towards the burrow entrance at four meters on a 50-centimeter wooden

stick. Thirty-second videos were automatically recorded when an animal was detected in the camera trap field of view. The 30-second videos were then analysed by a blind-to-the-experiment student who counted the flying and walking females, and the time they spend on the ground. To avoid the bias of considering breeders or transient individuals, we only counted individuals flying at a maximum distance of four meters from the burrow entrance, and individuals showing exploration behaviours on the ground such as walking in the direction of the burrow, moving head in all directions. Similarly, we looked at the attractiveness for predators. Brown skua are territorial and all four experimental burrows were in the territory of a couple (CG, FB, and TZ observations). We thus counted how many times the male or female brown skua came near the experimental burrows and the time they spent. In total, 21 visits of skuas and 19 females were detected during the 20 nights of the experiment: 12 females flying and 7 females walking.

Statistical analyses

Analyses results were implemented under the R software environment version 3.4.4 (R Core Team, 2018). To assess the attractiveness of "lone" and "group" playbacks, we used three Mann-Whitney tests to compare the number of females on the ground, the number of females flying, and the time females spent on the ground considering the playback type ("lone" / "group"). Similarly, we used two Mann-Whitney tests to compare the number of skuas on the ground and the time they spent considering the playback type ("lone" / "group"). Raw data are available in annex, in Tables A1 to A4.

Results

Attractiveness of male calls on females

Results of the two-choice experiments showed that "group" playbacks did not significantly attract more females on the ground (W = 133; *p*-value = 0.33; Figure 1A) nor females flying (W = 143; *P*-value = 0.68; Figure 1B) than "lone" playbacks. In average, females did not spend significantly more time close to burrows where we broadcast "group" playbacks than close to those where we broadcast "lone" playbacks (W = 4; *P*-value = 0.84; Figure 1.C).

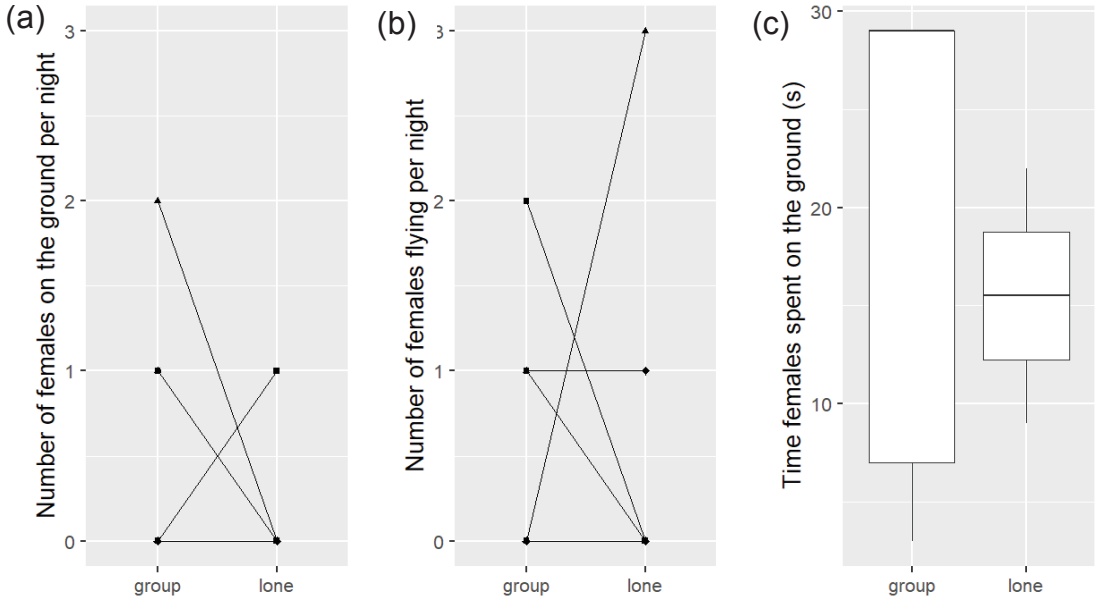


Figure 1. Attractiveness of the stimulus ("lone"/"group" playbacks) assessed with A: the number of females on the ground; B: the number of females flying; C: the time females spent on the ground. Each symbol corresponds to a burrow. Lines connect the two burrows used simultaneously each night for the two-choice experiment.

Attractiveness of male calls on predators

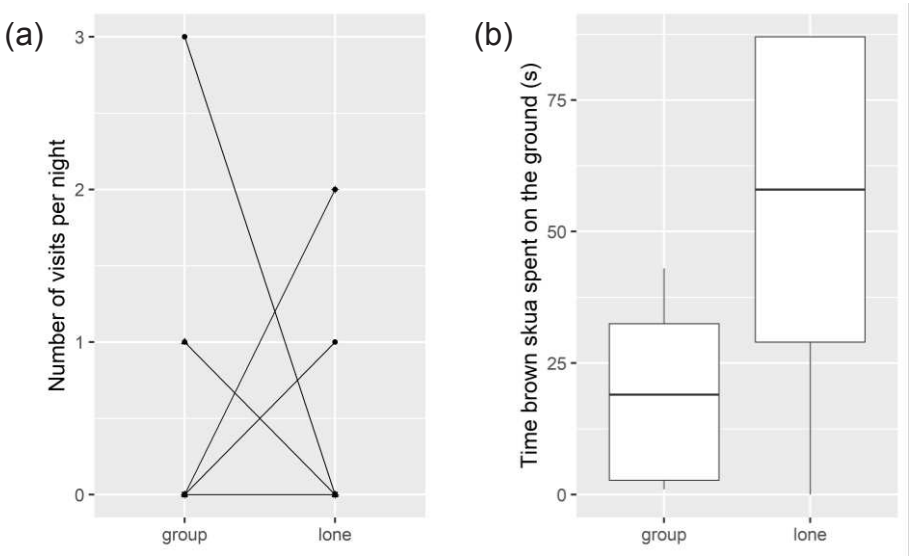


Figure 2. Attractiveness of the stimulus ("lone"/"group" playbacks) assessed with (a) the number of visits by brown skuas; (b) time brown skuas spent on the ground. Each symbol corresponds to a burrow. Lines connect the two burrows used simultaneously each night for the two-choice experiment.

Results of the two-choice experiments showed that "group" playbacks did not significantly attract more brown skuas on the ground (W = 164.5; *p*-value = 0.64; Figure 2.A) than "lone" playbacks. However, they spent more time in average close to burrows where we broadcast "lone" playbacks than close to those where we broadcast "group" playbacks (W = 24.0; *P*-value = 0.03; Figure 2.B).

Discussion

We aimed to assess whether male clustering within breeding colonies may be related to female mate choice in Antarctic prions. Using an attractiveness experiment on the field, we compared the attractiveness of four males calling in partial synchrony and males calling in isolation. Although our experimental design successfully attracted females, results showed no significant effect of the numbers of males calling on the average number of females flying or walking close to the burrow, nor on the average time spent by females on the ground nearby. Grouped callers and lone callers equally attracted predators of Antarctic prions. Nonetheless, predators spent more time in proximity to lone callers.

Our results showed no relationships between the number of attracted females (either walking or flying) and the number of males calling, contrary to our first hypothesis. Based on previous studies on anurans (Bates et al., 2010; Rehberg-Besler et al., 2017) and insects (Hartbauer et al., 2014), we expected females to be preferentially attracted by males advertising in group. The absence of relationships in Antarctic prions may suggest that calling synchrony is not advantageous in this species. One explanation may be that overlap does not increase the active vocal space of male calls, although it seems very unlikely that the physic effect called "Beacon effect" does not apply to petrel calls (Bradbury, 1981; Buck & Buck, 1966). Another explanation – more plausible – is that signal detectability is not the main determinant influencing female mate choice, as we first assumed considering that Antarctic prions live in environmental conditions constraining vocal communications.

Our results showed no relationship between the number of males calling and the time females spent on the ground. This absence of relationship between time on the ground and play-backed male calls have been found in previous attractiveness experiments in blue petrels, a burrowing petrel ecologically and phylogenetically close to Antarctic prions (Gémard et al., 2021). We hypothesized that, once the female lands, additional signals may be needed. For instance, males vocally react to females calls, likely to show motivation and sexual arousal (e.g. female-directed calls: Gémard, et al., *in press*) and possibly to guide the female to the burrow (Storey, 1984). Olfactory signals may also guide females to the burrow and/or indicate the presence of the caller (e.g. burrow or body odour: Bonadonna & Nevitt, 2004; Leclaire et al., 2017; Mardon et al., 2010). In absence of these signals, females would not benefit to stay

on the ground where it is vulnerable to predation (Mougeot & Bretagnolle, 2000). Although our results are consistent with previous studies, they should be interpreted carefully due to the small sample size.

Our results showed that the number of Antarctic prions calling did not influence the number of visits by its main predator, the brown skua. It supports the idea that brown skuas opportunistically detect and locate Antarctic prions using their calls, as previously shown (Mougeot & Bretagnolle, 2000). Nonetheless, brown skuas spent more time close to burrow of lone caller, perhaps because grouped callers cause confusion and prevent the predator to concentrate on an individual (Lehtonen & Jaatinen, 2016). After hearing a skua call, burrowing petrels decrease their vocal activity, likely to reduce conspicuousness (Mougeot & Bretagnolle, 2000). Hence, there is no mobbing in this species, but vocalizing in synchrony with conspecifics may be a strategy of self-predation avoidance based on the dilution effect. Even though there may be a dilution effect in male groups, it does not seem to be an influent determinism in female mate choice.

Based on our results, we may hypothesize that female mate choice is not driven solely by the detectability of male calling nor by the advantages provided by the group including reduced predation risk. One may hypothesize that females may choose males on information carried by their calls. In Antarctic prions, male calls carry information about the caller identity, morphological characteristics and sexual motivation (Gémard et al., 2019, 2021). These characteristics related to potential male qualities may influence female mate choice, as amply demonstrated in birds (Catchpole & Slater, 2008). We may thus hypothesize that informative content of male calls is the most discriminant factor in female mate choice, regardless of its range of detection. Similarly, in another burrow-nester seabird, the Manx shearwater (*Puffinus puffinus*), females are not preferentially attracted by males calling outside, even though they are more detectable than males calling from their burrow (Storey, 1984).

Contrary to other seabirds, Antarctic prion bachelors do not form “clubs” like Larids, nor “prebreeding aggregations” like gulls, nearby or adjacent to the colony (Kharitonov & Siegel-Causey, 1988). Bachelors and breeders seem randomly distributed within the breeding colony of Antarctic prions. Nonetheless, when looking carefully we found opposite patterns of bachelor distribution and looked for prospective factors. This present study indicates that female preference for one of these patterns cannot explain them. Further alternative factors may explain bachelors’ nest site selection, for

instance microhabitat preferences, or even sympatry. Patterns of nest formation in burrow-nesters remains unclear and further work is needed to fully understand the colony phylogeny and ontogeny in burrow-nester seabirds (Kharitonov & Siegel-Causey, 1988).

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

Permits – Experiment described was made in compliance with guidelines established by both IPEV and CNRS for the Ethical Treatment of Animals. 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. The Ethical Committee of Reserve Naturelle des Terres Australes et Antarctiques Françaises (TAAF) reviewed and authorized the experiment.

Data availability – Data generated for this study are available in supplementary material.

Authors' contributions – All authors made substantial contributions to conception of experiment, analysis and interpretation of data, and critical review of the manuscript. CG, FB and TA contributed to the study conception and design. CG, AL, and TZ performed material preparation and data collection. CG analysed the data. The first draft of the manuscript was written by CG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Appendices

Table A1. Raw data of the number of Antarctic prion females *P. desolata* attracted by the "group" and "lone" playbacks, respectively mimicking a four-male group and a lone male calling.

Julian date	Burrow ID	Playback	Flying female	Walking females
1	107	lone	0	0
1	113	group	0	0
2	110	lone	0	0
2	113	group	0	0
3	113	lone	0	0
3	110	group	**1**	**2**
4	107	lone	0	0
4	110	group	0	1
5	110	lone	0	0
5	107	group	0	0
6	107	lone	**1**	0
6	110	group	**1**	0
7	110	lone	0	0
7	107	group	0	0
9	112	lone	0	**1**
9	110	group	0	0
10	113	lone	**1**	0
10	107	group	0	0
11	107	lone	0	0
11	113	group	0	0
12	112	lone	0	**1**
12	107	group	0	0
13	107	lone	0	0
13	112	group	0	0
357	107	lone	**1**	0
357	110	group	**1**	0
358	110	lone	**3**	0
358	107	group	0	0
359	112	lone	0	0
359	113	group	0	0
360	113	lone	0	0
360	112	group	**1**	**1**
361	110	lone	0	0
361	112	group	**2**	0
363	113	lone	0	0
363	107	group	0	0
364	107	lone	0	0
364	113	group	0	0
365	112	lone	0	0
365	107	group	0	**1**

Table A2. Raw data of the time Antarctic prion females *P. desolata* spent on the ground nearby the burrow where "group" and "lone" playbacks were broadcast, respectively mimicking a four-male group and a lone male calling.

Julian date	Burrow ID	Playback	Duration (s)
3	110	group	29
3	110	group	3
4	110	group	7
9	112	lone	9
12	112	lone	22
360	112	group	29
365	107	group	29

Table A3. Raw data of the number of brown skuas (*S. antarcticus)* attracted by the "group" and "lone" playbacks of its prey (Antarctic prions *P. desolata*), respectively mimicking a four-male group and a lone male calling.

Julian date	Burrow ID	Playback	Predators
1	107	lone	0
1	113	group	0
2	113	group	0
3	110	group	0
3	113	lone	2
4	110	group	0
5	107	group	3
5	110	lone	0
6	107	lone	1
6	110	group	0
7	107	group	4
7	110	lone	4
9	112	lone	0
10	113	lone	0
11	107	lone	0
12	107	group	3
12	112	lone	0
13	107	lone	2
13	112	group	0
357	107	lone	0
357	110	group	1
358	107	group	1
358	110	lone	0
359	112	lone	0
359	113	group	0
360	112	group	0
360	113	lone	0
361	110	lone	0
361	112	group	0
363	107	group	0
363	113	lone	0
364	107	lone	0
364	113	group	0
365	107	group	0
365	112	lone	0

Table A4. Raw data of the time brown skuas *S. antarcticus* spent on the ground nearby the burrow where "group" and "lone" playbacks of its prey (Antarctic prions *P. desolata*) were broadcast, respectively mimicking a four-male group and a lone male calling.

Julian date	Burrow ID	Playback	Duration (s)
5	107	group	29
5	107	group	1
5	107	group	29
6	107	lone	4
7	107	group	43
7	107	group	43
7	107	group	43
7	107	group	2
7	110	lone	87
7	110	lone	87
7	110	lone	87
7	110	lone	87
3	113	lone	29
3	113	lone	0
12	107	group	6
12	107	group	10
12	107	group	2
13	107	lone	58
13	107	lone	58
358	107	group	3
357	110	group	28

CHAPTER IV

BURROW EFFECT ON CALL PROPAGATION AND ATTRACTIVENESS

(photo credits : Jean-Yves Barnagaud)

In blue petrels and Antarctic prions, males vocalize from their burrow. As a hollow structure, burrow is likely to modify these signals, and consequently the sound modification related to the burrow may be an additional source of information for females. Considering the crucial role of the burrow in burrowing petrels' breeding ecology, it may influence female mate choice. In this chapter, I explored the effect of the burrow on male call propagation, and I compared the attractiveness of burrows with different dimensions.

ARTICLE 6

Burrow effect on call propagation and its influence on female mate choice in the blue petrel *Halobaena caerulea*

Charlène Gémard[a,b*], Léo Maucourt[a], Francesco Bonadonna[a], Thierry Aubin[b]

*Correspondence: C. Gémard, CEFE-CNRS UMR 5175, 1919 route de Mende, 34295 Montpellier, France.

E-mail address: charlene.gemard@cefe.cnrs.fr (C. Gémard)

[a] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[b] Neuro-PSI-CNRS, UMR 9197, Université Paris-Saclay, 91405 Orsay, France

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Abstract

The key in animal communication is that receiver gets the signal sent by the emitter through the environment. Receivers may use information carried by signals to make decisions and react accordingly. Nonetheless, attenuation and degradation processes constrain communication by modifying the signal structure and impairing its informative content. Few anurans, insects, and bats use particular hollow structures of their environment as natural amplifiers to improve the propagation of their vocal signals and thus increase their detectability by conspecifics. In a burrow-nester seabird, the blue petrel (*Halobaena caerulea*), burrow has a crucial role in breeding ecology and possibly in male-female vocal communication. Here we investigated whether particular burrow characteristics: (i) improve the propagation of male calls; and (ii) influence female mate choice. A propagation experiment in natural burrows showed that male calls propagate on long distances, suggesting a large active space. The spectral structure of calls is less degraded than amplitude and frequency modulations over distance, emphasizing the relevancy of this parameter in coding strategy in blue petrels. Calls emitted from burrow with large chamber and/or large tunnel are less degraded with distance. A two-choice test showed that females are preferentially attracted by calls emitted from shallow than deep burrows, but the chamber volume had no effect on female attractiveness. We discuss the hypothesis that burrow detectability related to its dimensions may not be as influential in female mate choice as previously hypothesized.

Keywords: burrow, sound propagation, mate choice, seabirds, blue petrels

Introduction

Acoustic signals including calls, songs, and mechanical sounds, are ubiquitous in animal kingdom. One of their main advantages is to travel without a trace on great distances despite obstacles. They are thus involved in long-range signalling and mediate a wide variety of behaviours at the basis of social interactions, including mate choice, group cohesion, predator avoidance, and territoriality (Catchpole & Slater, 2008). Nevertheless, acoustic signals suffer from environmental constraints that affect their transmission from emitters to receivers. Considering the implications of acoustic signals in animal social interactions, a bad transmission impairing the informative content of the signal may have strong consequences on fitness. Theoretically, sexual selection should thus favour signals propagating efficiently in the environment (Marten et al., 1977).

The most important environmental constraint on sound signal propagating is the geometric attenuation caused by spherical spreading. In theory, the sound pressure level of a signal drops by six decibels per doubling of distance in the atmosphere (inverse square law: Wiley & Richards, 1982). Several factors accentuate this predicted attenuation such as temperature gradients, humidity, heterogeneities, obstacles on the transmission path. This extra attenuation is called excess attenuation, an umbrella term for a number of habitat-induced effects (Larsen, 2020). During propagation, signals may also suffer from modifications of their spectral and/or temporal structure. The echo, which modifies the temporal parameters and amplitude of acoustic signals, is a well-known example of degradation by reverberation. Spectral parameters of acoustic signals are sensitive to degradation and attenuation too. Low frequencies (under 2 kHz) generally propagate further than high frequencies, most absorbed by the atmosphere (Naguib & Wiley, 2001; Marler & Slabbekoorn, 2004). Low frequencies emitted close to the ground are filtered and degraded too (e.g., “ground effect”: Morton, 1975; Marten et al., 1977).

Signal attenuation and degradation are major problems in long-range communication. Most often, species limit these problems by using strategies to optimize signal transmission. Some strategies consist in modifying the signal design according to the physical properties of the environment. For instance, vocalizations emitted are lower-pitched in forests than in open habitats because dense vegetation filters high frequencies. Similarly, vocalizations are often higher-pitched in urban areas than in natural habitats

as a consequence of low-pitched anthropic noises (Kirschel et al., 2009; Luther & Derryberry, 2012; Slabbekoorn et al., 2007). In noisy habitats, the well-known Lombard effect occurs when signallers increase the amplitude of their vocalizations accordingly with the ambient noise to increase the signal-noise ratio and thus the active space of the signal (reviewed in birds in Brumm & Zollinger, 2013).

Another strategy to lessen signal degradation during propagation consists in choosing an appropriate signalling site and taking advantage of its physical properties. To illustrate, natural hollow structures such as leaves, trunks, burrows, have resonant properties and amplify all or part of acoustic signals. The Spix's disc-winged bat (*Thyroptera tricolor*) calls from tubular leaves, similarly to acoustic horns. The particular shape and resonant properties of such leaves enhance the call amplitude up to 9 dB and increase frequencies about 30 kHz (Chaverri & Gillam, 2013). *Eusophus* frogs call from burrows which amplify their own vocalizations but also those of their conspecifics from outside (Muñoz & Penna, 2016; Penna & Solís, 1996). In burrowing crickets, males use underground burrows as sound baffle. This system reduces attenuation and spreading loss during sound transmission (Forrest, 1982).

The first studies on sound propagation took place in coastal environments (Henry, 1878 in Douglas & Conner, 1999), which are considered as restricting for sound propagation. Tubenose seabirds, also called petrels (Procellariiformes), are mainly burrow-nesters: 65% of tubenoses live in underground burrows during the breeding period (Warham, 1990). Burrows consist in two parts: the access tunnel, cylindrical; and the spherical chamber. Before seeking for mates, male petrels dug their burrow themselves using their legs and beak, or they appropriate an unoccupied burrow. Burrow has a double function: it protects its occupants (adults, egg or chicks) from the strong temperature variations, bad weather, and terrestrial predators like skuas and gulls. After pairing, pairs renew to the same burrow year after year (Warham, 1990).

In burrowing petrels, burrow should also hold a central place in vocal communication, particularly in pair formation. Bachelor males seeking for potential mates vocalize at night from the chamber of their burrow, likely to attract females and potentially repel other males (Bretagnolle, 1996; Catchpole & Slater, 2008; Gémard et al. *in press*). In another burrow-nester petrel, the Manx shearwater (*Puffinus puffinus*), burrow acts as a natural amplifier that increases amplitude at its entrance. However, it does not increase the propagation distance of the signal and the wall of the burrow may filter particular

frequencies (Storey, 1984). To go further, we here propose to: (i) study the propagation of male call; (ii) assess the effect at long range of the burrow structure on calls emitted from the chamber; (iii) investigate the influence of burrow characteristics on female mate choice. Here, we focused on a burrowing petrel: the blue petrel (*Halobaena caerulea*). We hypothesized that the degradation of the acoustic structure of calls, especially in amplitude and frequency domains, should vary with the burrow structure (Muñoz & Penna, 2016; Penna & Solís, 1996, 1999). Burrows that reliably propagate signals on long distance should be more detectable and thus more attractive for females.

Material and methods

Study site and species

We carried out our experiments in the natural colony of blue petrels (*Halobaena caerulea*) of the Ile Verte (49°51′S, 70°05′E), Kerguelen archipelago, South Indian Ocean. Fieldwork was performed during two consecutive breeding seasons. We carried out propagation experiments and took measurements of natural burrows the 26th December 2018. We installed artificial burrows, carried out propagation experiments and two-choice tests from 30th November 2019 to 17th December 2019.

Propagation experiment

Propagation experiment consisted in broadcasting calls of petrels in burrow chambers to describe the natural degradation of the sound at several distances from the burrows. We broadcast the signals during the day, in ideal climatic conditions (no rain, wind speed < 5 km/h) to limit atmospheric turbulences on sound propagation.

We used the signal-processing software Avisoft SASLab Pro v5.2.11 (Specht, 2017) to build four signals of four males, recorded in the same colony in 2013. Each of the four calls consisted in five phrases separated by a silence of 200 ± 60 ms (all uncertainties units in mean ± SD otherwise stated; total duration: 5.5 ± 1.6 s). We broadcast all four calls in natural burrows in the blue petrels' colony. We choose eight representative but easily accessible natural burrows with a single tunnel. We also selected an artificial burrow (no. 99, Table 1) installed and occupied during the previous breeding season 2018-2019 to compare the sound transmission with natural burrow. For the nine burrows, we measured the length, width and height of the tunnel, and the chamber using a metal rule. We estimated the tunnel

volume using the formula for the volume of an elliptical cylinder: $V = \pi \times a \times b \times h$, with *a* the length of the major half-axis base, *b* the length of the minor half-axis base, and *h* the cylinder height. We also estimated the chamber volume by filling it with vermiculite and weighting the vermiculite quantity needed. Finally, we calculated the resonance frequency of each burrow using the formula for a Helmholtz resonator, which is the best approximation of a petrel burrow: $f = \frac{c}{2\pi}\sqrt{\frac{S}{LV}}$ with *c* the sound speed (340 m/s), *S* the area of the burrow entrance (section in m²), *L* the tunnel length (in m), and *V* the chamber volume (in m^3). The characteristics of each burrow are given in Table 1.

Table 1. Characteristics of blue petrels' burrows. Measurements in centimetres, volumes in litres.

Burrow	Tunnel volume (L)	Tunnel length (cm)	Tunnel height (cm)	Tunnel width (cm)	Chamber volume (L)	Chamber length (cm)	Chamber height (cm)	Chamber width (cm)	Resonance frequency (Hz)
94	6.01	63.00	9.00	13.50	5.29	40.00	14.00	40.00	91.59
99*	3.69	53.00	8.25	10.75	5.96	32.00	17.00	32.00	80.38
67	7.27	65.00	9.50	15.00	11.16	56.00	14.00	26.00	67.23
106	3.92	56.00	8.50	10.50	3.61	33.00	22.00	10.00	100.79
EU	7.54	60.00	10.00	16.00	6.33	32.00	14.00	32.00	98.45
EF	1.94	45.00	5.50	10.00	8.02	41.00	17.00	30.00	59.22
EJ	2.04	41.00	5.50	11.50	9.20	40.00	10.00	20.00	62.12
FF	1.22	27.00	5.50	10.50	10.07	43.00	15.00	28.00	69.91
90	5.88	72.00	6.50	16.00	8.60	34.00	20.00	29.00	62.17
Mean ± SE	***4.4 ± 2.2***	***53.6 ± 13.1***	***7.6 ± 1.7***	***12.6 ± 2.4***	***7.6 ± 2.3***	***39.0 ± 7.2***	***15.9 ± 3.4***	***27.4 ± 8.0***	***76.9 ± 15.5***

*Artificial burrow

We used a speaker JBL Flip 4 (frequency response: 60 Hz - 12000 Hz ± 5 dB) connected to a Sony NWE393B placed in the burrow chamber. The volume occupied by the speaker is close to the volume occupied by a blue petrel (about 0.7 L). Playback was broadcast at a natural sound pressure level (66 ± 9 dB: Gémard et al., 2019) and then recorded at each distance by 6 omnidirectional microphones Sennheiser K6-ME62 (frequency response: 20–20 000 Hz ± 2.5 dB). The first microphone was at the entrance of the burrow and the others at each doubling distance: 4, 8, 16, 32, and 64 m. Microphones were placed on metal sticks at 1m30 above the ground to avoid ground effect and mimic the perception of a flying female. Microphones were connected to an eight-channel recorder Roland R-88 (sampling frequency: 44.1 kHz, dynamic: 16 bits) using remote control transmitters Sennheiser EW110-G3.

Recorded calls were analysed using Avisoft SASLab Pro v5.2.11. They were first down-sampled from 44.1 to 11.025 kHz to increase the precision of frequency measurements. On each phrase of each call, we measured three acoustic parameters describing the whole phrase structure: Amplitude Modulations (AM), Frequency Modulations (FM), and Spectral Structure (SP). These three parameters are likely to be crucial in female mate choice as their sensitivity to attenuation and degradation processes makes them determinant for the active space of the signal (Marten et al., 1977; Larsen, 2020). We measured AM, FM, and FFT, on the envelope, the sonogram, and the linear amplitude spectrum (resolution: 1.0 ms, 43.0 Hz, 0.17 Hz, with FFT length = 1024), respectively. For each parameter, the measurements of the five phrases of a same call were averaged.

Artificial burrows

Because the dimensions and structure of natural burrows cannot be accurately controlled, we used artificial burrows to test whether particular characteristics of the burrow modify the call transmission and/or are attractive to females. Artificial burrows are made of a clay-pot chamber (volume = 4.8 L) and PVC-gutter tunnel (volume = 5 L). We buried four artificial burrows at the beginning of the 2019- 2020 breeding season, at the edge of the colony to simulate natural males in a natural habitat, while limiting vocal interferences from blue petrels and human disturbances in the colony. Two artificial burrows were buried at 16 cm (hereafter referred as “deep”), and two at 8 cm (“shallow”) from the surface. We covered them with the existing soil and vegetation to avoid bias in sound propagation related to vegetation density. To check whether sound propagation in natural and artificial burrows was similar, we carried out a second propagation experiment in the four artificial burrows following the same protocol and using the same equipment. As blue petrel calls were not recordable (i.e., below the background noise) after 16 m in most cases, we focused on shorter distances this time and recorded the play-backed calls at the burrow entrance, 2, 4, and 8 m (Figure A1).

Two-choice experiment

We used two-choice experiments to compare the attractiveness of male calls broadcast in regard to different burrow characteristics. Experiments were carried out during the birds’ activity (10:00 pm to 03:00 am). It consisted in broadcasting the same playback in two different burrows at the same time

(e.g. deep *versus* shallow burrow). To do so, we used the same equipment that we used in propagation experiment: a JBL Flip 4 speaker connected to a Sony NWE393B placed in the burrow chamber. The broadcast signals were the four signals already used for the propagation experiments. We broadcast a call every 40 s, to respect the natural call rate observed in our bird population (Gémard et al., 2021).

We chose to test two characteristics that may influence the sound propagation and the breeding success of blue petrels: depth and chamber volume. We hypothesized that deep burrows are advantageous because they are more difficult to excavate for predators. Burrows with a small chamber may be more advantageous for temperature regulation, especially in species with a particular incubation routine like blue petrels (Chaurand & Weimerskirch, 1994). We first tested the burrow depth and compared the attractiveness of "deep" burrows (16-centimeter deep) versus "shallow" burrows (8-centimeter deep). In a second step, we reduced the chamber by adding two litres of soil in the chamber, and we compared the attractiveness of reduced versus unreduced burrows following the same protocol.

We used the number of attracted individuals (in flight and on the ground) as a proxy of the burrow attractiveness. We photographed attracted blue petrels in a four-meter range around the burrow entrance using phototraps. To do so, we placed a phototrap on a 30-centimeter wooden stick, at four-meter from the entrance. Photos were analysed by a blind-to-the-experiment student that counted the number of females approaching the burrow while flying or walking on the ground. In total, we pictured 23 females the 17 nights during which the experiment took place.

Statistical analyses

All statistical analyses were implemented in the R environment version 3.6.2 (R Core Team, 2018).

Propagation experiment

First, we graphically checked the correlations between the burrow characteristics (Figure A2). Based on the correlation matrix, we chose to keep the chamber volume and the tunnel volume to describe the burrow structure in the next analyses. Second, the average measurements obtained at each distance were compared to the average measurements obtained at the entrance of the burrow using a Pearson correlation (Mathevon et al., 1996). We used the obtained correlation coefficient as an index of sound degradation (hereafter referred as "CCI"). We used a beta regression model to fit our index of sound degradation CCI, which was beta-distributed (i.e. with a continuous distribution on the finite range 0 to

1 with a peak on the right end; Bolker et al., 2009). The independent variables are the chamber volume, the tunnel volume, and the distance. Models assumptions were graphically checked (Zuur & Ieno, 2016).

Two-choice experiment

We used GLM with Poisson distribution to model the number of attracted females (either on the ground or flying) according to the burrow characteristics. Due to small sample size, we realized four independent models to test the effect of burrow depth (shallow/deep) or chamber volume (reduced/unreduced) on the number of females on the ground or the number of females walking. Models assumptions were graphically checked (Zuur & Ieno, 2016).

Results

Propagation experiment

Results of the propagation experiment in blue petrel burrows show a classical pattern of sound propagation (Figure 1). Distance had a negative effect on the CCI of the three acoustic parameters: AM, FM and SP, meaning that the longer the distance, the worst the parameter degradation (Figure 1, Table 2). The SP of calls seems less degraded and attenuated with distance whereas AM and FM rapidly decrease. SP variations between burrows are smaller than AM and FM variations (Figure 1, Table 2). Natural and artificial burrows had similar degradation pattern graphically (Figure 2, Figure A1).

Table 2. Beta regression results. *p* values under 0.05 in bold.

	Estimate	SE	*z* value	*p* value
Amplitude Modulations (AM)				
Intercept	1.467	0.446	3.291	0.001
Chamber volume	- 0.010	0.043	- 0.222	0.824
Tunnel volume	**0.200**	**0.045**	**4.421**	**< 0.001**
Distance	**- 0.172**	**0.016**	**- 10.909**	**< 0.001**
Frequency Modulations (FM)				
Intercept	0.779	0.448	1.739	0.082
Chamber volume	**0.091**	**0.044**	**2.065**	**0.039**
Tunnel volume	**0.092**	**0.045**	**2.039**	**0.042**
Distance	**- 0.129**	**0.015**	**- 8.579**	**< 0.001**
Spectrum (SP)				
Intercept	0.785	0.063	12.418	< 0.001
Chamber volume	**0.015**	**0.006**	**2.420**	**0.018**
Tunnel volume	**0.014**	**0.006**	**2.199**	**0.031**
Distance	**- 0.019**	**0.002**	**- 9.914**	**< 0.001**

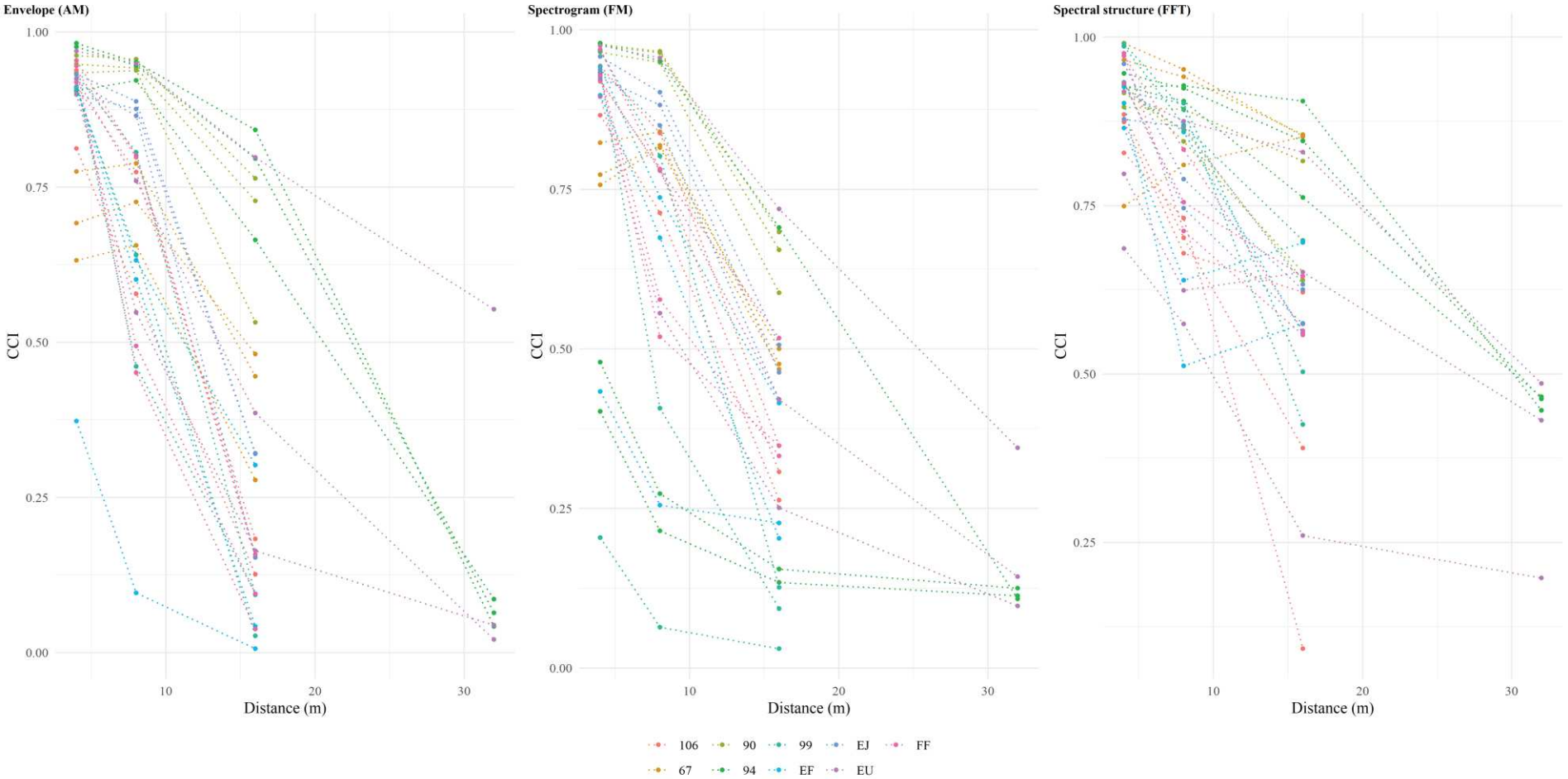

Figure 1. Degradation of three acoustic parameters of male calls in the blue petrel *Halobaena caerulea*: Amplitude Modulations (AM), Frequency Modulations (FM), Spectral Structure (SP). Each colour indicates a burrow. Lines link the measurements taken on the same call in a same burrow.

Calls propagated further in the burrows no. 94 and EU (up to 32 m whereas calls were not recordable after 16 m in other burrows: Figure 2). Sound propagation is also better in burrows no. 67 and 90 than in other burrows. These four burrows have a tunnel volume higher than the mean volume (table 1). Results of the beta regressions show that the tunnel volume has a positive effect on the CCI of the three acoustic parameters, suggesting that they are less degraded when sound is emitted from burrow with a big tunnel (Table 2). The chamber volume has a positive effect on the CCI of the FM and FFT too. The effects of the chamber and tunnel volumes are similar with the same magnitude (Table 2).

We obtained similar results with the propagation carried out in artificial burrows: CCI of AM and FM quickly decrease with distance, whereas FFT is steadier. Calls propagate further in unreduced burrows than in burrows with a reduced chamber (Figure A1).

Two-choice experiment

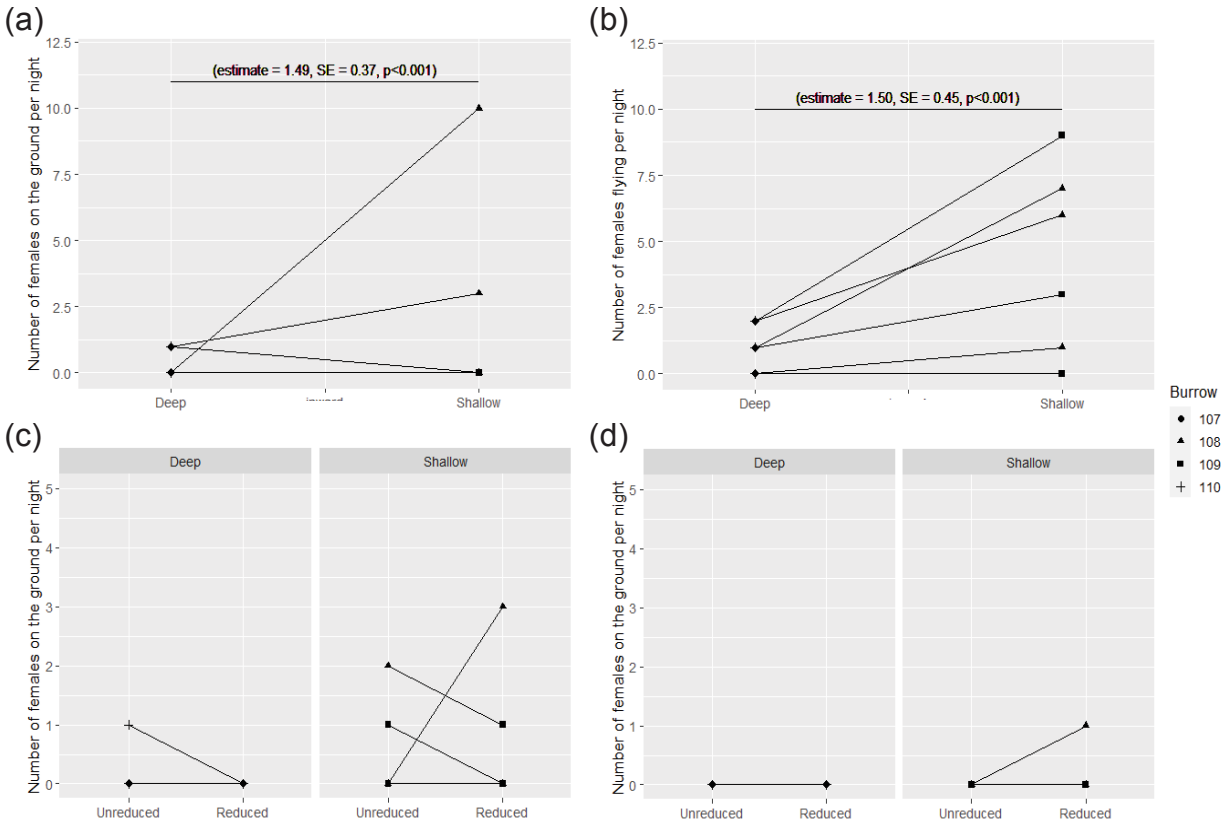

Figure 2. Attractiveness of burrows with different characteristics to females: (a) number of females on the ground according to burrow depth; (b) number of females flying according to burrow depth; (c) number of females on the ground according to burrow volume; (d) number of females flying according to burrow volume.

Results of the two-choice experiment show a significant effect of the burrow depth on the number of females attracted (Figure 2). Shallow burrows attracted in average more females on the ground and flying than deep burrows (estimate = 1.49, SE = 0.37, $p < 0.001$; estimate = 1.50, SE = 0.45, $p < 0.001$, respectively). No significant effect of the reduction of the chamber volume was found on females on the ground or flying (estimate = -0.22, SE = 0.71, p=0.75; estimate = 1.16, SE = 0.80, $p = 0.14$, respectively; Figure 2).

Discussion

Prior works highlighted the effectiveness of hollow structures in long-range signalling, mostly in insects and anurans. In this study, we aimed to assess whether burrow characteristics have an effect on the propagation of male calls in a burrow-nester seabird, the blue petrel *H. caerulea*. Using a propagation experiment in natural and artificial burrows, we found that three acoustic parameters measured – AM, FM, and SP – quickly degrade and/or attenuate as distance increases, especially AM and FM. The degradation/attenuation pattern was similar for artificial and natural burrows. The volumes of the tunnel and chamber are positively related to the modification of the FM and spectral structure over distance. The volume of the tunnel is also positively related to AM modification over distance. The spectral structure was less degraded with distance and varied less between burrows than AM and FM. Resonance frequency of burrows are about 76 Hz, and thus outside the petrel spectrum. In a second part, we tested the attractiveness of two burrow characteristics, depth and chamber volumes, using a two-choice experiment. We found that females are preferentially attracted by male calls emitted from a shallow burrow than a deep burrow. We found no significant effect of the chamber reduction on female attractiveness.

Male calls were recorded up to 32 meters, showing that they have a large active space (i.e. maximum distance at which the receiver can detect the signal from the background noise, Marten et al., 1977; Brenowitz, 1982) and they are thus likely to be involved in long-range signalling. The active space of male calls is difficult to estimate because: (i) petrels are likely to have better auditory abilities than microphones but so far, they are unknown; and (ii) we carried out call propagation in ideal conditions, but blue petrels breed in noisy colonies in windswept areas. For example, atmospheric turbulences and

hetero/conspecific interferences are two sources of background noises that mask the signal and reduce its detectability. Moreover, as experimentally shown in songbirds, detection does not imply discrimination and the distance at which a female blue petrel may discriminate a male call in the hubbub of the colony is smaller than the detection range (Brenowitz, 1982; Dabelsteen et al., 1993).

During transmission through the atmosphere, male calls are degraded and attenuated with the distance, like any acoustic signals. AM and FM structures are the most degraded. Several attenuation and degradation processes, including absorption and scattering, mainly affect amplitude and high frequencies (Naguib & Wiley, 2001; Wiley & Richards, 1982). Even though the blue petrel spectrum is quite low (frequency range between 300 and 1000 Hz; mean F0 ± SD: 466.6 ± 64.2 Hz), frequency and amplitude modulations in male calls are severely degraded over distance. Similarly, in starling songs (*Sturnus vulgaris*) low frequencies in the 0 - 1 kHz range are strongly attenuated (Mathevon et al., 1997). It suggests the existence of additional sources of frequency attenuation and/or degradation. For instance, the petrel calls are emitted from underground burrows and it would be unlikely that the ground effect (Morton, 1975) does not apply on these low-pitched calls.

Compared to AM and FM, the spectral structure is the less degraded parameter in calls of male blue petrels during the signal propagation. Spectral structure is thus the most detectable and discriminable parameter over distance and may code for information of interest. This result is consistent with previous studies that highlight the implication of energy spectral distribution (i.e. fundamental frequency and frequencies corresponding to energy quartiles) in coding pieces of information about the caller, such as the individual identity, and aggressive and sexual motivations (Gémard et al., 2019; Gémard et al. *in press*). Moreover, the spectral structure is less affected by the burrow characteristics than AM and FM are. Spectral structure of male calls may thus reliably provide static and dynamic information of interest in long-range interactions, regardless of the burrow characteristics.

Most notably, females are preferentially attracted by shallow burrows than deep burrows. Because the sound attenuation by the chamber walls is less pronounced in shallow burrows than deep burrows, the former may be more detectable, and thus more attractive. This result is consistent with sexual selection theory stating that signals propagating efficiently should be favoured because they are more detectable and they reliably convey the information more (Marten et al., 1977). Nonetheless, results also

show that females are similarly attracted by calls emitted from large burrows than small burrows, although the former propagate sound better. It suggests that detectability is not the only determinant criteria in female mate choice. It would be consistent with previous studies suggesting that the most detectable male calls are not necessarily the most attractive to females (Gémard et al., 2021). Another explanation is that the burrow detectability is more related to its depth than its dimensions. It would be consistent with the fact that resonant frequency of petrel burrow is outside the spectrum of male calls, meaning that burrows do not amplify particular frequencies of interest, contrary to burrows of *Eusophus* frogs (Muñoz & Penna, 2016; Penna & Solís, 1996, 1999).

To sum up, in blue petrels, male calls emitted from burrows may have a large active space. Their spectral structure, which code information of interest for females, is less degraded than the AM and FM over distances. These results emphasize the implication of male calls in long-range signalling between males and females. Burrow has an effect on call propagation and particular characteristics (volumes of chamber and tunnel) slightly limits the degradation of AM, FM, and spectral structure. Occupying structure with particular acoustic properties may thus be a strategy to improve the signal propagation. Nonetheless, burrows enhancing male call propagation do not preferentially attract females, suggesting that detectability may not be the main criterion in female mate choice.

Besides male call propagation, burrow might have further advantages in petrel vocal communication. In bats and frogs, particular song posts also amplify the incoming vocalizations (Chaverri & Gillam, 2013; Penna & Solís, 1996). To go further, in blue petrels, we may hypothesize that the burrow amplifies incoming vocalizations of conspecifics but also predators. After hearing a brown skua call, blue petrels decrease their vocal activity likely to reduce conspicuousness and limit predation risks (Mougeot & Bretagnolle, 2000). Amplification of vocalizations emitted outside the burrows may thus help predation avoidance and/or female detection. Further studies are needed to fully understand the functional role of the burrow in long-range signalling in burrowing petrels, and its implication in their breeding ecology.

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Competing interests – Authors declare they have no competing interests.

Permits – 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.

Data availability – Data will be available from an online data repository after publication.

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Appendices

Figure A1. Degradation of three acoustic parameters of male calls in artificial burrows of blue petrel *Halobaena caerulea*: Amplitude Modulations (AM), Frequency Modulations (FM), Spectral Structure (SP). Each colour indicate an artificial burrow. Empty circles represent burrows after chamber reduction, full circles burrows without chamber reduction. Lines link the measurements taken on the same call in a same burrow.

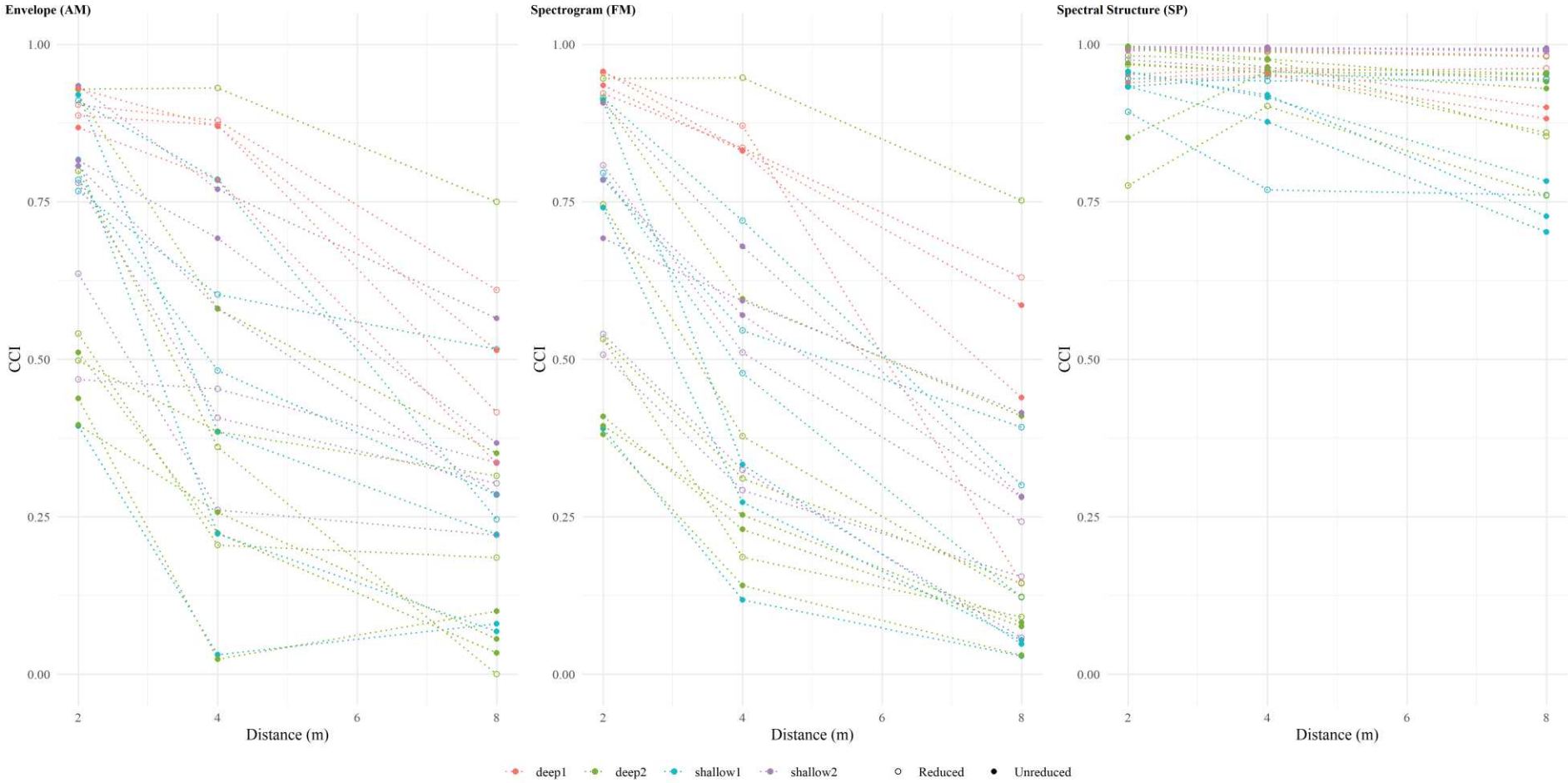
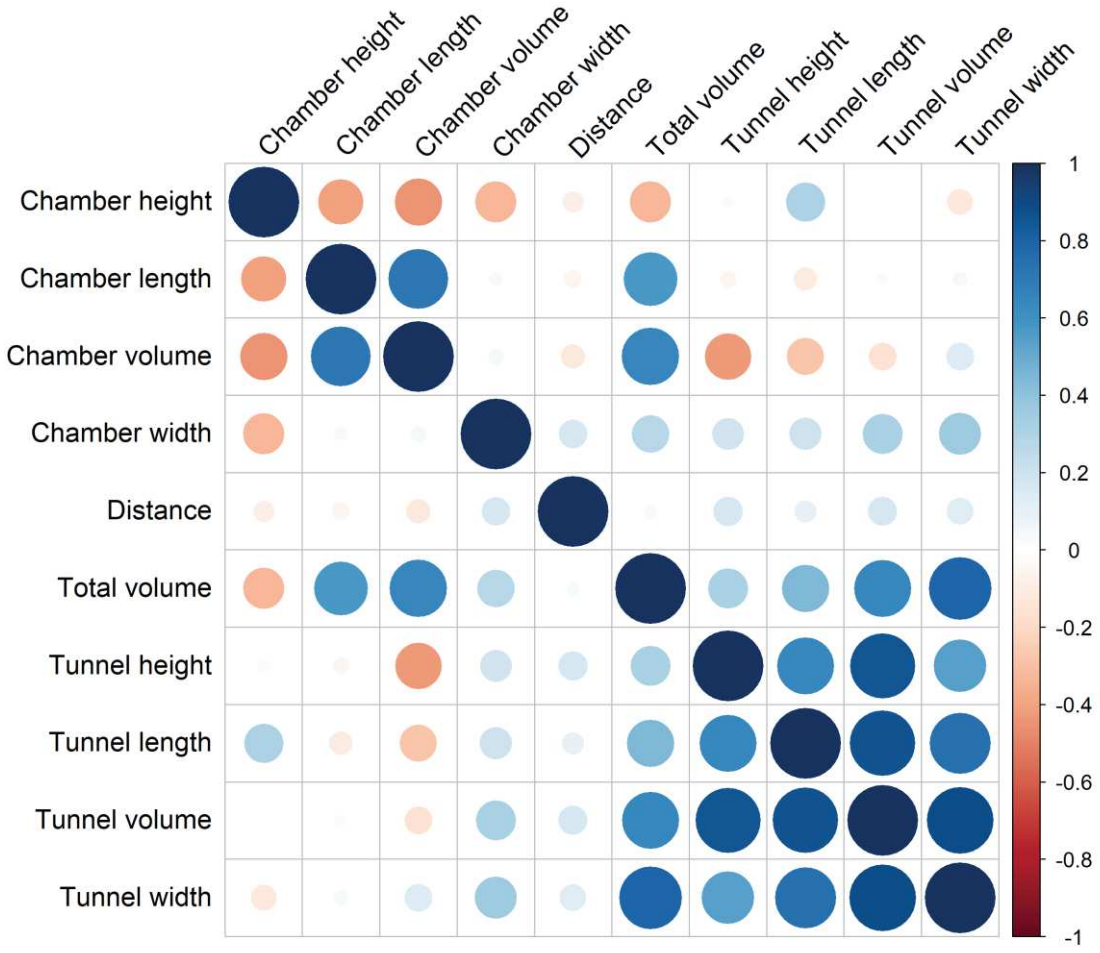


Figure A2. Correlation matrix with the characteristics of both parts of the burrow (tunnel, chamber) in the blue petrel *Halobaena caerulea*.



GENERAL DISCUSSION

(photo credits: Guilhem Battistella)

BRIEF REMINDER OF THE CONTEXT

Mate choice in burrowing petrels

Blue petrels *H. caerulea* and Antarctic prions *P. desolata* are burrow-nester seabirds that breed during the austral summer in crowded colonies close to the Antarctic Convergence. These long-lived birds are characterized by long partnerships with little extra-pair copulations (Quillfeldt et al., 2012), rare divorces and high nest fidelity (Bried et al., 2003; Warham, 1990). After pairing, pairs lay a single egg per year with no possibilities of clutch replacement and with a high bi-parental investment. In these species with a particular breeding ecology, breeding success relies on a perfect synchrony and a strong cooperation between mates (Bried & Jouventin, 2001; Warham, 1990). Choosing the wrong mate would lead to a low breeding success and consequently would have a negative effect on the individual fitness. Nonetheless, changing partner and/or breeding site have negative consequences too (Bried & Jouventin, 2001). The choice of a lifetime mate is thus crucial in burrowing petrels.

Reviewing and analysing the biology of these species, the non-formalised opinion of some researchers is that mate choice implies two steps relying on two communication channels separated in space and time: acoustic and olfactory. In a first step, long-range interactions between females in flight and males in their burrow rely on vocalizations from both sexes. In a second step, short-range interactions after female has landed and penetrated in the burrow may rely on additional signals including vocal duets and olfactory signals (Bonadonna et al., 2009; Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012). In this thesis, we got interested in the first step (i.e., long range interactions based on male calls), practically unknown, while the second step benefits from the last 20 years of research. Male calls are likely to attract females in burrow and may be the only channel for burrowing petrels to communicate on long distances (Bretagnolle, 1996; Warham, 1990, 1996), as nocturnality, distance, and burrow as a physical barrier impair the transmission of signals in other sensory modalities. Nonetheless, the propagation of vocal signals is constrained by several factors: vocal interferences of heterospecifics and conspecifics due to coloniality, climatic factors limiting sound

propagation, calling from an underground hollow structure modifying the sound, and predation pressure limiting the vocal activity in the colony.

Questions and hypotheses

In burrowing petrels, male calls seem to be at the heart of the first step of mate choice but their implications have been understudied. Do they influence female mate choice and if so, how? Using playback experiments in the field, I assessed the implications and determinisms of the only major call of bachelor males in male - female interactions. More precisely, I tested whether: (i) male calls actually attract females and if so, how; (ii) parameters of calls vary with the social context to ensure different functions despite the apparent stereotypy of calls; (iii) parameters of calls code for information of interest about the caller and/or its burrow.

Summary of the main results

In a first chapter, I investigated the relationships between acoustic parameters of male calls and static information about the caller characteristics. In both blue petrels and Antarctic prions, results show that spectral and temporal parameters of male calls encode information about the individual identity, the body size, and the bill and wing morphology of the caller.

In a second chapter, I assessed vocal variations related to motivational state of the caller in both species. Results show that males vocally react to the presence of a conspecific, either male or female, by producing male-directed and females-directed calls. These directed calls are characterized by different acoustic variations in both spectral and temporal domains. I tested whether males react similarly to any females and I found that the female-directed vocal response depends on the female proximity. The closer the female, the more intense the male vocal reaction. In birds, this is the very first evidence that males use the frequency shifts and/or tempo variations induced by the Doppler Effect in female flight calls as a distance cue to modulate their vocal response.

In a third chapter, I showed that static and dynamic pieces of information in male calls actually influence female mate choice in blue petrels. Females are more attracted by calls with particular acoustic characteristics including high-pitched calls, calls emitted with a high rate and possibly by calls with few syllables. The total duration of the call and the syllable rate of the call, however, have no influence on female attraction. Results also show that grouped and lone callers equally attract females.

In a fourth and last chapter, I investigated male-call propagation and the effect of the burrow on calls emitted from inside. Male calls propagate on long distances (a few dozen meters). Burrow, as a hollow structure, has an influence on call propagation. During propagation, envelope and frequency modulations of male calls are strongly degraded over distance, while the spectral structure is less degraded. Calls emitted from high-volume burrows (i.e., with a large chamber and/or large tunnel) are less degraded than calls emitted from small burrows. The propagation difference between burrows with large and small chambers does not influence female mate choice. Nonetheless, females are preferentially attracted by calls emitted from shallow burrows.

CODING STRATEGY IN MALE CALLS

As stated by the Mathematical Theory of Communication of Shannon & Weaver (1949), calls of blue petrel and Antarctic prion males encode a wide variety of information, including static information about caller's stable characteristics. For instance, in both species, male calls encode an individual signature (Chapter I), as shown in other seabirds (Aubin et al., 2007; Aubin & Jouventin, 2002; Bretagnolle, 1989; Charrier et al., 2001; Favaro et al., 2015, 2017; Jouventin et al., 1999; Robisson et al., 1993; Searby, 2004) and many other animal species (Charrier et al., 2003, 2009; Mathevon et al., 2010). Individual vocal signature in our two studied species is multi-parametric and mostly coded by the energy distribution and syntactic parameters (Chapter I), but not by the frequency value of the fundamental although this parameter is highly individualised in many other species, especially terrestrial mammals (Charlton et al., 2020). The vocal signature in burrowing petrel calls might provide the basis for individual vocal recognition (i.e., when an individual discriminates individuals from each other), required in many social behaviours (Tibbetts & Dale, 2007). Vocal individual recognition would thus

be added to chemical recognition (Bonadonna & Nevitt, 2004) and the two channels of communication may be used at different times/spaces. Nonetheless, individual vocal recognition highlighted in mate and parent-offspring interactions in many mammals and birds, including seabirds (Carlson et al., 2020), remains unknown in burrowing petrels and poorly studied in Procellariforms in general (Brooke, 1978; Curé et al., 2011). Besides vocal individuality, male calls provide information about the body size and bill and wing morphology of the caller. This information is coded in temporal parameters and syntax in blue petrels; in energy distribution and temporal parameters in Antarctic prions (Chapter I).

In blue petrels and Antarctic prions, male calls encode dynamic information, depending on the social context. Motivation of the caller, either sexual or aggressive, is coded by a mix of spectral and temporal parameters, and mostly by the length of the call (phrase number) (Chapter II). More precisely, directed vocalizations of blue petrels and Antarctic prions are longer than spontaneous undirected vocalizations, indicating a change in the motivational state of the emitter, as shown in mammals, songbirds, and non-songbirds (Briefer, 2020; Mager et al., 2012; Martín-Vivaldi et al., 2004; Morton, 1977; Sossinka & Böhner, 1980). Among directed vocalizations of our study species, male-directed calls are even longer than female-directed calls. This observed decrease in call duration from negative (e.g., territorial interactions) to positive situations (e.g., sexual interactions) is consistent with studies in other birds and mammals (Briefer, 2020).

In blue petrels and Antarctic prions, static and dynamic information is not coded by single, independent acoustic parameters in male calls, but rather by a set of acoustic parameters in both physical domains (temporal/spectral). It suggests an elaborate multi-parametric coding strategy based on information redundancy despite an obvious call stereotypy. Redundancy of information may be a vocal adaptation to communicate and reliably transmit information in the noisiness of the colony (Shannon & Weaver, 1949), as shown in other colonial seabirds (e.g., king penguins *A. patagonicus*: Jouventin et al., 1999). Vocal individuality in male calls (Chapter I) may also be an adaptation of vocal communication in noisy environments with many conspecifics and heterospecific interferences. Individuality enhances detection because familiar sounds are easier to detect and discriminate in the background noise (*cocktail party effect*: Cherry, 1957). In blue petrels and Antarctic prions, each male has a vocal signature

providing information about its individual identity. Nonetheless, individual signature does not imply individual recognition (Townsend et al., 2010) and so far this possibility has not been tested in burrowing petrels. In other colonial seabirds, vocal individual signature is the basis of social behaviours implying individual recognition such as parent-offspring and mate reunion (Aubin et al., 2007; Aubin & Jouventin, 2002; Bretagnolle, 1989; Favaro et al., 2015, 2017; Jouventin et al., 1999; Robisson et al., 1993; Searby, 2004). In blue petrels and Antarctic prions, breeders have a physical place to meet and they remain silent in the nest after pairing, likely to minimize the risks of being detected by predators. In addition, a chemical signature exists and individuals are able to recognise it in petrels (Bonadonna et al., 2009; Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Mardon et al., 2010). Hence, the individual vocal signature may have another function than mate recognition, for instance in bachelor discrimination. Females may profit from discriminating males to avoid visiting the same potential mate several times. In male-male interactions for burrow defence, discriminating neighbour males may allow a vocal adjustment (*dear-enemy phenomenon*: Fisher, 1954; Temeles, 1994).

In blue petrels and Antarctic prions, male calls are degraded and attenuated during their propagation at long range, even in ideal climatic conditions (Chapter IV). Consequently, vocal strategies in these species may be adaptations for long-range signalling. For instance, producing stereotyped calls with a steady call rate increases the chances to be detected when a female flies nearby and/or to find a window of silence to maximise call propagation. This vocal strategy has been documented in many animals living in noisy environments, including other seabirds (Aubin & Jouventin, 1998; Jouventin et al., 1999; Lengagne et al., 1999). Another vocal adaptation of long-range signalling is the coding of relevant and discriminant information in the least degraded acoustic parameters (Brenowitz, 1982; Mouterde, 2020). In calls of male blue petrels and Antarctic prions, temporal parameters and spectral structure encode information and they are less degraded by environmental factors than amplitude and frequencies. Temporal parameters of male calls do not seem to be modified by the burrow (Chapter IV) nor by obstacles in the propagation path as male calls propagate in open areas without (or with very few) obstacles. Spectral structure of calls is less degraded and less sensitive to the characteristics of the burrow than modulations of amplitude and frequencies (Chapter IV).

Besides environmental constraints, vocal signals in blue petrels and Antarctic prions may have evolved under predation pressures because their main predator, the brown skua *S. antarcticus*, is an acoustically-oriented predator (Moncorps et al., 1998; Mougeot & Bretagnolle, 2000). The intense vocal response when a conspecific is present may be a strategy to optimize vocal investment while limiting predation risks for both the emitter and the receiver (Chapter II). Despite a small number of observations, our results show no significant differences in predator attraction between deep and shallow burrows, although the latter should be easier to excavate (Chapter IV), nor by lone males and grouped males calling, although the latter are theoretically easier to detect on large distance (*signal enhancement hypothesis*: Alexander, 1975; Chapter III). Skuas might be more attracted by short calls than long calls (Chapter II) and they spend more time nearby lone callers which are easier to locate precisely (predator-confusion effect; Chapter III). These results taken together suggest that skuas might favour the closest and the most easily locatable preys, but not the most detectable on large distance. This is consistent with our field observations that skuas mostly walk through the petrel colony when hunting at night and would thus favour preys at short distance.

In blue petrels and Antarctic prions, coded information and coding strategy are similar (Chapters I and II). The similarity between both species may be due to similar physiological and anatomical constraints (see "General Methods"). Another explanation is that both species share the same environmental constraints related to the burrow-nesting system, predation risks, climatic interferences, and caller physiology (Warham, 1990, 1996). Both hypotheses are not mutually exclusive.

MALE CALLS AND SEXUAL SELECTION

As stated by the dual-function hypothesis, male calls in songbirds ensure the double function of attracting potential mates and repelling rivals and/or intruders, corresponding to the two main mechanisms of the sexual selection. In blue petrels and Antarctic prions, male calls are likely to occupy these two functions as well. As a reminder, sexual selection theory states that the chosen sex (usually males) display and advertise to attract the choosy sex (usually females) that selects only certain potential mates (Andersson, 1994). In burrowing petrels, males vocally advertise from their burrow. James (1985)

found that females were more attracted by burrows in which he broadcast male calls than by empty burrows. He deduced that calls spontaneously produced by males are highly attractive to females. To go further and to test whether male petrel calls are actually sexual signals actively selected by females, Bretagnolle (1996) proposed four conditions I detailed hereafter: (i) existence of a vocal sexual dimorphism; (ii) male calls actually attract females; (iii) vocal differences between sexes are perceived; and (iv) a given acoustic parameter is related to a selected male trait.

First, previous works already highlighted the existence of a sexual dimorphism in vocalizations of petrels (Bourgeois et al., 2007; Bretagnolle, 1996; Curé et al., 2011) and seabirds in general (e.g., kittiwake *R. tridactyla*: Aubin et al., 2007; king penguin *A. patagonicus*: Kriesell et al., 2018). In blue petrels and Antarctic prions, the dimorphism is mainly syntactic but it can be temporal and/or spectral in other petrels (unpublished data; Bretagnolle, 1996; Curé et al., 2011).

Second, in all attractiveness experiments of the present thesis, females were successfully attracted by broadcast male calls, in spite of the total absence of a real male and the use of freshly installed artificial burrows (Chapter III). It means that male calls are attractive to females and at this step of mate choice there is no need for additional signals, such as further vocal signals (e.g., a vocal response from the male to the female presence) or olfactory signals/cues (e.g., body or nest odour). These results are consistent with a wide literature on the attractiveness of male calls to females in Tetrapods. Nonetheless, further signals, including female-directed calls produced by males, may be involved in the next step of mate choice when females have landed and walk on the ground toward the burrow entrance. These additional signals may provide further information, including motivational state of the caller (Chapter II), and may help females finding the burrow entrance (Storey, 1984).

Third, previous playback experiments showed that the vocal dimorphism leads to sex vocal recognition in burrowing petrels. Females respond preferentially to same-gender conspecifics in blue petrels and Antarctic prions (unpublished data), and other burrowing petrels (Bretagnolle & Lequette, 1990; Curé et al., 2011; Taoka & Okumura, 1989). In blue petrels and Antarctic prions, bachelor males too discriminate females and males calls, as they vocally react according to the sex of the signaller

(Chapter II). Subtle sound differences are perceived by females because few acoustic parameters of male calls, including high call rate and high frequencies, preferentially attract females (Chapter III).

Finally, acoustic parameters of male calls are related to male traits. Genevois & Bretagnolle (1994) previously highlighted the relationship between tempo and body condition. To go further, I highlighted relationships between other acoustic parameters (phrase duration and syntax in blue petrels; energy distribution, phrase rate and phrase duration in Antarctic prions) and body size, bill and wing morphology (Chapter I). In soaring birds travelling long distance to feed and to store energy, anatomical structures related to feeding efficiency (bill) and flight capacity (wings) may be related to male qualities (Chastel et al., 1995; Klages & Cooper, 1992; Weimerskirch et al., 1995).

Therefore, male calls of blue petrels and Antarctic prions fulfil all four criteria of sexual signals proposed by Bretagnolle (1996). In the literature, calls of male burrowing petrels have been thought as sexual signals with the purpose of attracting potential mates for a long time, but this is now confirmed experimentally in the most natural conditions possible. Besides their sexual function, male calls may ensure a territorial function. As stated by the sexual selection theory, males compete with each other to attract females and to gain resources including hierarchical status, food, and nest sites. In burrowing petrels, there is no hierarchical organization, males do not feed at the colony and they do not hold feeding territories at sea, indicating that males do not compete for these resources. Males may compete for burrows as breeding sites, suggesting that colonies are mosaics of small territories vocally defended.

Previous studies in burrowing petrels showed that males vocally react to the presence of another male and I observed similar reactions in blue petrels and Antarctic prions. Moreover, in blue petrels and Antarctic prions, male-directed calls differ from spontaneous and female-directed calls. They are characterized by spectral and temporal variations related to their competitive motivation (Chapter II). The major variation is the increase of the number of phrases per call, which is an indicator of territoriality in oscines and other non-oscines. Both bachelor and breeder males produce male-directed calls when vocally challenged by another male, suggesting that these calls have a territorial function. Differences in male-directed calls of bachelors and breeders may be explained by weight variations because breeders

store energy, while bachelors do not. Nonetheless, I also cannot exclude the fact that male-directed calls of bachelors vary from those of breeders because they have the double function of deterring intruders to protect the burrow and repelling rivals for female attention.

Male calls are considered as signals implied in male-male competition if they fulfil four criteria described by Cate et al. (2002): (i) there is an inter-individual difference in acoustic parameters; (ii) this difference correlates with the competitive ability of the emitter; (iii) some signal variations are only produced by highly-competitive males; (iv) receivers perceive the signal variation and respond accordingly with the perceived quality of the sender. In blue petrels and Antarctic prions, an individual signature has been highlighted in male-directed calls, showing that acoustic parameters vary between individuals (Chapter I). These acoustic variations are related to male morphology but relationships between morphology, competitive ability and acoustic parameters have not been addressed. Further works are thus needed to fully investigate the function of male calls in male-male interactions.

ACOUSTIC BASIS OF FEMALE PREFERENCE FOR MALE CALLS

In both blue petrels and Antarctic prions, female mate choice is non-random and occurs in several steps. The start point is when a female hears a male call to rely on for potential mate evaluation. Selectivity is likely to occur at this step, when female is still flying, because once landed it is exposed to ground-hunting predators. Based on the game theory, female should thus land on the ground only if it provides benefits and compensates the predation costs (Smith, 1984). After female has landed and vocally signalled its presence, female-directed calls of the male may help females to locate the burrow entrance (Storey, 1984) and possibly give complementary information. One may wonder how selectivity occurs and which acoustic parameters of male calls are favoured by females.

Theoretically, the decision to land by females despite a high predation risk may rely on static and dynamic information carried by male calls. Outcomes of the theory were confirmed using attractiveness experiments in the field and results in blue petrels show that male calls do not equally attract females. Females have a clear preference for high-pitched calls, calls emitted at a high call rate, and possibly calls with few syllables (Chapter III). These parameters may correlate with the caller mating success in natural

conditions. Mean pitch of calls is related to bill morphology: males with a long, thin bill produce high-pitched calls (Chapter I). In filter-feeding seabirds, like blue petrels, bill morphology influences feeding efficiency (Klages & Cooper, 1992) and consequently the reproductive success. Call pitch is also related to the caller motivation, as a high-pitched first syllable may be a sign of sexual motivation in female-directed calls (Chapter II). A high call rate is a sign of endurance and good body conditions in many birds (Catchpole & Slater, 2008; Searcy & Beecher, 2009) and possibly an indication of good-quality males because it increases detectability and predation risks (Mougeot & Bretagnolle, 2000; Zahavi, 1975, 1977). Surprisingly, female blue petrels are not preferentially attracted by long calls nor calls with a high syllable rate, two parameters described as indicators of mass and body condition in burrowing petrels (Genevois & Bretagnolle, 1994). One may hypothesize that body mass and/or condition is not a reliable trait in burrowing petrels because it highly varies during the breeding season. Hence, female mate choice may be influenced by other male qualities and/or the detectability of male calls.

Highly detectable signals are theoretically more attractive to females, especially in noisy environments, because they are easier to discriminate and to locate in the background noise (Marten et al., 1977). In a previous section, we have seen that males calling with a high call rate, more detectable than males calling less frequently, preferentially attract females in blue petrels. The more calls produced, the more chances to be perceived and the less risks to be masked by other callers. In species forming breeding aggregations in noisy environments, the production of easily-detectable calls may be more advantageous for signallers and receivers than the coding of information by subtle signal variations. One may thus hypothesize that detection is a determinant criterion. Nonetheless, long calls, low-pitched calls and grouped callers did not significantly attract more females (Chapter III), although they theoretically increase the detectability of the caller (Wiley & Richards, 1982). Similarly, male calls emitted from a burrow with a large chamber have a larger active space than calls emitted from a small burrow, but they are equally attractive to females (Chapter IV). These results suggest that the informative content of male calls is more determinant in female mate choice than the detectability of the calls, although detectability may help females reliably decode the information coded in male calls.

In blue petrels, burrow properties have an influence of sound propagation and thus its detectability, as shown for burrows or cavities in insects, anurans, and bats (Chaverri & Gillam, 2013; Muñoz & Penna, 2016; Penna & Solís, 1999). Female blue petrels are more attracted by calls emitted from burrows close to the surface, either because they are more detectable (Chapter IV) and/or because shallow burrows provide a benefit that has not been documented yet. Females are not influenced by the volume of the burrow chamber, although large burrows propagate calls further than small burrows, and calls coming from large burrows are less degraded than calls coming from small burrows. These findings suggest that at the early step of mate choice, females in flight are not influenced by call-propagation properties of male burrows. It would be surprising that burrow is not an influential element in female mate choice due to its close relationship with the breeding success of its occupants. Burrow protects against climatic turbulences (wind, rains) and hides from predators (Jouventin & Mougin, 1981; Warham, 1990). It also acts as an incubator, keeping the incubation chamber at a steady temperature when both adults are absent and the egg stays non-incubated (Warham, 1990). Therefore, a plausible hypothesis would be that females mate choice is based on a two-step process: in a first step, flying females evaluate potential mates on their calls, regardless of the caller and burrow detectability and, in a second step, females evaluate male burrow when visiting it. Mate choice in fiddler crabs (*Austruca annulipes*) is similar to that in blue petrels: females attracted by male signals visit male burrow or not. If so, both adults perform synchronous displays in the burrow and female assesses the burrow quality (Backwell et al., 1999).

MUTUAL MATE CHOICE?

According to the sexual selection theory, the choosy sex is stimulated and attracted by sexual advertisement of the other sex. In burrowing petrels, females are supposed to be the choosy sex because they are attracted by male calls accordingly with the informative content of calls (Chapters I and III). However, after hearing a female flight call, males vocally react to the female presence and produce female-directed calls characterized by acoustic variations (Chapter II). It suggests that females stimulate males too, somehow. Blue petrels and Antarctic prions are long-lived species known for their partnership and nest fidelity, which equally share parental responsibilities between parents (Warham, 1990, 1996).

Hence, it is expected that mate choice is mutual (parental investment theory: Trivers, 1972). Both males and females should thus seek for a partner that maximises their chances of successful mating and with which they would form a well-synchronized pair (Warham, 1990). If mate choice is mutual in burrowing petrels, when and how does it take place? One hypothesis is that males evaluate females using the information carried by female flight calls. Males thus remain silent when a low-quality female flies around. Another hypothesis is that males may react to any flying females, but they adjust their vocal response according to the female quality. So far, we do not know whether males adjust their vocal investment according to the female quality, but we do know that their vocal response is more intense when the female is close or getting close, than when the female is flying away. Males use the frequency shifts and/or tempo variations of the Doppler Effect in female flight calls as an auditory cue of distance (Chapter II).

According to Bried & Jouventin (2001), if males are choosy, selection is more likely to occur when both adults perform duets in the burrow (unpublished data; Warham, 1996). Duets allow mates to test their compatibility and learn their respective vocalizations (Nelson & Baird, 2001). Moreover, because of the close proximity in the burrow, both adults may exchange further signals in different sensory channels providing further information, such as olfactory signals which influence mate choice in blue petrels (e.g., MHC genotype in body odour: Leclaire et al., 2017; Strandh et al., 2012), or visual and tactile signals as shown in other seabirds (Nelson & Baird, 2001). Therefore, if mutual mate choice occurs when both adults are in the burrow, it is unlikely that female-directed calls are related to male mate choice, but the function of these calls would rather be to convince females to visit the male calling. The more females visit the burrow, the more chances to find a suitable mate for males. This hypothesis would also explain why the time females spent on the ground is not related to the acoustic parameters of broadcast calls in attractiveness experiments (Chapter III).

CONCLUSIONS

Blue petrels and Antarctic prions are burrow-nesters, breeding in dense colonies where climatic factors and vocal interferences from conspecifics and other birds impair the propagation of vocal signals. In spite of these environmental constraints, acoustic is a main sensory channel for bachelors to communicate. More precisely, male calls are implied in both main mechanisms of the sexual selection theory: female mate choice and male competition for burrow and mate. As Marler (1955) stated, animal vocalizations "*have not been chosen arbitrarily but they are directly adapted in structure to the function they have to perform*". A comparison of vocal strategies and adaptations between these two species highlights similarities. In both species, static (identity and morphology) and dynamic (aggressive/sexual motivation) information carried by spontaneous male calls are encoded at different syntactic levels and in the two physic domains (temporal/spectral). It suggests that similar environmental constraints and selective pressures have similarly driven the evolution of vocal signals and have resulted in a complex and redundant coding strategy, adapted to noisy environments.

The encoded static and dynamic information in acoustic parameters of male calls, as potential indicators of male quality, and the caller detectability influence females prospecting for a lifetime mate. Female mate choice is likely to take place in two steps separated in space and time, and relying on different signals. A first selection step occurs when females are still in flight and evaluate males calling in their burrow based on their calls. At this moment, females choose to land and to visit the male or not, likely to minimize the time spent on the ground where they are vulnerable to brown skuas. After landing, females walk on the ground toward the burrow entrance, guided by female-directed calls of males. In absence of a male vocal response, females fly away, suggesting that besides their guiding function, female-directed calls provide further information through temporal and spectral variations, such as the caller sexual motivation. A second step occurs when both adults are in the burrow and perform intense vocal duets. Adults in close proximity are likely to exchange other signals such as olfactory signals (body odour, nest odour). If burrow properties influence female mate choice, it is likely to occur at this step too.

In burrowing petrels, mate choice is likely to be mutual considering their monogamous system but so far, there is no evidence that males respond to certain females only and/or vary their response intensity with the female quality. Yet, the intensity of the males' vocal response is related to the female proximity, suggesting that they have the ability to extract information in female flight calls and to adjust their vocal response accordingly. It may be a strategy to maximise the chances of being detected by females. The mutual selection is more likely to occur during the second step of mate choice, when both adults are in the burrow exchanging vocal and olfactory signals, providing further information and allowing potential mates to test their compatibility.

Burrowing petrels represent a good opportunity to study the functioning and evolution of a signalling system combining the role of hollow structures on vocal signal propagation with vocal strategies in noisy environments. This thesis is a first step in our understanding of the implication of vocal signals in mate choice in monogamous-for-life and colonial species breeding in a hollow structure and in noisy environments. Two results presented here - the use of Doppler Effect as a distance cue and the structural modification of the calls according to the motivation state of the caller in two non-oscine species - are particularly new in animal vocal communication. Although this work is a product of fundamental research, knowing which burrows combined with which calls indicate a good-quality male may have applications in restoration of seabird colonies. Broadcasting calls may attract birds and encourage them to recolonize colonies and/or to establish new colonies (i.e. social attraction), as shown in seabirds by recent studies (Buxton et al., 2016; Hamblin et al., 2019; Swinnerton et al., 2018).

PERSPECTIVES

To dig deeper into the burrow function

First, experiments and acoustic analyses conducted here aimed to assess the overall propagation pattern of male calls, as a first step in our investigations of the burrow role in petrel communication. Surprisingly, results of our propagation experiment show an absence of resonance effect by the burrow on male call, contrary to results obtained in anurans (Muñoz & Penna, 2016; Penna & Solís, 1996, 1999). Further ongoing analyses should allow me to go deeper and to highlight more subtle acoustic variations

related to the burrow dimensions. More precisely, a comparison between the structure of calls emitted from a burrow and outside the burrow will provide complementary information about the effect of the burrow on sound propagation. Measures of call amplitude at different distances will provide evidence about the absence or existence of a megaphone effect, as shown in Manx's shearwaters (*P. puffinus*) and anurans (Muñoz & Penna, 2016; Penna & Solís, 1996, 1999; Storey, 1984).

Second, our investigations on the burrow function suggest no influence of the burrow dimensions on female mate choice. One hypothesis to test is that other relevant burrow characteristics or a combination of several characteristics may influence female mate choice. For instance, in Kerguelen petrels (*Aphrodroma brevirostris*), the burrow orientation is determinant when choosing a site to dig or a burrow to squat as burrows oriented towards the East are less exposed to strong winds (Mougin, 1969). Another important factor could be the tunnel inclination that prevents inundation risks (Warham, 1996). A second hypothesis to test is that burrow properties do not influence females when they are still flying, but more likely when they are in the burrow, as shown in fiddler crabs (Backwell et al., 1999). To this end, the design and analysis of the attractiveness experiments could be modified to consider further behavioural factors, such as the time spent or the female behaviour inside the burrow. Therefore, further investigations are needed to assess the implication of the burrow in petrel social interactions. Understanding the role of the burrow in burrow-nesters could have applications in the conservation and management of seabird colonies, for instance when restoring colonies or when creating artificial burrows, more and more popular in population monitoring and research experiments.

To study multimodal communication

Results of the present thesis suggest that male calls are not the only signals implied in mate choice in burrowing petrels. Further signals may be involved in short-range signalling between bachelor male and female, after the attracted female has landed. Female-directed calls from males may be signals stimulating females to penetrate the burrow. Additional signals using other communication channels may be involved too, thanks to the proximity between emitter and receiver. In burrowing petrels, previous studies highlighted the olfactory abilities and the use of olfactory signals in social interactions

and burrow location. (Bonadonna et al., 2004, 2009; Bonadonna & Sanz-Aguilar, 2012; Leclaire et al., 2017; Mardon & Bonadonna, 2009; Strandh et al., 2012). Hence, it seems likely that burrowing petrels use composite signals, especially in short-range communication (Partan & Marler, 2005). Evidences in burrowing petrels show that information, such as the individual identity, are carried both by vocal and olfactory signals (redundant information). Using redundant composite signals may be beneficial for both emitter and receiver because they decrease the costs of mate choice by limiting the risk of misclassification (Candolin, 2003). Further information was investigated in burrowing petrels and found in a single modality only, such as the CMH in body odour. The hypothesis that vocal and olfactory signals provide multiple messages cannot be excluded. There is thus a need for further investigations to study the function of each modality of these composite signals and to assess whether one modality overrides the second. One may hypothesize that acoustic channel first provides information and attracts attention; then olfactory channel provides further information (e.g., histocompatibility between potential mates). A similar signalling system exists for mother-offspring recognition in Australian sea lions (*Neophoca cinerea*). Both pups and females use vocal signals when apart and olfactory signals in close proximity (Wierucka et al., 2018). Exploring multimodal communication would be a promising lead for future investigations in burrowing petrels.

To explore the individual vocal recognition

A recent review highlighted vocal recognition in mammals and birds, including very few seabirds (Carlson et al., 2020). Previous studies showed that few burrowing petrels discriminate the calls of their predators (Mougeot & Bretagnolle, 2000) and use the vocal sexual signature of their conspecifics to modulate their vocal response, for instance in aggressive interactions (Bretagnolle, 1996; Taoka et al., 1989; Curé et al., 2011). In blue petrels and Antarctic prions, male calls carry the individual identity of the caller but we still ignore whether they are actually able to discriminate individually their conspecifics or not. In these species, vocal recognition may be implied in male interactions and/or in mate recognition. Males vocally react to calls of other males, but one may hypothesize that bachelors do not react to calls of neighbouring males or reply with an adjusted vocal investment (*dear-enemy phenomenon*). During the incubation in the burrow, partner shifts are silent in both species. However,

how partners find each other from one year to the next is a mystery, especially if they had to switch for another burrow. We know that breeders come back to the colony during the “prenuptial return”, few months before the start of the breeding season (Warham 1990, 1996), but we ignore how they communicate and if so, which signals and channels are involved. The possibility that mates recognize each other using vocalizations is not excluded. We aimed to carry out playback experiments combined with a non-invasive heartbeat recorder on both breeding males and females to test whether: (i) mates recognize each other and (ii) bachelor males discriminate familiar and unfamiliar males. We thus started a collaboration with an electronic institute of the University of Montpellier to this end. The recorder development was more difficult than expected due to technical reasons and is still in progress. Consequently, individual recognition in burrowing petrels have not been explored in the present thesis and the experiment will be carried out in a future field season.

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APPENDICES

APPENDIX 1: PUBLISHED VERSION OF ARTICLE 1

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Article

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

Charlène Gémard, Thierry Aubin and Francesco Bonadonna

C. Gémard (https://orcid.org/0000-0002-8019-5842) ✉ (charlene.gemard@cefe.cnrs.fr), and F. Bonadonna, CEFE-CNRS, Montpellier, France. – T. Aubin, Neuro-PSI CNRS, Orsay, France.

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Acoustic communication in burrowing petrels has been poorly studied. However, as for many other bird species, acoustic communication seems to play an essential role in social interactions during the breeding season of these seabirds. Bachelor males call from their burrow, likely to attract females, but also when vocally challenged by other males. Calling in the breeding colony exposes petrels to high predation risks and thus it should provide an important benefit. The present study focuses on the informative content of males' calls in the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata*, two monogamous petrel species producing a single egg per year. We tested the hypotheses that acoustic parameters of a male's calls 1) reflect phenotypic characteristics, and 2) bear an individual vocal signature. To do so, we first tested on both species the relationships between seven morphometric measurements and 11 acoustic parameters using multivariate analyses. Second, we performed a between-class analysis and calculated the potential of individuality coding (i.e. the ratio between intra- and inter-individual variabilities) for acoustic parameters in both spectral and temporal domains. Results show acoustic parameters (especially energy quartiles, call duration, and syllable or phrase rate) reflect the caller's body size, bill morphology and wing morphology in both species. Considering the seeming pertinence of wing morphology, we suggest wing area may be a more relevant trait to consider than wing length when studying soaring birds. The results support the idea that energy quartiles, phrase rate and call duration also code for individual identity. Information carried by males' calls might play a role in social interactions, such as burrow defence (e.g. male-male competition, neighbour-stranger discrimination) and/or female mate choice.

Keywords: vocal communications, sexual selection, identity, phenotypic features, seabirds, petrels

Introduction

Knowing how animal communication systems work is crucial to understanding social behaviours. Indeed, social interactions are mediated by signals in one or several modalities, such as acoustic, olfactory or visual (Bradbury and Vehrencamp 1998). Among these, vocal signals provide information mainly to conspecifics, but not exclusively (see Magrath et al. 2015 for a review). Signals carry different kinds of information, stable

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information on long-term (e.g. species, sex, social status, group membership, phenotypic characteristics: Searcy and Nowicki 2005) and temporary information through acoustic modulations (e.g. motivation: Morton 1977, emotion: Briefer 2018). Vocalizations may also bear stable individual signatures to allow efficient discrimination among individuals (Beecher 1989, Tibbets and Dale 2007), particularly in social species. For instance, it has been shown in rodents that alarm calls contain more individual information in species living in large groups than species living in small ones (Pollard and Blumstein 2011).

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

Several acoustic parameters have been shown to reflect a singer's characteristics linked to overall male quality, and there is evidence that females are attracted by specific acoustic parameters related to male qualities (see Nowicki and Searcy 2004 for a review). A well-known example is the fundamental frequency (or pitch) which negatively correlates with body size (Galeotti et al. 1997, Mager et al. 2007, Favaro et al. 2017, Kriesell et al. 2018). In many species, larger males have a higher breeding success because body mass is an indicator of physical strength and/or foraging success (Chastel et al. 1995, Salton et al. 2015) and females rely on fundamental frequency as a sexual signal (review in Cardoso 2012). Besides frequency parameters, females rely on song output structure, complexity and vocal performance (Nowicki and Searcy 2004). For instance, they are attracted by songs constituted of many and/or complex elements (Martín-Vivaldi et al. 2000, 2004) which may indicate a male in good body condition (Martín-Vivaldi et al. 1998). Females are also attracted by males that perform challenging songs (i.e. with a high rate and/or a large frequency bandwidth), that indicates body size, age and endurance (Ballentine et al. 2004, Ballentine 2009, Byers et al. 2016).

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

Among Procellariidae, burrowing petrels occupy deep burrows and are active, at the colony, at night during the breeding period (Warham 1990). In this context, visual communication seems strongly restricted whereas olfactory and vocal signals may be used for long-range communication. The role of olfaction has been investigated in petrel social interactions. Studies suggest that the chemical signature of nests is used by mates to find their own burrow (Bonadonna et al. 2001, 2004), and that individual body's odour carries individuality signals and some genetic information that may influence mate choice (Bonadonna and Nevitt 2004, Bonadonna and Sanz-Aguilar 2012, Leclaire et al. 2017). Comparatively, acoustic communication has been poorly studied so far. For some burrowing-petrel species, vocal communication is extremely costly because it exposes callers to an increased risk of predation (Mougeot and Bretagnolle 2000). However, during pair formation, bachelor males looking for a mate intensely vocalize at night from their burrow, while females fly and call over the colony (Bretagnolle 1990, Warham 1996). These costly calls are likely to be reliable sexual signals that attract and/or stimulate suitable mates (Bretagnolle 1990), but we still ignore which one, between male or female, stimulates the other. Petrels also vocalize after being vocally challenged by a conspecific close to the entrance of their burrow. These vocalizations might be aggressive signals to defend the own burrow (occupied year after year) from intruders (Warham 1990, 1996). According to Bretagnolle (1996), burrowing petrels have a small vocal repertoire. For instance, genera *Halobaena* and *Pachyptila* produce a single major call produce in both sexual and agonistic interactions.

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

high predation pressure by the brown skua (Mougeot et al. 1998). We tested the hypotheses that acoustic parameters in both temporal and spectral domains of petrel calls 1) reflect morphological characteristics, and 2) bear an individual vocal signature.

Material and methods

Studied species

Blue petrels (*H. caerulea*) and Antarctic prions (*P. desolata*) are monogamous medium-sized (about 190 and 160 g, respectively) seabirds belonging to the Procellariidae. They spend most of their life at sea but they breed in dense colonies on coastal grass slops. These long-lived seabirds do not reach sexual maturity for five years and a couple of years is needed for establishing stable pair-bonds. They show a high partner fidelity, low extra-pair paternities, and divorces are rare. After pairing, pairs produce a single egg per year. From incubation (50 d in blue petrels, 45 in Antarctic prions) to fledging (50 and 53 d, respectively), they exhibit bi-parental cares. Partners regularly alternate fasting period in the burrow and feeding trips at sea (Warham 1990, 1996, Brooke 2004).

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

Study location

Fieldwork was performed in a small sub-Antarctic island (Ile Verte, 49°51′S, 70°05′E) of the Kerguelen Archipelago, in the southern Indian Ocean, where blue petrels and the Antarctic prions gather in stable colonies during the breeding season. We conducted the study during the 2017 and 2018 birds' incubation period (25 November 2017 to 12 December 2017 and 27 November 2018 to 20 December 2018 for blue petrels; 23 December 2017 to 16 January 2018 and 25 December 2018 to 13 January 2019 for Antarctic prions).

Playback procedure and recording of provoked calls

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

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

The recording equipment was composed of an omnidirectional Sennheiser K6-ME62 microphone (frequency response: 20–20 000 Hz $\pm$ 2.5 dB) connected to a Marantz PMD 660 digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). The microphone was positioned on the ground, at the burrow entrance, and one randomly selected synthesized call was broadcast at a natural sound pressure level ($\pm$ 67 dB, measured on 111 calls from 54 males with a sound level meter) using a TASCAM DR-07MKII digital recorder (sampling frequency: 44.1 kHz, dynamic: 16 bits). Calls emitted in reply by the burrow owner were recorded during the playback and two minutes after the end of the

playback stimulus. If the focal individual did not reply, the playback was repeated every 30 s, up to three times.

Morphometric measurements

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

Head and tarsus measurements (CL, BD, HL and TL) were taken using a calliper with an accuracy of ±0.1 mm. Wing length was measured with a stainless-steel rule with an accuracy of ±1.0 mm. To limit measurement biases, a single person (CG) took each measurement three times and calculated the mean. We also took standardized pictures of both sides of the right wing for each tested individual, using a digital camera (Olympus TG-610). Wing area was then measured by a single person (CG) by counting the number of calibrated pixels using ImageJ image analysis software version 1.52a (National Inst. of Health, USA). Correlation scores between morphometric measurements and summary are given in Supplementary material Appendix 1 Fig. A1, Table A1, respectively.

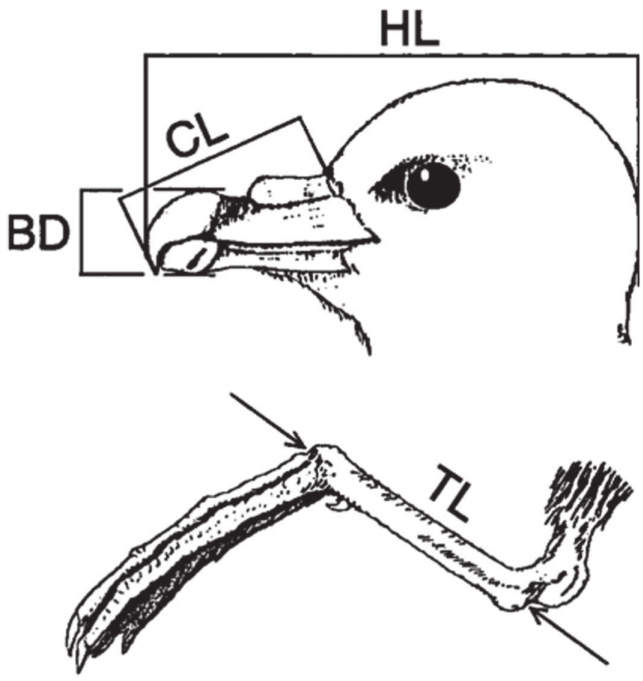

Figure 1. Tarsus and head measurements from Cramp and Simmons (1977), taken on blue petrels and Antarctic prions: head length (HL), bill depth (BD), bill length (CL) and tarsus length (TL).

We chose morphometric measurements likely to be indicators of body size and/or to have an effect on call production based on the literature, and/or may be important in the biology of the species. Head size has been used as an indicator of body size in swallows (Winkler and Allen 1996, Patel et al. 2010) and nestling growth in blue tits (Plummer et al. 2013). Similarly, tarsus and wing lengths are good indicators of body size in passerines (Senar and Pascual 1997, Gosler et al. 1998), although it has not been documented if these indicators are suitable in seabirds. Bill is considered as the end of the vocal tract and its morphology (length and depth) may influence sound production. Bill is also the small petrels' feeding means (Warham 1996), as they filter small crustaceans at the surface of the water, and may thus influence feeding efficiency (Klages and Cooper 1992). Wing area seems a relevant morphological trait because petrels are a soaring species and travel great distances at sea to feed (Cherel et al. 2002).

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

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

Acoustic analysis

Calls recorded were first down sampled at 11.025 kHz to increase the precision of frequency measurements and high-pass filtered (Cutting frequency: 0.10 kHz, FFT filter) to remove the background noise. We described calls at a phrase level by measuring 11 acoustic parameters in the temporal and frequency domains (see Table 1 for abbreviations and description), on oscillograms and spectra of the signal-processing software Avisoft–SASLab Pro ver. 5.2.11, respectively (Specht 2017). Temporal variables were automatically extracted on the amplitude envelopes using the 'Pulse Train Analysis' function, with a resolution of 0.09 ms (hysteresis: +30 dB; start/end threshold: −30 dB). Settings were not manipulated during measurements, except the threshold which was manually adjusted to detect all syllables. Mean fundamental frequencies and variables describing energy spectral distribution were automatically extracted on linear amplitude spectra with a resolution of 22 Hz (FFT length: 512, Blackman window) (Fig. 2). Automatic extractions are based on clear criteria preliminarily set, insuring objectivity in element demarcation and thus replicable measurements (Fischer et al. 2013). Syllables and phrases were counted on sonograms (Fig. 2). Correlation scores between acoustic-parameter measures and summary are given in Supplementary material Appendix 1 Fig. A2, Table A2, respectively.

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

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

Statistical analysis

We implemented all analyses results under the R software environment version 3.4.4 (R Core Team) with the ade4 package (Dray and Dufour 2015).

Relating acoustic parameters and morphological traits

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

We investigated covariance among morphometric measurements and acoustic parameters with a co-inertia analysis

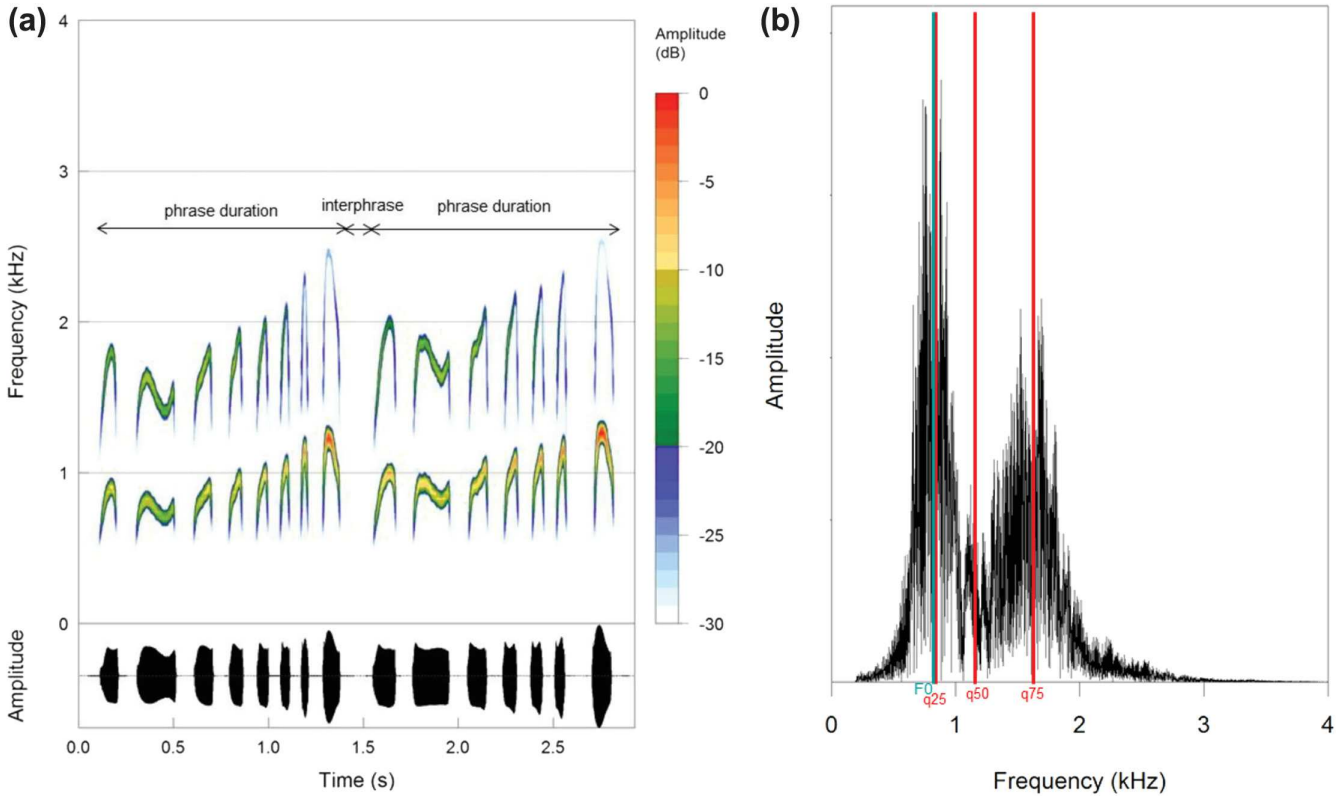

Figure 2. (a) Sonogram (top) and oscillogram (bottom) of a male blue petrel call constituted of two phrases. (b) Linear amplitude spectrum of a call phrase. Red lines indicate energy quartiles and blue line indicates the mean frequency of the phrase.

(CIA), an ordination method designed to reveal the co-structures among two data tables (Dolédec and Chessel 1994, Dray et al. 2003). A summary table of acoustic and morphometric data are given in Supplementary material Appendix 1 Fig. A1, Table A1, respectively. We first summarized the morphometric measurement table with the two first axes of a normed principal component analysis (PCA_1), which explained together 55.5% for blue petrel (32.2 and 23.3% for $PC_1 1$ and $PC_1 2$, respectively) and 60.6% of total inertia for Antarctic prion (34.6 and 26.0% for $PC_1 1$ and $PC_1 2$, respectively). We ordinated the acoustic-parameters table with a between-class analysis (PCA_2), a PCA which accounts for the clustering of object (here phrases) by a grouping factor (here individuals), similarly as in a redundancy analysis (Dolédec and Chessel 1987). We retained the two first axes of the PCA_2 in both species (28.2% and 24.7% of variance explained by $PC_2 1$ and $PC_2 2$, respectively, in blue petrel; 34.6% and 24.9% in Antarctic prion). We built the CIA as an ordination of PCA_1 and PCA_2. Overall similarity between the two ordination tables was assessed by the RV coefficient, a correlation coefficient between two sets of variables recorded from the same sample (0: no similarity, 1: equal tables).

Individual signature

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

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

Results

Relation between acoustic parameters and morphological traits

In blue petrels, the RV coefficient of the CIA between morphometric measurements and acoustic parameters is 0.34. The first two axes of the CIA explained 51.0% and 22.8% of total variance, respectively. The first CIA axis shows the duration and the syllable number of the phrase are mainly related to head and bill length (HL, CL). More precisely, males with a small head (HL) and a short bill (CL) produce short calls with few syllables. The second CIA axis shows rhythm and syllable rate are related to both wing measurements (WL, WA). More precisely, males with short, large wings produce slow (i.e. low phrase rate) calls with long syllables (i.e. high rhythm) and short interphrase silences. Frequency parameters are weakly related to the chosen morphometric measurements (Fig. 3).

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

Tables of CIA scores for both species are given in Supplementary material Appendix 1 Table A3.

Individual signature

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

The total inertia explained by the differences between males in blue petrels and Antarctic prions was 74% and 65%, respectively, showing that the chosen acoustic parameters allow a significant vocal discrimination of individuals ($p < 10^{-5}$ in both species). Composite plots of BCA analyses are given in Supplementary material Appendix 1 Fig. A3.

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

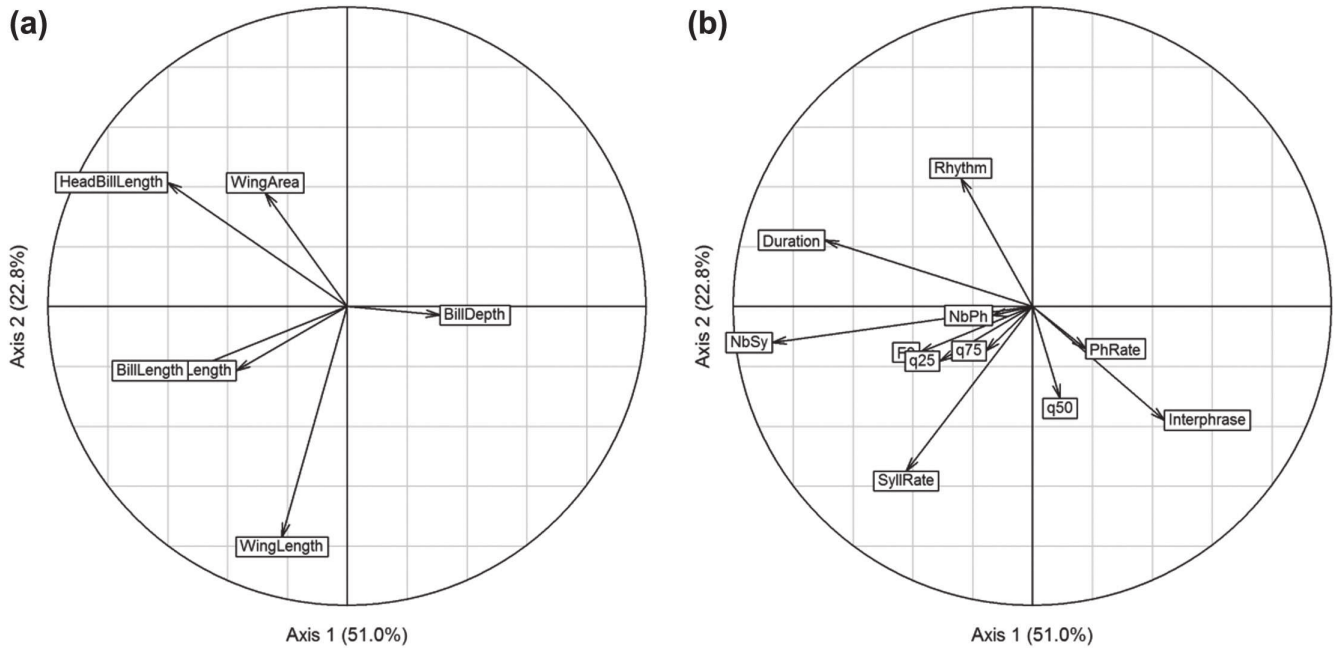

Figure 3. In blue petrels, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.

Discussion

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

Relationship between acoustic parameters and morphological traits

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

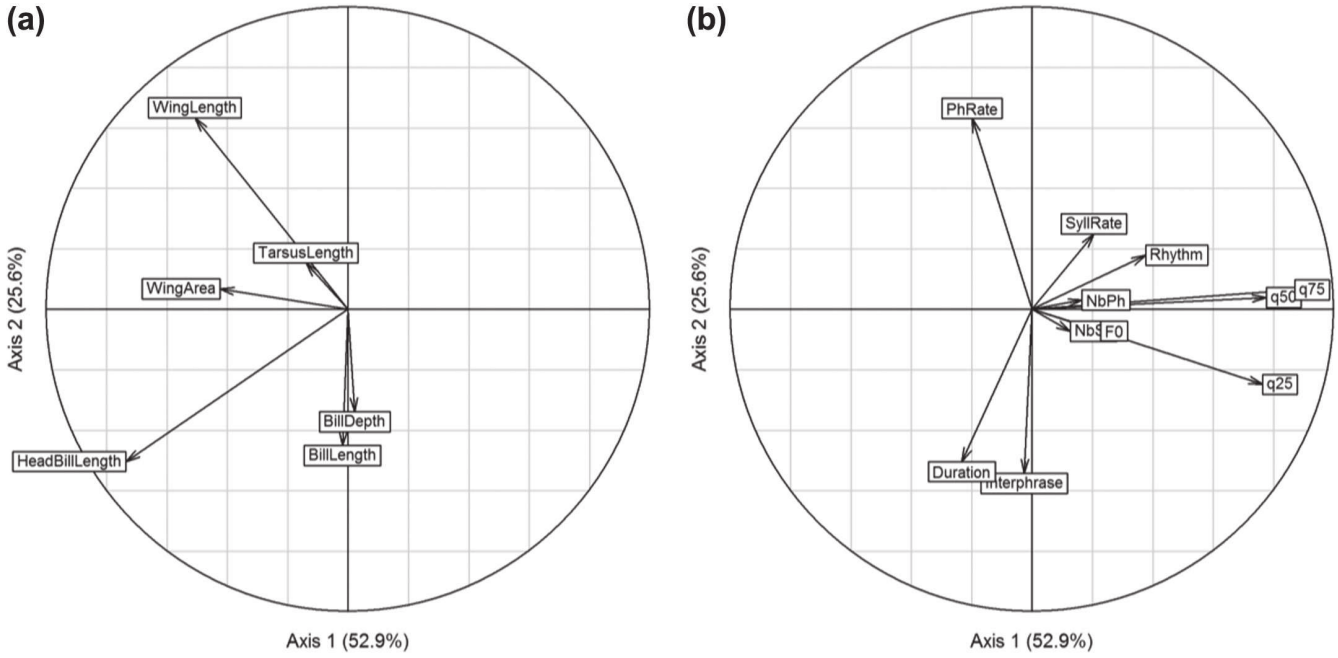

Figure 4. In Antarctic prions, correlation circles of CIA showing relationships between the two first components of the CIA and (a) the morphometric measurements, and (b) the acoustic parameters of male calls.

Table 2. Potential of individual coding (PIC) for the acoustic parameters measured on blue petrel (top) and Antarctic prion (bottom) calls. Abbreviations of acoustic parameters as in Table 1. PIC values above 2.0 are in bold.

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

relevant considering the feeding ecology (bill morphology, wing morphology) of these species.

Specifically, frequency parameters (i.e. fundamental frequency and energy quartiles) are related to bill morphology, especially head-bill length, in both species even though the relationship is weak in blue petrels. Males with a short head and bill produce low-pitched calls in blue petrels whereas they produce high-pitched calls in Antarctic prions. Relationship between bill morphology and frequency is unclear in birds and both opposite patterns have been observed in many species (Palacios and Tubaro 2000, Laiolo and Rolando 2003, Christensen et al. 2006). Other studies have found no relationships between frequencies and bill morphology (Garcia and Tubaro 2018). We can hypothesize that cues that may inform females on this male characteristic might be important as bill morphology influences feeding efficiency in these filter-feeding species (Klages and Cooper 1992).

Head-bill length is also a body size indicator, suggesting frequencies are related to body size. This frequency–body size relationship has been illustrated in many species at the light of the source-filter theory (Taylor and Reby 2010). This theory states that vocal signals result from a two-stage production: the source signal is generated by membrane vibrations in the vocal organ (larynx in mammals or syrinx in birds), and subsequently filtered by the vocal tract and the mouth/nostrils (Fant 1960). Consequently, the anatomy of the 'source', particularly the length and mass of vibrating membranes, shapes the fundamental frequency. Muscular interactions changes the airflow in the 'source' and thus influence temporal parameters such as rhythm, duration and amplitude. The 'filter' influences the formants, i.e. the resonant frequencies (Titze 1994, Taylor and Reby 2010). Although this theory is valid in mammals, the relationships between frequencies and body size remains unclear in birds (Galeotti et al. 1997, Mager et al. 2007, Favaro et al. 2017, Kriesell et al. 2018 but see Patel et al. 2010).

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

Results show a strong relationship between acoustic parameters and wing morphology, especially wing length in both species, and wing area even though this relationship is weaker in blue petrels. We thus suggest that for soaring seabirds, which travel great distances at sea to feed, wing morphology is a relevant parameter to be considered (Cherel et al. 2002). We can hypothesize that cues that may inform females on this male characteristic might be important as wing morphology is correlated with foraging behaviour (Hertel and Ballance 1999) and reproductive costs (Mauck and Grubb 1995). In other Procellariidae, a reduction of parents' flying abilities (e.g. clipping feather tips, removing flight feathers, adding extra weight) affects the incubation routine and results in a decrease of their body condition and/or a deterioration of chick condition (Saether et al. 1993, Weimerskirch et al. 1995, Navarro and Gonzáles-Solís 2007).

Blue petrels and Antarctic prions form lifelong monogamous bonds. Pair bonding takes up to two years and partners equally share parental care during the incubation period (Chaurand and Weimerskirch 1994a, Warham 1990, 1996). Sexual maturity is reached tardily (around seven years), they show low fecundity (one single egg per year without a replacement clutch), and extra-pair paternity is extremely rare (Jouventin and Mougin 1981, Warham 1996). Consequently, choosing the 'wrong' mate affects fitness more than in species that change mates at each breeding. Females should rely on attractive and reliable cues to evaluate the quality of a potential partner (Darwin 1871, Smith 1991). As in many bird species, males' calls are likely to be sexual signals that attract and/or stimulate a potential mate (Bretagnolle 1990). Especially as they are highly vocal, despite the predation cost, and as living in burrows prevents visual communication on long-range. We hypothesize, thus, that the information contained in male calls about the caller body size may have a significant role in sexual selection. In blue petrels, bigger males at the beginning of the breeding season have a higher breeding success (Chastel et al. 1995). Moreover, calls contain information about wing morphology, which may be linked to reproductive success in these soaring birds (Saether et al. 1993, Weimerskirch et al. 1995, Navarro and Gonzáles-Solís 2007).

Individual signature

Our results suggest that individuality in calls of males of both species is coded by several parameters in spectral (energy quartiles) and temporal domains (phrase rate and duration). Individual identity coded by frequency parameters has been shown in numerous species

(Robisson et al. 1993, Jouventin et al. 1999, Charrier et al. 2001, 2004, Favaro et al. 2017). Among these parameters, the fundamental frequency often codes for individual signature in many birds, likely because it is linked to anatomical structure of the vocal tract (Fletcher and Tarnopolsky 1999). Nevertheless, our results show that fundamental frequency has the lowest PIC value and that its correlation with morphological traits is weak. This is consistent with previous studies on blue petrels (Genevois and Bretagnolle 1994), although a negative correlation between mass and fundamental frequency has been highlighted in the snow petrel (Guillotin and Jouventin 1980).

In many seabirds, vocal identity is crucial in social interactions, such as mate reunion or kin recognition (e.g. Spheniscidae: Robisson et al. 1993, Jouventin et al. 1999, Aubin and Jouventin 2002, Procellariidae: Barbraud et al. 2000, Curé et al. 2011, Stercorariidae: Charrier et al. 2001, Laridae: Mathevon et al. 2003). However, in burrowing petrels, finding relatives and nest sites seems not based on vocal signals. As they return from their foraging trip at sea, petrels rely on olfactory signals to find their burrow (Bonadonna et al. 2001, 2004) and take the place of their mate incubating in the burrow, without emitting any call (FB and CG personal observation). Therefore, vocal signature does not seem to be involved in mate reunion. Vocal signatures do not systematically imply recognition (Townsend et al. 2010). So far, there is no clear evidence that burrowing petrels vocally recognize conspecifics as shown in other seabird families (e.g. Spheniscidae: Robisson et al. 1993, Jouventin et al. 1999, Aubin and Jouventin 2002, Procellariidae: Barbraud et al. 2000, Curé et al. 2011, Stercorariidae: Charrier et al. 2001, Laridae: Mathevon et al. 2003). Nonetheless, vocal signature could be used in neighbour/stranger discrimination processes. Indeed, blue petrel and Antarctic prion males call from their burrow in crowded colonies (respectively up to 0.7 and 1.4 burrows m^{-2} according to Croxall and Prince 1980). The significant costs of calling behaviour (Mougeot and Bretagnolle 2000) suggests that males should call only when necessary, for instance in the presence of a stranger male not belonging to the neighbouring community, to avoid higher predation risks and useless energy expenditures. This 'dear-enemy phenomenon' (Fisher 1954) has been documented in many territorial songbirds where males are less aggressive with neighbours than with strangers when defending their breeding territory (Temeles 1994). One hypothesis is that territory owners adjust their aggressive behaviour according to the familiarity and/or threat degrees and thus minimizes fighting costs (Temeles 1994).

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

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

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1rn8pk0pk> (Gémard et al. 2019).

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

Permits – This study was performed according to 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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Supplementary material (available online as Appendix jav-02270 at <www.avianbiology.org/appendix/jav-02270>). Appendix 1.

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APPENDIX 2: PUBLISHED VERSION OF ARTICLE 4

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ORIGINAL ARTICLE

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

Charlène Gémard[1,2] · Thierry Aubin[2] · Eliette L. Reboud[1] · Francesco Bonadonna[1]

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Abstract

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

Significance statement

Mate selection process is largely unknown in burrowing petrels due to their cryptic life at the colony. Here, we examined the implication of vocal signals in mate choice in the blue petrel *Halobaena caerulea*. We used an experimental setting based on a two-choice test to show that male calls are sexual signals attracting females. As expected, broadcasting male calls attracted females. Despite the apparent stereotypy of male calls, their acoustic parameters transmit pieces of information that may influence females' preference. We found that females are more attracted by high call rate and high-pitched calls. This is the first evidence of the implication and influence of vocal signals in mate choice in burrowing petrels.

Keywords Vocal communication · Sexual signal · Attractiveness · Mate choice · Seabird · Blue petrel

Introduction

In animal species, mating is not random and the probability of mating with a given individual of the opposite sex increases with some behavior patterns (Halliday 1983). According to theoretical and empirical studies, in many species, both males and females should profit from being choosy when selecting their mating partner (Andersson 1994; Bakker and Pomiankowski 1995; Courtiol et al. 2016). They rely on attractive signals that inform them about the signaler's qualities (Smith 1991). Although sexual signals are often multimodal, the implication of vocal signals in mate choice has been well documented in many taxa (reviewed in Bradbury and

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✉ Charlène Gémard
charlene.gemard@cefe.cnrs.fr

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

[2] Equipe Communications Acoustiques, UMR 9197, Neuro-PSI-CNRS, Université Paris-Saclay, Bat.446, 91405 Orsay, France

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Vehrencamp 2011). Male vocalizations, apart from their role in male-male competition, attract potential mates in insects (Walker 1957), fish (Amorim 2006), frogs (Ryan 1980), bats (Knörnschild et al. 2017), songbirds (Mountjoy and Lemon 1991), and non-songbirds (Gibson 1989; Martín-Vivaldi et al. 1999).

Mate choice using vocalizations is influenced by (i) the selection of certain acoustic parameters in the absence of the signaler and (ii) that these acoustic parameters correlate with mating success in natural conditions (Searcy and Andersson 1986). Well-known examples of attractive acoustic parameters in birds and mammals are a low fundamental frequency (F0 or pitch), a high vocalizing rate, long vocalizations, and vocalizations consisting in many elements (reviewed in Nowicki and Searcy 2005). These parameters reflect some overall qualities, such as morphological characteristics (e.g., body size: Ballentine et al. 2004; Ballentine 2009; Byers et al. 2016; Favaro et al. 2017; Kriesell et al. 2018; bill morphology: Christensen et al. 2006), endurance, and fighting abilities (McComb 1991). These parameters are also related to breeding success in natural conditions (Chastel et al. 1995; Salton et al. 2015). For instance, in red deer (*Cervus elaphus*), females are preferentially attracted by high roaring rate and low-pitched roars, emitted by large males, which have a better reproductive success than small males (Reby et al. 2010). In several songbird species, females are more attracted by males singing with a high song rate, which have a better territory quality, body condition, or feeding rate, and thus a higher reproductive success (reviewed in Marler and Slabbekoorn 2004).

Most of our knowledge on vocal signal implication in mate choice focuses on songbirds. Comparatively, non-songbirds, such as seabirds, have been poorly documented, although mate choice is crucial in these species due to their particular breeding ecology (reviewed in Bried and Jouventin 2001; Schreiber and Burger 2001). Seabirds have distinct feeding and nesting areas: they feed at sea, while they breed on land. This implies obligatory bi-parental care and cooperation between mates during the whole breeding cycle. Burrowing petrels (Procellariiformes) are colonial seabirds breeding in self-dug burrows on coastal grass slopes (Warham 1990), to which they show a high fidelity year after year (Bried and Jouventin 2001). These monogamous species also show lifelong fidelity to their mate, and divorces and extra-pair copulations are rare (Jouventin and Mougin 1981; Warham 1990, 1996; Quillfeldt et al. 2012). Moreover, parental investment is high despite the small clutch size (one egg per year with no possibility of replacement clutch) and reproductive success is based on parents' cooperation and synchrony (Warham 1990, 1996). Consequently, with respect to species that can change partner at each breeding, correcting possibly wrong choices, choosing the wrong partner will affect the lifelong fitness more drastically in petrels than in other species.

Mate choice in burrowing petrels appears to rely on male calls, emitted at night from burrows while females fly calling over the colony. After hearing a male call, females can land close to the sound source, then enter the caller's burrow. On the contrary, empty burrows do not attract females (James 1985). Females visit several males for a couple of years before pairing (Bretagnolle 1996), suggesting that the mate choice by females is active, and that male calls attract and/or stimulate potential mates (Bretagnolle 1990; Warham 1990). More precisely, female mate choice may be influenced by information carried by male calls, such as the caller's morphological characteristics (Genevois and Bretagnolle 1994; Gémard et al. 2019), linked to male overall qualities and reproductive success. For instance, big blue petrel males with a long, thin bill produce high-pitched calls consisting of many syllables. Because bill morphology may determine the filtering surface in filter-feeding species like petrels, these males might have a better filter-feeding efficiency (Klages and Cooper 1992). Blue petrel males with long and thin wings (i.e., high aspect ratio: Pennycuick 1982) produce fast calls (high syllable rate). Considering the soaring flight mode of petrels, these males may be able to travel over longer distances to feed (Pennycuick 1982). Consequently, they may have a better feeding rate (Chastel et al. 1995; Weimerskirch et al. 1995). Nevertheless, calling in the colony may be considered intriguing as this behavior exposes petrels to predators, especially the brown skua (*Stercorarius antarcticus*) which uses the calls of petrels (mostly blue petrels *Halobaena caerulea* and prions *Pachyptila* spp.) to locate and catch them (Mougeot and Bretagnolle 2000b).

Considering the high predation cost associated with their production, vocal signals should play a major role in mate choice. Despite the seeming implication of male calls in mate choice, vocal communication in burrowing petrels has been poorly studied so far, likely due to constraints associated with fieldwork in remote locations and their particular breeding ecology (nocturnal and burrowing habits). A recent study suggests that acoustic parameters of male calls reflect qualities and mating success but the hypothesis that females actually show a preference for these parameters has never been tested. Here, we experimentally tested by playback experiments with modified calls: (i) the role of male calls in mate attraction and (ii) the role of certain acoustic parameters of male calls in mate choice. Among burrowing petrels, the blue petrel is a good candidate to assess this question because it is highly vocal and suffers from a high predation pressure (more than 70% of the brown skua diet: Moncorps et al. 1998; Mougeot et al. 1998). Based on our previous study on the informative content of blue petrels' calls (Gémard et al. 2019), we hypothesized that females should be attracted by males producing long calls with many syllables and a high syllable rate. According to the handicap theory (Zahavi 1975, 1977), females may also

be attracted by males that take large risks of predation, for instance by calling at a high call rate and/or producing long calls as shown in other species (Johnstone 1995; Zuk and Kolluru 1998).

Material and methods

Study area

We conducted the fieldwork on a small island of the Kerguelen Archipelago (Ile Verte: 49° 510′ S, 70° 050′ E), southern Indian Ocean. In blue petrels *H. caerulea*, bachelor males and females are vocally active and actively prospecting for a mate in the colony, at night, throughout the breeding season (Warham 1996), although the daily activity in the colony is dependent of the moon phase and cloud cover (Mougeot and Bretagnolle 2000a). We conducted the fieldwork during the birds' incubation period, from November 27 to December 27, 2018.

Studied species

In blue petrels, callers are mainly bachelor males and females, although breeders call when they are vocally challenged by a conspecific, likely to defend their burrow (Warham 1996). Their calls consist of distinct and repeated sections called "phrases." Phrases are themselves composed of indivisible units organized in a particular order, called "syllables" (Bretagnolle 1996; Catchpole and Slater 2008). There are four types of syllable (mentioned as A, B, C, D, in their order of appearance), distinguishable by the shape of their frequency modulations. Each syllable is produced once per phrase, except syllable C which is repeated between two and twelve times per phrase depending on the individuals (see Bretagnolle 1996; Gémard et al. 2019 for spectrograms).

Playback procedure

To assess whether particular acoustic parameters play a role in female mate choice, we used a two-choice playback experiment to compare the attractiveness of chosen acoustic parameters, one by one. The experimental design consists in broadcasting two stimuli from inside two artificial burrows simultaneously. The two stimuli (i.e., the stimuli dyad) are two modified versions of a same call, whose tested acoustic parameter has been either decreased ("low version" of the call) or increased ("high version"). We chose five acoustic parameters to test, related to morphological characteristics and possibly to reproductive success in blue petrels according to a previous study (Gémard et al. 2019): call rate (number of calls per minute), call duration (in seconds), frequency spectrum (in Hertz), number of syllables per phrase, and syllable rate (number of syllables per second).

To build the playbacks, we first chose two representative male calls (hereafter call1 and call2) of the studied population in 2017. Call1 and call2 were chosen among recorded calls to have syntax, temporal parameters, and frequencies close to the mean values of the population, based on measurements of 38 acoustic parameters (Appendix 1). For both call1 and call2, we modified the five acoustic parameters (call rate, call duration, frequency spectrum, number of syllables per phrase, syllable rate) one by one, by either decreasing or increasing them, while letting the other parameters unchanged (Table 1; Fig. 1). We made the modifications of acoustic parameters of call1 and call2 using the signal processing software Avisoft-SASLab Pro v 5.2.11 (Specht 2002). More precisely, in the temporal domain, we modified the number of syllables by manually removing or adding the last C syllables and we modified the call duration by adding or removing phrases among the call. We modified the syllable rate by cutting or inserting inter-syllable silences. In the spectral domain, we modified the frequency spectrum by shifting up or down the frequency spectrum of ± 50 Hz using the Avisoft tool "frequency shift" (Fig. 1). To avoid extreme values and bias related to supra stimulus, we increased/decreased the acoustic parameters in the natural range previously observed in the studied colony (Table 1; Appendix 1). Considering five acoustic parameters, this gave us five dyads of stimuli consisting in a low-parameter call and a high-parameter call, for both call1 and call2.

For each of the five acoustic parameters, a trial consists in broadcasting a stimuli dyad in a same burrow twosome during two consecutive nights (Fig. 2). The stimuli dyad is composed of the same call in two versions: one with a given acoustic parameters increased ("high" version) and the other with the same acoustic parameter decreased ("low" version). During the first night of the trial, the low version was broadcast in a burrow, and the high version in the other burrow of the twosome. During the second night of the trial, the same stimuli dyad was broadcast in the same burrow twosome but we shifted the "low" and "high" versions. The playbacks for a given acoustic parameter thus were done on two successive nights. For example, if we consider the given parameter "frequency spectrum" and the burrow twosome A, the high-pitched version of the call was broadcast in the burrow Aa and the low-pitched version in the burrow Ab during the first night. During the second night, the low-pitched version was broadcast in Aa and the high-pitched version in Ab (Fig. 2). Basically, each night, we performed a binary choice experiment where flying females had the choice between the two versions of the same call. With this design, the possible burrow effect is taken into account while habituation during the two nights of a trial is unlikely to occur. We first carried out the two-choice experiments in the twosome "A" (made of

Table 1 Dyads of experimental signals modified to test the attractiveness of five different acoustic parameters

Acoustic parameter	Low	High
Call rate	1 call/3 min	1 call/3 s
Call duration	2 phrases	8 phrases
Frequency spectrum	Frequencies decreased by −50 dB*	Frequencies increased by +50 dB*
Number of syllables per phrase	2 syllables C	6 syllables C
Syllable rate	Duration of inter-syllable silences doubled*	Duration of inter-syllable silences halved*

* Modifications of frequency spectrum and syllable rate are proportional to the original values of these parameters

burrows Aa and Ab) with stimuli dyads created from the original call1. We then repeated it in the burrow twosome "B" (made of burrows Ba and Bb) with stimuli dyads from call2. The binary choice tests in the burrow twosome B was performed, depending on the parameter, 6 to 26 days after the burrow twosome A. The order or presentation of stimuli dyads was randomized and thus differed between the two burrow twosomes. In total, we carried out 10 trials (two per

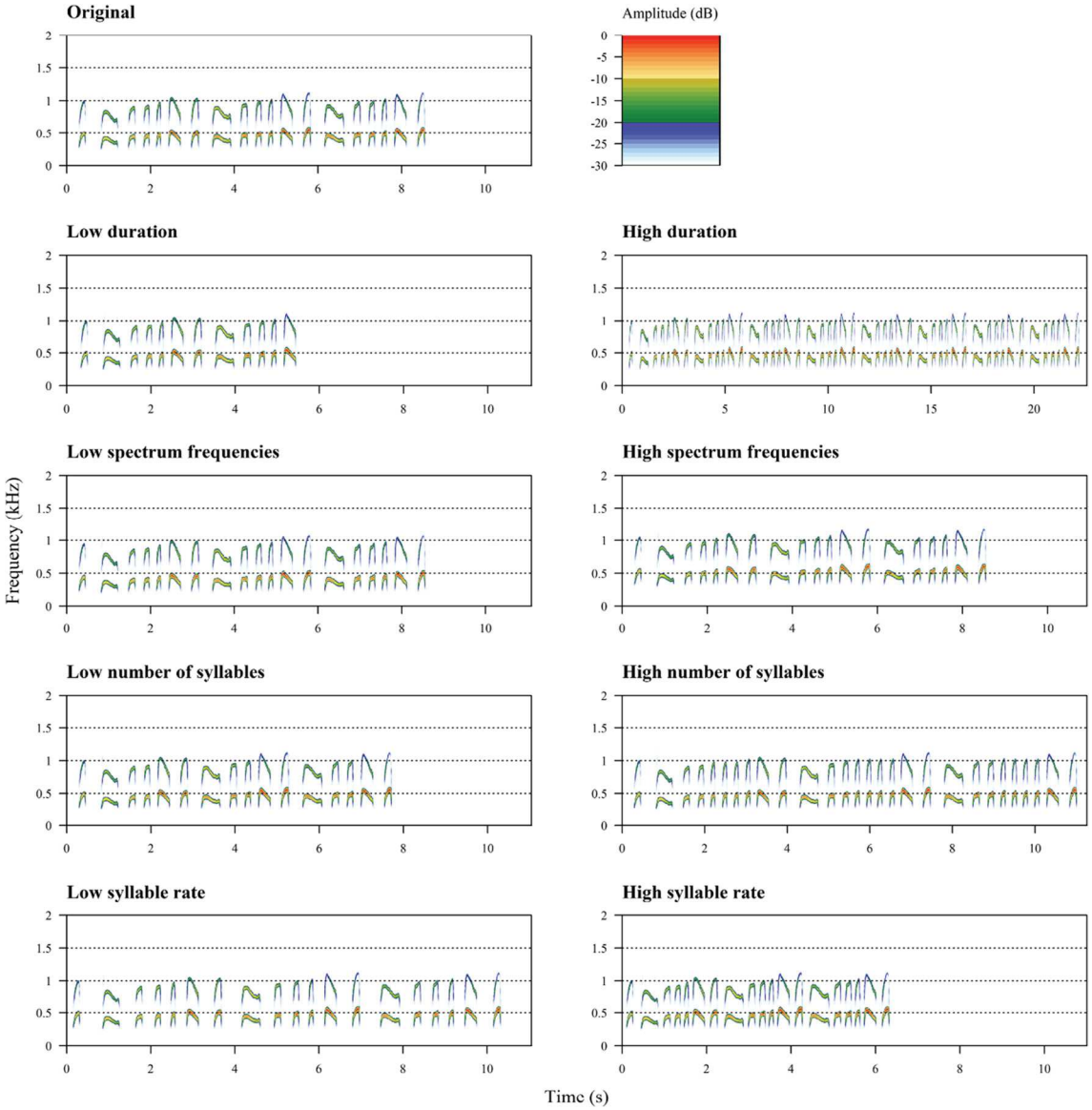

Fig. 1 Spectrograms of the stimuli dyad to broadcast, created from an original representative male call of the studied population of blue petrels (call1). On the left, the chosen acoustic parameters have been decreased; on the right increased

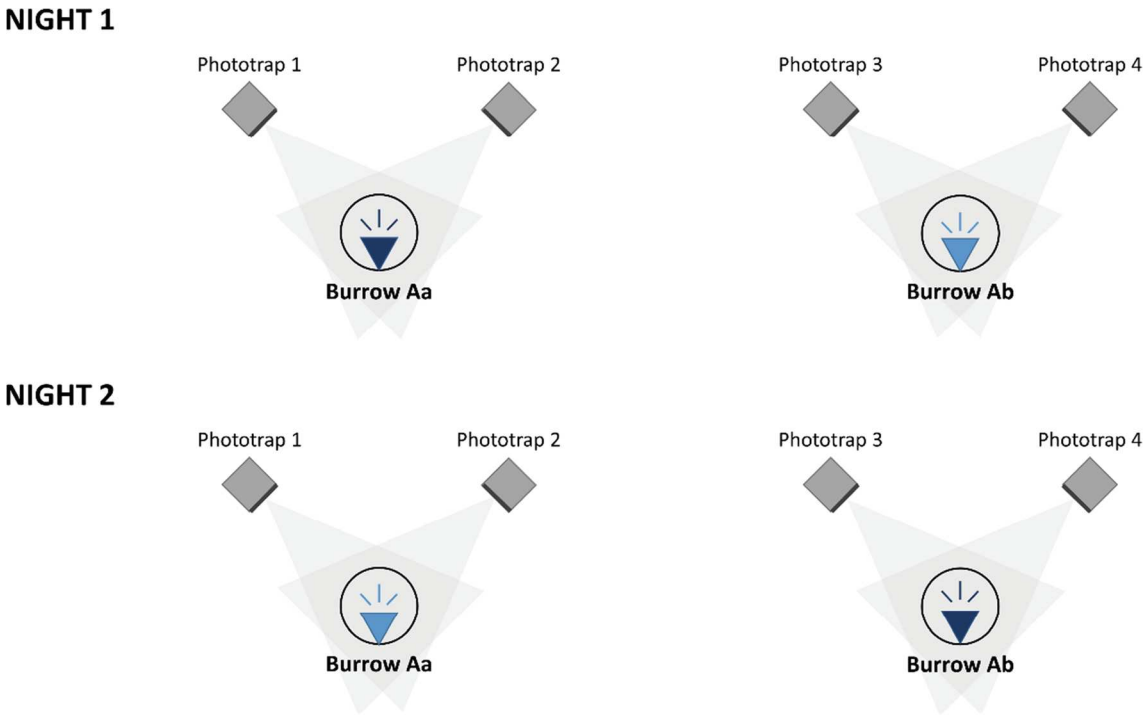

Fig. 2 Experimental design of the two-choice playback experiment. Both burrows of a twosome (circles) are equipped with two phototraps (gray squares) with overlapped visual ranges (gray triangles). A trial consists in testing a given acoustic parameter during two consecutive night. During the first night, a low-version (light blue triangle) and a high-version (dark blue triangle) of a male call (i.e., the stimuli dyad) are broadcast in burrows. During the following night, call versions to broadcast are shifted

chosen acoustic parameters) during 20 nights using four burrows organized in two twosomes.

Stimuli were emitted from the burrow chambers using a Sony NWE393B connected to a JBL Flip 4 speaker (frequency response 70–20000 Hz ± 5 dB). The volume occupied by the speaker is close to the volume occupied by a blue petrel (about 0.7 L). Playbacks were broadcast during the most intense vocal activity (10:00 pm to 3:00 am, unpublished data) at a natural amplitude (mean ± SD: 66 ± 9 dB, measured at the entrance of burrows with an A-weighted decibel-meter Lutron SL-4001 on 115 spontaneous calls from 24 bachelor males in the studied population) and a natural call rate (a call every 40 s, unpublished data from 21 bachelor males in the studied population), except when we specifically tested the call rate attractiveness.

Two-choice playback experiments were carried out in four unoccupied artificial burrows (i.e., two twosomes) because they offer the advantage of limiting biases of sound propagation caused by volume differences. Artificial burrows were installed during the previous breeding season in the colony (2017). They consisted in a chamber made of a clay pot diameter 30 cm upside down, a 66-centimeter tunnel made of two end-to-end half fired-clay wine rack, and a 30-centimeter PVC pipe diameter 125 mm above the chamber to easily reach the birds and/or the egg. They were buried at a depth of 40 cm and covered by the existing vegetation. A wooden board and a stone recovered the hole above the chamber, as the other monitored burrows of the colony (see Appendix 2 for pictures). During the 2018 breeding season, 75% of artificial burrows installed in 2017 were occupied by breeding petrels. The two burrows of a twosome were at least 5 m apart and had different orientation to avoid the influence of sound propagation from a burrow to the other burrow.

To record female behaviors at proximity of the tested burrows, we equipped each burrow with two infrared phototraps (Bushnell Nature View Essential HD Camera) (Fig. 2; Appendix 3). We placed phototraps 50 cm above the ground on wooden sticks at equidistance of the burrow entrance. We oriented phototraps toward the burrow entrance. We used phototraps in video mode with both automatic detection (i.e., 1-min record after movement detection) and "Field Scan" option (i.e., automatic 1-min record every 5 min). Videos were analyzed by a blind-to-the-experiment student with VLC media player 2.1.5 Rincewind. In several burrowing-petrel species, bachelor females use a two-step approach: first flying and landing close to the sound source, then listening to calls until they reach the source by walking (Storey 1984). Here, for each night and each burrow, we counted the number of females flying close to the burrow and the number of females on the ground. We calculated the total time each female spent on the ground. To limit the risk of considering breeders shifting and transient individuals, we only considered individuals flying at a maximum distance of 5 m from the burrow entrance, and individuals showing exploration behaviors on the ground,

e.g., calling, walking, moving head in the direction of the burrow (Appendix 4). Although there is no sexual dimorphism in blue petrels, bachelor males competing for burrow are scarce at this advanced stage of the breeding season (Warham 1990). Recorded prospecting individuals were thus considered females.

Data analyses

All analysis results were implemented under the R software environment version 3.4.4 (R Core Team 2018). Raw data are available in Appendices 5 and 6.

We statistically compared the attractiveness of the "low version" and the "high version" of each of the five acoustic parameters using three distinct models. The dependent variables — one per model — were the number of females flying close to the burrow, the number of females on the ground close to the burrow, and the time females spent on the ground. To model the number of females flying as a function of the independent variables, a Negative Binomial General Linear Model (NB GLM) with a log link function was used as our count data was overdispersed and zero inflated. To model the number of females on the ground, a Poisson GLM with a log link function was used because Poisson distribution is typically used for count data. To model the time females spent on the ground, a linear model from the *lme4* R package (Bates et al. 2015) was used. The "total time" variable was previously log-transformed to normalize its distribution. In the three models, independent variables consisted in three categorical variables: burrow twosome (A or B), and the interaction between acoustic parameter and condition (low or high). Model assumptions were verified by checking the dispersion parameter for the two first models (respectively 1.02 and 4.12) and by plotting residuals versus fitted values for all three models (Appendices 7, 8, and 9). For each of the three models, we created a contrast matrix based on Tukey contrasts with a Bonferroni-Holm correction method for multiple testing.

Results

Results showed significant differences between the maximum and the minimum in two acoustic parameters. More specifically, a high call rate attracted more flying females than a low call rate (estimate (SE) = 2.12 (0.90), $z = 2.35$, $p = 0.02$; Fig. 3). High-pitched calls attracted more flying females than low-pitched calls (estimate (SE) = 1.94 (0.89), $z = 2.18$, $p = 0.03$; Fig. 3). Based on the model parameters, calls with phrases made of few syllables might also be more attractive than calls with phrases of many syllables, although the relationship is not significant (estimate (SE) = −1.94 (1.03), $z = -1.88$, $p = 0.06$; Fig. 3). The call duration did not influence the average number of flying females per night (estimate (SE) = −0.25 (0.84), $z = -0.30$, $p = 0.77$; Fig. 3). Burrow twosome A was significantly more attractive than burrow twosome B (estimate (SE) = −2.06 (0.42), $z = -4.9$, $p < 0.001$).

Results show that a high call rate significantly attracted more females on the ground than a low call rate (estimate (SE) = 1.22 (0.51), $z = 2.41$, $p = 0.02$: Fig. 4). The call duration, frequency spectrum, number of syllables per phrase, and syllable rate were not significantly related to the number of females on the ground per night (respectively: estimate (SE) = −0.46 (0.31), $z = -1.49$, $p = 0.14$; estimate (SE) = 0.18 (0.35), $z = 0.52$, $p = 0.60$; estimate (SE) = −1.79 (1.08), $z = -1.66$, $p = 0.10$; estimate (SE) = −0.34 (0.41), $z = -0.81$, $p = 0.42$; Fig. 4). Burrow twosome A was significantly more attractive than burrow twosome B (estimate (SE) = −0.47 (0.18), $z = -2.61$, $p = 0.009$).

Results show that the time females spend on the ground was not significantly influenced by the five acoustic parameters tested ($F_{10–81} = 1.27$, $p = 0.26$, $r^2 = 0.03$; Fig. 5). The time females spent on the ground was not significantly different between the two burrow twosomes (estimate (SE) = −0.47 (0.30), $z = -1.60$, $p = 0.11$).

Discussion

We aimed to assess the role of male calls in female mate choice, and the attractiveness of certain acoustic parameters of male calls (call rate, call duration, frequency spectrum, number of syllables per phrase, and syllable rate) in blue petrels. Our two-choice playback experiments with modified calls successfully attracted females. The results indicate that more females were attracted by the high-pitched calls, by high-rate versions of the call exemplars tested, and possibly by modified calls with few-syllable phrases. We found no relationship between acoustic parameters and time females spent on the ground exhibiting exploratory behaviors.

Results show that in blue petrels, male calls attracted potential mates even in absence of the caller. Similar results have been found in many taxa, including non-songbirds such as sage grouses and hoopoes (Gibson 1989; Martín-Vivaldi et al. 1999). Previous studies have assessed that olfactory signals contain genetic information about the signaler, and that they are likely to influence mate choice (Bonadonna and Nevitt 2004; Bonadonna and Sanz-Aguilar 2012; Leclaire et al. 2017). We thus hypothesize that both vocal and olfactory signals may influence mate choice but with a different timing: first, male calls may attract flying females, then olfactory signals may play a role when females land and/or when both male and female are in the burrow.

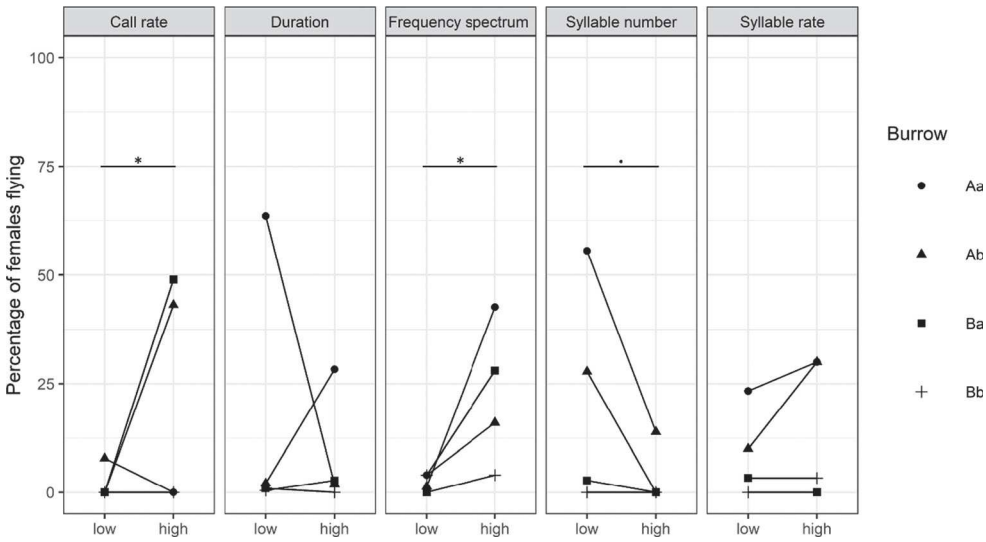

Fig. 3 Number of blue petrel females flying at a maximum distance of 5 m from the burrow where modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow twosome where we broadcast a stimuli dyad. *p<0.05, ·0.05<p<0.01

Results suggest that males calling with a high rate attract more flying females and more females on the ground. Similar results have been found in mammals and birds (McComb 1991; Riebel 2009). One possible explanation would be that males producing many frequent calls are easier to locate in dense and noisy colonies (up to two burrows per m^2: Brothers 1984) because the repetition of calls helps the female walking on the ground to locate the source of emission (Storey 1984). Producing redundant vocal signals is a communication strategy in response of misdetection and/or misclassification in noisy environment ("cocktail-party effect": Cherry 1957; Aubin and Jouventin 1998; Jouventin et al. 1999; Lengagne et al. 1999). A high call rate is also indicative of the signaler's sexual motivation in many birds, including burrowing petrels (Catchpole and Slater 2008; Searcy and Beecher 2009; CG et al. unpubl. data). Nonetheless, bachelor petrels face a high predation pressure and a high call rate also increases the risk of being detected by predators (Mougeot and Bretagnolle 2000b). The handicap principle states that good-quality males take larger risks than other males to produce sexual signals (Zahavi 1975, 1977). Based on this theory, we could hypothesize for the blue petrels too that females are preferentially attracted by males that produce frequent calls, and thereby are more exposed to predation.

Our results also indicate that females are preferentially attracted by high-pitched calls when they fly over the colony. One possibility is that calls higher in frequency make the emitter easier to locate (Dooling 1982; Park and Dooling 1991; Klump 2000). Low frequencies are usually easier to detect because they are less attenuated by distance and less attenuated and/or degraded by environmental constraints than high frequencies (Marten et al. 1977). Nonetheless, male calls are emitted from burrows in burrowing petrels and low frequencies are attenuated by the ground effect (Morton 1975; Marten et al. 1977).

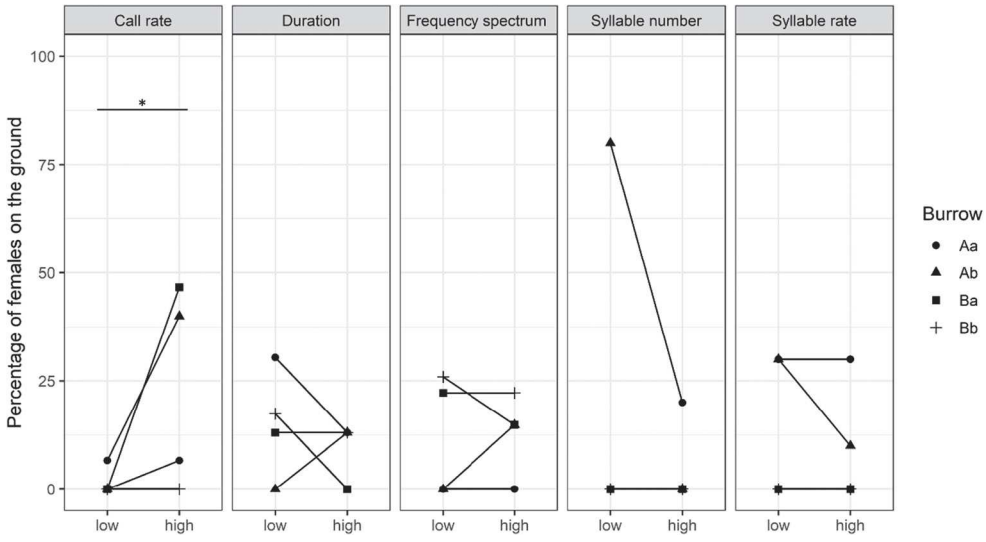

Fig. 4 Number of blue petrel females showing exploratory behaviors on the ground at proximity of the burrow where modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow twosome where we broadcast a stimuli dyad. *p<0.05

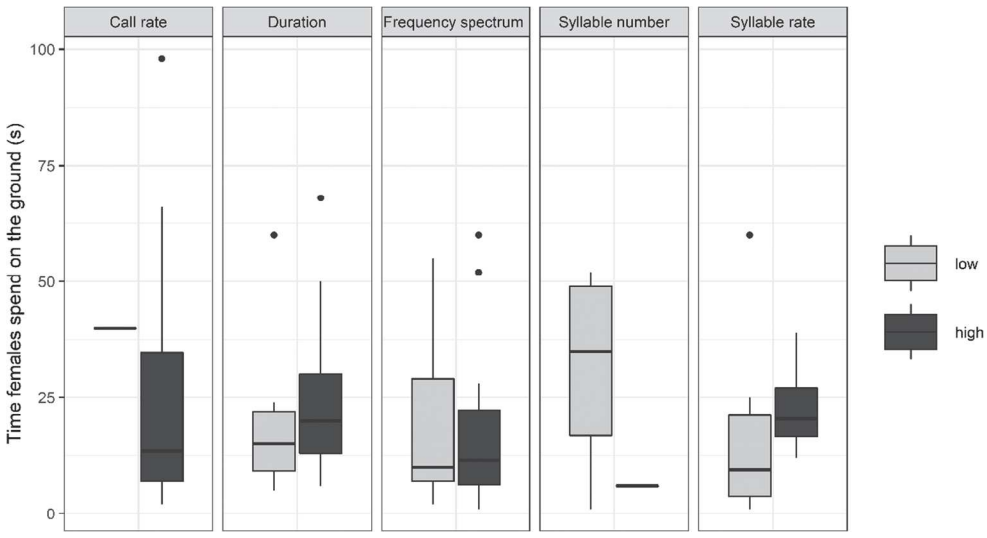

Fig. 5 Time spent by blue petrel females showing exploratory behaviors on the ground, at proximity of the burrow where modified calls of male blue petrel were broadcast. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to 1.5*IQR and outliers

Moreover, some animal species are more sensitive to high frequencies but so far, little is known about how call frequency affects the ability of petrels to localize calls. Another possibility is that high-pitched calls indicate males of good quality, as shown in many taxa, including tortoises (Galeotti et al. 2005), passerines (Cardoso 2012), and mammals (Reby et al. 2010). In blue petrels, big males with a long, thin bill produce high-pitched calls (Gémard et al. 2019). Because bill morphology may determine the filtering surface and efficiency (Klages and Cooper 1992), these males might have a better filter-feeding efficiency and consequently a better reproductive success.

Our results suggest that calls made of few-syllable phrases might be attractive to females. They contradict our assumptions that females may be preferentially attracted by long calls with many syllables. For example, in another non-songbirds, the hoopoe *Upupa epops*, songs with many syllables are more attractive than songs with few elements as it is indicative of the singer's body condition (Martín-Vivaldi et al. 1998, 2000). Moreover, males producing long calls with many elements are easier to detect and to locate than males producing short calls with few elements (Brumm and Zollinger 2013), but this may be true for both potential mates and predators. We thus may hypothesize that females might be more attracted by males producing short calls with few syllables, but at a high call rate, as the result of a trade-off between predation avoidance and conspicuous sexual signaling.

Broadcast signals, regardless of the tested acoustic parameter, had no influence on the time attracted females spend on the ground, at the proximity of the burrow. In burrowing petrels, females vocalize towards the sound source (male in the burrow) when they are on the ground, and then walk following female-directed calls produced by males until they find the burrow entrance (Storey 1984). In blue petrels, males produce female-directed calls characterized by frequency and temporal modulations that may indicate their sexual motivation (CG et al. unpubl. data). Olfactory signals may also be involved in sexual signaling because previous studies have shown burrows have a chemical signature (Bonadonna et al. 2001, 2004), and individuals have a body odor containing genetic information (Bonadonna and Nevitt 2004; Bonadonna and Sanz-Aguilar 2012; Leclaire et al. 2017). Thus, we hypothesize that a necessary exchange of vocal and/or olfactory signals might take place before the female enters the burrow. In our experiments, we used a repetitive playback in an artificial burrow, so that we could not interactively reply in an appropriate way to a female close to the burrow, and no odors were emitted. In the absence of these vocal and olfactory stimuli, and considering the predation risks (Mougeot and Bretagnolle 2000b), females may fly rapidly away independently of the nature of the modified call emitted.

In summary, we showed for the first time in a burrowing petrel that males' calls with certain acoustic characteristics are attractive to females. More precisely, females flying over the colony are more attracted by males producing high-pitched calls and calling at a high rate. Flying females might also be attracted preferentially by calls consisting in few-syllable phrases rather than many-syllable phrases. These acoustic parameters are related to male bill morphology and may thus be linked to male qualities, such as feeding efficiency. Another explanation is that males producing high-pitched calls at a high call rate may be easier to locate. Females are also attracted by short calls with few syllables, which make the caller less conspicuous. It might indicate a trade-off between predation avoidance and conspicuous sexual advertisement to attract potential mates in the hubbub of the colony. The time spent by females exploring on the ground might be influenced

by additional signals, such as a vocal response from the male, olfactory signals, or both.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-02989-3.

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Code availability Not applicable

Author contribution All authors made substantial contributions to the conception of experiment, analysis and interpretation of data, and critical review of the manuscript. CG, FB, and TA contributed to the study conception and design. CG and FB performed material preparation and data collection. CG and ELR analyzed the data. The first draft of the manuscript was written by CG, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The dataset generated and analyzed during the current study is available in supplementary material.

Declarations

Ethics approval All experiments were approved by the French Ethical Committee (APAFIS#9496-201707131540776) after favorable recommendation of Comité d'Ethique pour L'Expérimentation Animale Languedoc-Roussillon (CEEA-LR), C2EA no. 36, and by the Ethical Committee of Reserve Naturelle des Terres Australes et Antarctiques Françaises (TAAF). The 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.

Consent to participate This article does not contain any studies involving human participants performed by any of the authors.

Consent for publication All the authors have approved the submitted version and have agreed both to be personally accountable for their own contributions and to ensure that questions related to the accuracy or integrity of any part of the work, even ones in which the authors were not personally involved, are appropriately investigated and resolved, and the resolution documented in the literature.

Conflict of interest The authors declare that they have no conflict of interests.

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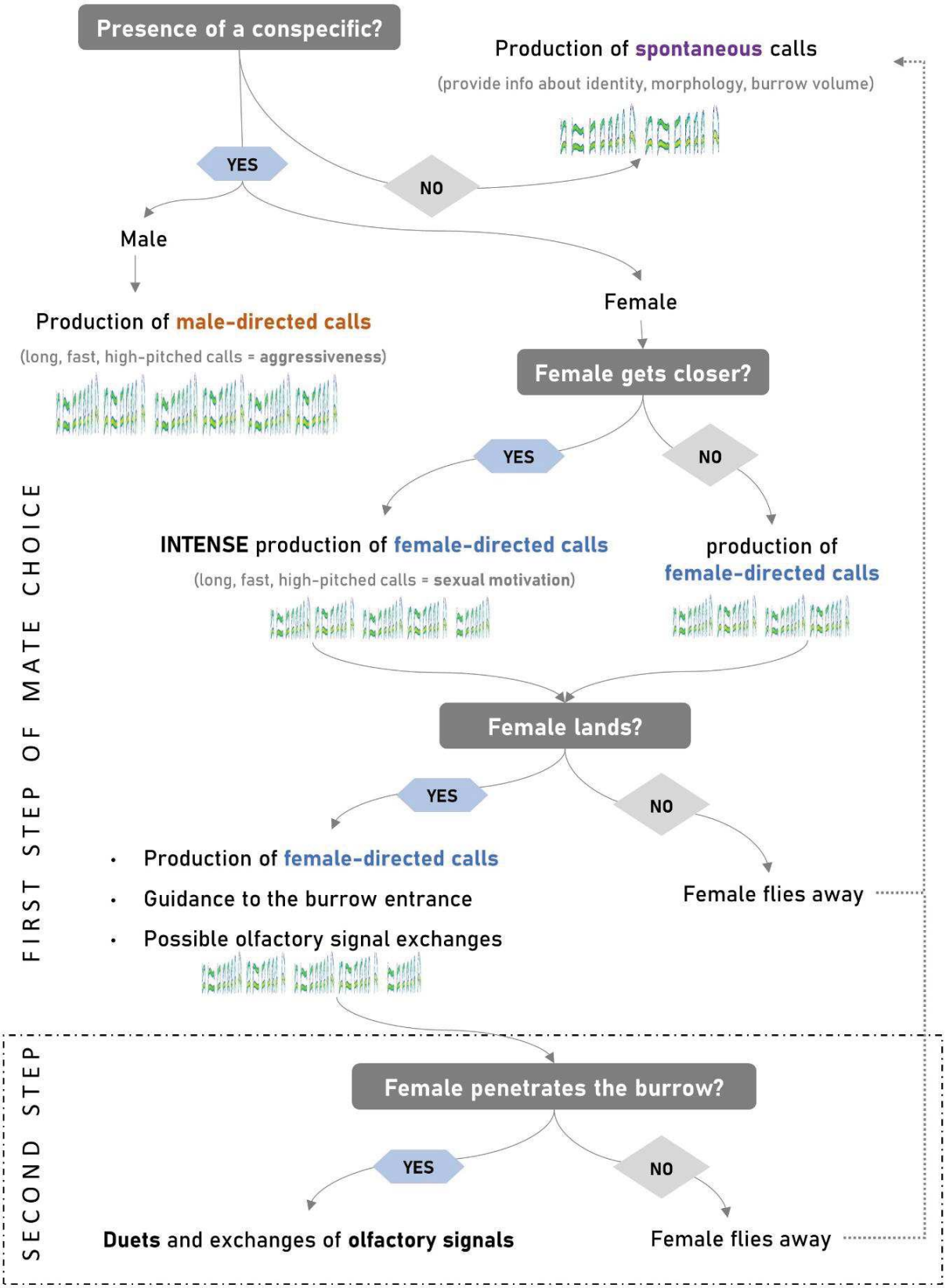
APPENDIX 3: SUMMARY DIAGRAM OF MALE VOCAL BEHAVIOUR AND FEMALE MATE CHOICE IN BURROWING PETRELS



GLOSSARY

ACTIVE SPACE: maximal distance at which the receiver detects the signal in the background noise. Also called *detection range* or *detectability*.

ATTENUATION: decrease in the intensity of a sound (Wiley & Richards 1982).

CALL: usually short and simple vocalizations with a larger range of functions (Catchpole & Slater, 2008). Not to be confused with *song*.

CHORUS: group of at least two individuals vocalizing in competition.

CUE: phenotypic traits (morphological, acoustic, olfactory, tactile, and behavioural) or resources (nest, territory) defended or produced by the signaller with a communicative potential, although its main purpose is not communication (Candolin, 2003).

DEAR-ENEMY PHENOMENON: mechanism by which individuals react less aggressively towards familiar conspecifics of neighbouring territories than towards unfamiliar individuals (Fisher 1954; Temeles, 1994).

DEGRADATION: modification of the structure of a sound (Wiley & Richards, 1982).

DETECTION RANGE: maximal distance at which the receiver detects the signal in the background noise. Also called *active space*. Not to be confused with *discrimination range*, as detectability does not imply discrimination (Wiley & Richards, 1982).

DISCRIMINATION RANGE: maximal distance at which the receiver detects **and** discriminates the signal in the background noise. Not to be confused with *detection range*. The *discrimination range* is usually shorter than *detection range* (Wiley & Richards, 1982).

DISPLAY: vocalizations, movements, and postures which have become adapted in physical form or frequency to subserve social signal functions (Moynihan, 1960).

DUAL FUNCTION HYPOTHESIS: theory stating that birdsongs have two main function, which are attracting potential mates and repelling rivals (Catchpole & Slater, 2008).

GROUND EFFECT: sounds are reflected and attenuated (especially frequencies under 2 kHz) by the surface and vegetation of the ground above which they propagate (Marten et al., 1977; Morton, 1975).

HANDICAP PRINCIPLE: theory stating that showy signals, displays, and ornaments are honest indicators of the signaller quality because they are costly to maintain (Zahavi, 1975, 1977).

INDIVIDUAL RECOGNITION: process through which individuals modulate behaviour based on cues that differ between individuals.

MATE CHOICE: one of the two main mechanisms of the sexual selection, relying on a selection of high-quality mates by the choosy sex (usually females) (Andersson, 1994).

MESSAGE: subset of information carried by a signal.

MOTIVATIONAL-STRUCTURAL RULES: hypothesis stating that the physical structure of vocalizations provides information about the emitter motivation. Vocalizations emitted in hostile contexts are usually harsh and low-pitched, whereas vocalizations in friendly contexts are high-pitched (Morton, 1977).

NOISE: interfering abiotic and biotic sounds that may blur or mask an acoustic signal (Brumm & Zollinger, 2013).

PARENTAL INVESTMENT THEORY: theory stating that the sex with the highest investment in offspring (usually female) is the choosy one, generating a reproductive competition (Trivers, 1972).

RECEIVER: also called *receptor*, individual that perceives the signal and extracts its message.

RESPONSE: change of mental or physical state of the receiver after perceiving a signal (Cherry, 1957).

SEABIRD: birds living in and making their living from the marine environment, which includes coastal areas, islands, estuaries, wetlands, and oceanic islands (Shreiber & Burger, 2002).

SENDER: also called *communicator* or *signaller*. Individual that transmits a signal.

SENSORY SPECIALIST: animal that rely predominantly on one sensory modality.

SENSORY DRIVE: ecological selection for efficient signal transmission (Wilkins et al., 2013).

SEXUAL DIMORPHISM: difference between males and females in the expression of a trait.

SEXUAL SELECTION THEORY: differential reproductive success resulting from competition for mates and fertilizations (Darwin, 1871).

SIGNAL: behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms (Otte, 1974; see Rendall et al., 2009 for a review).

SIGNAL DETECTABILITY: distance at which the signal is still discriminable from the background noise. Also called *propagation distance*, *active space*, and *effective range*.

SIGNAL DISCRIMINATION: ability to classify correctly a signal based on its temporal, spectral, structural characteristics.

SIGNAL-TO-NOISE RATIO: difference between the amplitude of the background (ambient noise) and the amplitude of a given signal (Klump, 1996). Sometimes abbreviated S/N in literature.

SONG: long, complex vocalizations produced by males in the breeding season (Catchpole & Slater, 2008). Not to be confused with *call*.

SOURCE-FILTER THEORY: theory stating that vocal signals result from a two-stage production, with the glottal wave generated in the larynx (the source) being subsequently filtered in the supra laryngeal vocal tract (the filter). Therefore, independent information about the signaller is coded in the glottal wave (mostly characterized by the fundamental frequency) and the spectral envelope (mostly characterized by the vocal tract resonances or formant frequencies; Fant, 1960).

VOCAL RECOGNITION: discrimination of an individual among others by its *vocal signature*.

VOCAL SIGNATURE: set of acoustic parameters in vocalizations that allows the *vocal recognition* of the emitter.

RESUME EN FRANCAIS

CONTEXTE

Comme Bradbury et Verhencamp (1998) le disent, la communication est « *la colle maintenant les sociétés animales* » car elle est le fondement chez la majorité des espèces de nombreux comportements sociaux tels le choix de partenaire, les stratégies anti-prédateurs, la reconnaissance parents-jeunes et la défense de territoires. Bien que la communauté scientifique ne soit pas unanime quant à sa définition, il est communément admis que la communication animale est un échange de signaux produits par un émetteur, perçus puis décodés par un ou plusieurs récepteurs (Bradbury & Verhencamp, 2011 ; Shannon & Weaver, 1949). Les signaux vocaux (chants, cris), comme tout signal, transmettent des informations codées par des paramètres acoustiques particuliers, qu'ils soient temporels (ex. rythmes, durées), fréquentiels (ex. valeur de la fréquence fondamentale, distribution spectrale d'énergie) ou syntaxiques. L'information est dite statique si elle perdure dans le temps, comme l'espèce, le sexe, les caractéristiques physiques ou l'identité individuelle de l'émetteur. L'information est dite dynamique si elle est liée à un stimulus environnemental tel que la présence de nourriture, d'un conspécifique ou d'un prédateur. Par exemple, la motivation agressive ou sexuelle de l'émetteur est une information dynamique.

Pour que l'information contenue dans le signal soit fiable et perçue par le récepteur, les paramètres acoustiques qui la codent doivent être conservés ou peu dégradés et peu atténués durant la propagation du signal (Larsen, 2020). Bien que les signaux vocaux aient la particularité de se propager sur de grandes distances, ils sont inéluctablement dégradés et/ou atténués par différents processus liés à des facteurs environnementaux biotiques et abiotiques (Marler & Slabbekoorn, 2004 ; Naguib & Wiley, 2001 ; Wiley & Richards, 1982). Par exemple, une végétation dense filtre les fréquences élevées des vocalisations, les obstacles produisent de l'écho, les turbulences climatiques atténuent le signal (Wiley & Richards, 1982). Les divers sons ambiants provoquent des interférences et masquent le signal (ex. vent, vocalisations de congénères ou d'autres espèces). Les environnements bruyants, comme les chorus matinaux d'oiseaux chanteurs, les environnements urbains ou les colonies d'oiseaux marins sont donc particulièrement contraignants pour la propagation des signaux vocaux (Naguib & Wiley, 2001). Plusieurs stratégies et adaptations vocales comme la stéréotypie, l'individualité et la redondance de

l'information améliorent la détectabilité et la discrimination d'un signal vocal, comme mis en évidence chez les oiseaux marins (ex. Aubin & Jouventin, 1998, 2002).

Les oiseaux marins représentent un exemple intéressant de communication vocale en milieu contraignant. En effet, ils se regroupent généralement en denses colonies de dizaines, centaines, milliers d'individus dans des zones climatiques turbulentes. Chez certaines espèces, la prédation est une contrainte supplémentaire. Par exemple, les pétrels fouisseurs comme les pétrels bleus (*Halobaena caerulea*), prions de la Désolation (*Pachyptila desolata*) et pétrels à tête blanche (*Pterodroma lessonii*) subissent une forte pression de prédation par le labbe subantarctique (*Stercorarius antarcticus*) qui repère ses proies grâce à leurs cris (Mougeot & Bretagnolle, 2000). En dépit des contraintes environnementales (prédation, colonialité, climat) qui limitent la communication acoustique, les pétrels sont extrêmement vocaux. Les cris seraient à la base de la communication à longue distance sur le site de reproduction puisque le terrier empêche l'utilisation de signaux tactiles et visuels, et les signaux olfactifs seraient utilisés à courte distance.

Chez les pétrels fouisseurs, les cris sont principalement émis la nuit par des individus à la recherche d'un partenaire, c'est-à-dire sexuellement matures mais non reproducteurs. Les mâles crient depuis leur terrier et les femelles en vol. Les cris de mâles sont susceptibles de stimuler et d'attirer les femelles dans le terrier. Les mâles produisent le même type de cri après avoir été provoqués par un congénère mâle à l'entrée de leur terrier, probablement pour le défendre contre les intrus (Bretagnolle, 1996 ; Warham 1990, 1996). Les cris des mâles semblent donc jouer un rôle crucial au cours de la saison de reproduction dans les interactions territoriales et sexuelles, notamment dans le choix de partenaire. Ce choix est déterminant chez ces espèces monogames à vie dont le succès reproducteur dépend de la bonne synchronie et coopération entre les partenaires qui se relaient pour incuber et nourrir le poussin. En cas d'échec, changer de partenaire s'avère long et coûteux (Bried & Jouventin, 2002).

Les pétrels fouisseurs représentent un passionnant système de communication vocale peu étudié et pourtant au cœur du processus de sélection sexuelle en milieux contraignants. De plus, la communication acoustique depuis une structure creuse a été documentée chez les insectes, chauves-souris et amphibiens mais assez peu chez les oiseaux, rendant les pétrels fouisseurs d'autant plus intéressants. Enfin, le fait

que ces espèces soient connues pour leurs capacités olfactives développées et l'usage de signaux olfactifs dans les interactions sexuelles rend l'utilisation de la communication vocale surprenante (Bonadonna et al., 2009; Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012).

OBJECTIFS

Malgré la supposée importance des cris des mâles dans la sélection sexuelle chez les pétrels fouisseurs, les déterminismes et implications de ces cris restent méconnus. Les objectifs de la présente thèse ont donc été de : (i) tester si les cris des mâles influencent le choix de partenaire par les femelles et si oui comment ; (ii) déterminer les paramètres acoustiques qui varient avec le contexte social et la fonction des cris ; et (iii) mettre en évidence les paramètres acoustiques qui codent pour des informations statiques telles que les caractéristiques physiques du mâle émetteur et/ou de son terrier. Pour répondre à ces questions, deux espèces de pétrels fouisseurs fortement prédatées et connues pour leurs capacités olfactives ont été étudiées : le pétrel bleu (*H. caerulea*) et le prion de la Désolation (*P. desolata*). Les oiseaux ont été étudiés grâce à une approche expérimentale combinant repasses, expériences d'attractivité à choix binaire et analyses statistiques multivariées, dans une colonie naturelle située sur l'archipel de Kerguelen pendant la période de reproduction (novembre à janvier).

PRINCIPAUX RESULTATS

Information statique contenue dans les cris des mâles

Dans la définition même du signal, la notion d'information codée dans le signal est primordiale. Le Chapitre I, point de départ de cette thèse, a pour objectif l'identification d'informations statiques contenues dans le cri des mâles. Ces derniers étant probablement à la base du choix de partenaire des femelles, nous avons fait l'hypothèse qu'ils contiennent des informations renseignant sur les qualités intrinsèques des mâles et leur identité individuelle, permettant aux femelles: (i) d'évaluer les qualités de l'émetteur comme partenaire à vie potentiel ; (ii) de discriminer les mâles les uns des autres. Les résultats de nos expériences de repasse ont montré que, bien que les cris des mâles soient fortement stéréotypés, ils contiennent des informations sur les caractéristiques morphologiques des mâles (taille, morphologie

de l'aile et du bec) et ces informations sont codées par une combinaison de paramètres acoustiques temporels, fréquentiels et syntaxiques. Plus précisément, chez le pétrel bleu, les mâles de plus grande taille avec un long bec et de longues ailes produisent des cris plus longs, rapides et avec de nombreuses syllabes. Chez le prion de la Désolation, les mâles de plus grande taille produisent des cris plus graves, longs, lents. Les cris des mâles contiennent également l'identité individuelle du mâle émetteur. La signature vocale est principalement codée par la durée et le rythme des phrases, et par la distribution spectrale. Enfin, les cris renseignent sur le statut reproducteur du mâle émetteur.

Information sur la motivation des mâles

Après avoir souligné dans le chapitre précédent l'information statique contenue dans les cris des mâles, le Chapitre II se concentre sur l'information dynamique, contexte-dépendante, contenue elle aussi dans le cri des mâles. Nous faisons l'hypothèse que des variations de structure acoustique des cris d'un même individu, liées à la présence d'un conspécifique mâle ou femelle, renseignent sur la motivation agressive ou sexuelle de l'émetteur. Pour aller plus loin, nous avons fait également l'hypothèse que les mâles réagissent plus intensément lorsqu'une femelle est proche, et donc plus susceptible de percevoir le cri du mâle et d'en extraire précisément l'information qu'il contient. L'effet Doppler dans le cri des femelles généré par leur vol rapide pourrait être un indice de distance pour les mâles. L'intérêt de ce deuxième chapitre est double puisqu'au-delà des pétrels fouisseurs, la plasticité vocale des oiseaux non-chanteurs, ainsi que la détection et l'utilisation de l'effet Doppler, ont été très peu étudiées dans le passé et sont donc des problématiques novatrices.

Nos expériences de repasse ont montré que chez les deux espèces étudiées, la motivation sexuelle ou agressive est une information dynamique que l'on retrouve dans les cris des mâles. Un changement de motivation chez le mâle soumis à la présence de conspécifiques se traduit par la production de cris plus longs que les cris spontanés et caractérisés par des variations de rythme et de fréquences chez les deux espèces. Plus précisément, la présence d'un autre mâle, perçu comme un potentiel rival, provoque la production de cris plus longs et plus aigus que les cris spontanés. La présence d'une femelle, perçue comme un potentiel partenaire, déclenche également la production de cris plus longs et plus aigus que les cris spontanés. Ils sont également plus lents (diminution du rythme) chez le pétrel bleu, rapides

(augmentation du rythme) chez le prion de la Désolation. Bien que les mâles répondent vocalement à la présence d'une femelle, l'intensité de la réponse dépend de la proximité de la femelle : plus la femelle est proche, plus la réaction est intense. Les mâles estimeraient la distance qui les sépare de la femelle grâce à des variations de fréquences et/ou de rythme liées à l'effet Doppler du cri de vol des femelles. Bien que de nombreuses espèces vocalisent en vol, ce résultat original est une première chez les espèces n'utilisant pas l'écholocation.

Influence du contenu informatif des cris sur le choix de partenaire des femelles

Après une identification des paramètres acoustiques des cris des mâles codant pour des informations potentiellement liées à la qualité des mâles (ex. morphologie, identité, condition corporelle), le Chapitre III vise à comprendre si ces paramètres identifiés sont particulièrement attractifs pour les femelles. Nos expériences d'attractivité, basées sur la repasse de différentes catégories de signaux, ont montré que les informations statiques et dynamiques contenues dans le cri des mâles influencent les femelles dans le choix de partenaire. Les femelles sont préférentiellement attirées par les mâles produisant des cris aigus, fréquents, et potentiellement constitués de peu de syllabes par phrase.

Au-delà des caractéristiques acoustiques du cri, nous avons cherché à déterminer si les femelles sont préférentiellement attirées par des mâles vocalisant en groupe ou au contraire des mâles isolés au sein de la colonie. Nous avons fait l'hypothèse que des mâles groupés sont plus attractifs car les cris émis en quantité ont plus de chance d'être perçus à distance et permettent aux femelles d'évaluer plusieurs partenaires potentiels à la fois. Contrairement à nos hypothèses, le nombre de mâles criant en synchronie partielle n'a pas d'incidence sur le choix de partenaire des femelles.

Rôle du terrier dans la communication vocale

La particularité des pétrels fouisseurs est l'occupation de terriers, creusés par leurs soins, au cours de la saison de reproduction. Bien que le lien entre production acoustique et cavité ait été documenté chez les amphibiens et les insectes tout particulièrement, les informations disponibles chez les oiseaux sont moindres. Dans le Chapitre IV, nous avons donc cherché à définir le rôle du terrier dans la propagation des cris des mâles et par conséquent à étudier son influence sur le choix de partenaire par

les femelles. Nous avons fait les hypothèses que les femelles sont préférentiellement attirées par : (i) les terriers de grand volume qui pourraient améliorer par un phénomène de résonance la propagation du son et seraient donc plus détectables ; et (ii) les terriers plus profonds qui pourraient être plus difficiles à excaver par les labbes et donc moins soumis à la prédation.

Notre expérience de propagation a montré que les cris des mâles se propagent à grande distance mais sont inévitablement atténués avec la distance. L'enveloppe et les modulations de fréquences sont les paramètres acoustiques les plus sévèrement dégradés, contrairement à la structure spectrale moins dégradée. Le volume du terrier a un effet positif sur la propagation du son puisque les cris des mâles émis depuis des terriers de grand volume (i.e. avec un large tunnel et/ou une large chambre) sont moins dégradés que ceux émis depuis de petits terriers. Cependant, notre expérience d'attractivité a montré que cette différence de propagation des cris n'est pas perçue par les femelles et/ou n'influencent pas les femelles dans leur choix de partenaire. Les femelles semblent toutefois préférer les terriers proches de la surface aux terriers profonds, contrairement à notre hypothèse de départ.

DISCUSSION

Contraintes environnementales et stratégies de codage de l'information

Comme énoncé par la « Théorie de la Communication Mathématique » de Shannon et Weaver (1949), les cris encodent des informations. Chez les pétrels bleus et prions de la Désolation mâles, ils encodent notamment la morphologie du mâle, son statut reproducteur, sa motivation sexuelle ou agressive et son identité individuelle. Ces informations sont codées par des combinaisons de paramètres acoustiques temporels, syntaxiques et fréquentiels. La redondance de l'information et le codage multiparamétrique sont des stratégies vocales adaptées aux milieux bruyants car elles limitent les risques de dégradation et augmentent la probabilité que les informations soient efficacement perçues (Jouventin et al., 1999). De plus, nos résultats montrent que les informations les plus discriminantes, telle la signature individuelle, sont codées par les paramètres les moins dégradés lors de la propagation du cri, à savoir la structure spectrale et les paramètres temporels. Ce résultat concorde avec les résultats d'études précédentes (Brenowitz, 1982; Mouterde, 2020). L'émission de cris stéréotypés à intervalles

réguliers chez le pétrel bleu et le prions de la Désolation augmente également les chances de détection par des récepteurs potentiels, comme montré chez le manchot royal *Aptenodytes patagonicus* (Aubin & Jouventin, 1998; Jouventin et al., 1999; Lengagne et al., 1999).

La signature vocale individuelle pourrait être une stratégie de communication en environnements bruyants car les vocalisations familières sont plus facilement détectables dans le bruit ambiant (effet « *cocktail party* » : Aubin & Jouventin, 1998 ; Cherry, 1957). Cette signature vocale s'additionnerait à la signature olfactive, dont l'existence et le rôle dans la reconnaissance individuelle ont été montrés chez plusieurs espèces de pétrels (Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Mardon et al., 2010; Mardon & Bonadonna, 2009). Toutefois, signature individuelle n'implique pas toujours reconnaissance individuelle (Townsend et al., 2010) et cette dernière n'a pas été testée chez les pétrels fouisseurs et très peu chez les Procellariiformes (Brooke, 1978; Curé et al., 2011).

Les vocalisations ne sont pas choisies arbitrairement mais adaptées dans leur structure à la fonction qu'elles assurent (Marler 1955). Une comparaison entre deux espèces phylogénétiquement proches, le pétrel bleu et le prion de la Désolation, souligne la similarité de leurs stratégies et adaptations vocales. Cela suggère que les contraintes dues à un environnement colonial bruyant ont guidé l'évolution des cris, résultant en un codage complexe basée sur la redondance de l'information et l'individualité.

Implications des cris de mâles dans la sélection sexuelle

Chez le pétrel bleu et le prion de la Désolation, les cris des mâles semblent jouer un rôle crucial dans les deux mécanismes principaux de la sélection sexuelle, la compétition entre mâles et le choix de partenaire par les femelles. Nos résultent montrent que les mâles, qu'ils soient reproducteurs ou non, répondent vocalement de manière intense à la présence d'un autre mâle (Chapitre II). Ces cris assurent vraisemblablement la défense du terrier face aux rivaux et/ou intrus (Bretagnolle, 1996). Dans le cas d'un mâle non reproducteur, ces cris pourraient également jouer un rôle dans la compétition vocale pour l'attraction des femelles. Toutefois, les signaux vocaux sont considérés comme impliqués dans la compétition entre mâles s'ils remplissent quatre critères énoncés par Cate et al. (2002) : (i) il existe des différences entre mâles au niveau de certains paramètres acoustiques; (ii) il existe des différences liées

à la compétitivité du mâle ; (iii) certaines variations acoustiques sont produites seulement par les mâles très compétitifs ; et (iv) les individus récepteurs perçoivent ces variations et répondent suivant la qualité de l'émetteur. Bien que nos résultats montrent l'existence de différences interindividuelles au niveau de paramètres acoustiques codant la morphologie et/ou l'identité de l'émetteur (Chapitre I), de futures études sont nécessaires pour tester expérimentalement si les cris des mâles sont des signaux territoriaux.

Pour que les cris des mâles des espèces étudiées ici soient considérés comme des signaux sexuels ayant une réelle influence dans le choix de partenaire, ils doivent remplir quatre critères (Bretagnolle 1996) : (i) existence d'un dimorphisme vocal sexuel ; (ii) discrimination vocale des sexes ; (iii) attirance des femelles par les cris des mâles ; (iv) relation entre un paramètre acoustique et un trait sélectionné chez les mâles. Premièrement, nous n'avons pas testé s'il existe un dimorphisme vocal sexuel chez les pétrels, caractéristique déjà bien documentée dans la littérature (Bourgeois et al., 2007; Bretagnolle, 1996; Curé et al., 2011). Deuxièmement, nos expériences de repasse montrent que les mâles perçoivent ce dimorphisme vocal et répondent différemment aux autres mâles et aux femelles (Chapitre II), corroborant les résultats de précédentes études (Bretagnolle & Lequette, 1990; Curé et al., 2011; Taoka & Okumura, 1989). Troisièmement, les cris de mâles diffusés au cours des différentes expériences d'attractivité ont attiré des femelles, bien qu'aucun mâle ne soit réellement présent et qu'aucun signal supplémentaire (ex. odeurs) ne soit diffusé (Chapitre III et IV). Enfin, nous avons montré que les paramètres acoustiques des cris des mâles sont étroitement liés à des caractéristiques morphologiques du mâle et qu'ils sont de potentiels indicateurs de bonne qualité. Par exemple, un cri rapide chez les pétrels bleus indique un mâle avec de longues ailes fines (Gémard et al., 2019 ; Chapitre I), susceptible de planer plus loin et d'assurer un meilleur nourrissage du poussin (Hertel & Ballance, 1999 ; Mauck & Grubb, 1995). De plus, certains cris diffusés étaient plus attractifs que d'autres pour les femelles selon leurs paramètres acoustiques (ex. cris fréquent, aigu, et constitué de peu de syllabes), suggérant un choix actif par les femelles en vol.

Nos expériences de repasse et d'attractivité ont donc montré expérimentalement que les cris des mâles des pétrels remplissent les quatre critères énoncés précédemment et sont des signaux sexuels jouant un rôle prépondérant dans l'attraction des femelles et le choix de partenaire. Les paramètres

préférés par les femelles permettent une meilleure détectabilité des cris mais sont également liés à des caractéristiques morphologiques du mâle émetteur. Cette première étape de choix de partenaire, lorsque la femelle en vol évalue le mâle grâce à son cri, suggère une première sélection accrue par les femelles basée sur la détectabilité et/ou le contenu informatif du cri. Cependant, les paramètres acoustiques testés n'ont pas permis de souligner ce qui encourage les femelles à rester au sol après s'être posées, suggérant l'intervention de signaux supplémentaires tels qu'une réponse vocale du mâle et/ou des signaux olfactifs.

CONCLUSION ET PERSPECTIVES

Le pétrel bleu et le prion de la Désolation sont des oiseaux marins nichant en terrier dans de denses colonies proches de la convergence Antarctique. Les interférences vocales de congénères et d'autres oiseaux, couplées aux turbulences climatiques caractéristiques de ces régions, contraignent la communication vocale. Pourtant, mâles et femelles à la recherche d'un partenaire à vie communiquent via des cris émis respectivement depuis les terriers ou en vol. Les résultats d'expériences de repasse menées dans le cadre de cette thèse soulignent les adaptations et stratégies vocales propices aux milieux bruyants présentes chez les deux espèces étudiées, comme la stéréotypie des cris, la redondance d'information, la présence d'une signature individuelle et le codage multiparamétrique. Ces résultats concordent avec ceux de précédentes études menées sur différentes espèces de manchots. Le terrier permettrait également d'améliorer la propagation du son émis depuis l'intérieur, tout particulièrement si la chambre et/ou le tunnel sont de grand volume.

Le pétrel bleu et le prion de la Désolation sont deux espèces monogames à vie et présentant un investissement reproducteur très élevé basé sur la coopération entre partenaires. Le choix de partenaire, d'une importance capitale, serait non-aléatoire. La théorie actuelle, bien que non formalisée, indique que le choix de partenaire s'effectue en deux étapes séparées dans le temps et dans l'espace et qu'il est basé sur des canaux sensoriels différents. Dans un premier temps, les femelles en vol reçoivent les cris spontanés des mâles. Les paramètres acoustiques de ces cris fournissent des informations d'intérêt, notamment l'identité et la morphologie du mâle émetteur grâce à une stratégie de codage multiparamétrique, permettant aux femelles de l'évaluer. Les femelles choisissent alors de se poser à

proximité de la source du cri ou non. La théorie des jeux prédit que les femelles se posent, et s'exposent ainsi à la prédation, seulement si le mâle est de bonne qualité. Les femelles en vol ou au sol signalent leur présence par des cris, provoquant une réponse vocale intense du mâle. Ces cris provoqués fournissent des informations supplémentaires, notamment sur la motivation sexuelle du mâle grâce à des variations acoustiques temporelles et fréquentielles, et guident rapidement les femelles jusqu'à l'entrée du terrier. Dans un second temps, la femelle pénètre le terrier où les adultes produisent des duos leur permettant de tester leur compatibilité et potentiellement d'apprendre leurs cris respectifs. La proximité des adultes dans le terrier permet l'échange de signaux olfactifs, contenant des informations supplémentaires et influentes dans le choix de partenaire, tel que le complexe majeur d'histocompatibilité (Leclaire et al., 2017 ; Strandh et al., 2012). Si les caractéristiques du terrier influencent la décision des femelles, l'évaluation du terrier a probablement lieu à cette étape, comme chez les crabes violonistes (*Austruca annulipes*), et non lorsque les femelles sont en vol.

La présente thèse apporte donc des résultats importants quant aux stratégies de communication vocale depuis une structure creuse particulière (terrier) et en milieu bruyant, ainsi que l'implication des signaux vocaux dans le choix de partenaire chez les pétrels fouisseurs. Deux résultats sont particulièrement notables en communication animale: l'utilisation des changements de fréquences et tempo dans les cris de vol (effet Doppler) comme indice de distance et la plasticité vocale liée à un changement motivationnel chez des oiseaux non-chanteurs. De ces résultats découlent plusieurs perspectives. Les conclusions de la présente thèse suggèrent la nécessité d'étudier le rôle de signaux supplémentaires, notamment olfactifs, lorsque les femelles sont au sol. De futures expériences nous permettront de creuser la piste de la communication multimodale et de tester si les informations contenues dans les signaux vocaux et olfactifs sont redondantes et si les deux canaux sensoriels sont nécessaires au choix de partenaire ou si l'un des deux est prépondérant. Enfin, bien que cette thèse soit le fruit de travaux de recherche fondamentale, définir le terrier « idéal » et le « cri type » de mâles de bonne qualité pourrait avoir des applications dans la restauration et conservation de colonies de pétrels grâce à la méthode d'attraction sociale (Buxton et al., 2016 ; Hamblin et al., 2019) ou dans l'amélioration du design des terriers artificiels, de plus en plus utilisés par les chercheurs et gestionnaires.

Abstract

As Bradbury & Verhencamp (1998) nicely said, communication is "*the glue that holds animal societies*" as it mediates many social behaviours in most species. Burrowing petrels offer a remarkable opportunity to study vocal communication in an environment that at a first glance seems unfavourable. Indeed, these seabirds gather in dense colonies during the breeding season. In spite of strong winds, vocal interferences from other birds, and presence of acoustically-oriented predators, calls are at the heart of sexual and territorial interactions. In this thesis, I studied two burrowing petrel species phylogenetically close: the blue petrel *Halobaena caerulea* and the Antarctic prion *Pachyptila desolata*, already known for their developed olfactory abilities. In spite of the climatic constraints and predation pressure, and in addition to olfactory communication, vocal communication should provide benefits, unknown so far. Using playback and attractiveness experiments on the birds' breeding ground in Kerguelen, I aimed to investigate the determinisms and implications of male calls in female mate choice. The results of this thesis reports (i) the coding of static (caller morphology and individual identity) and dynamic (motivation) information coded in both spectral and temporal parameters of male calls, (ii) how detectability of male calls, but mostly their informative content, influence females mate choice, and (iii) the role played by the burrow in call propagation and female mate choice. Both studied species show similarities in their vocal coding and strategies, suggesting that the same environmental constraints on long-range signalling have shaped similarly vocal signals. Considerable insight has been gained concerning the communication strategies in constraining environments and in burrow-nester seabirds, still under-studied.

Keywords: vocal communication, mate choice, information coding, seabirds, burrowing petrels

Résumé

Comme Bradbury et Verhencamp (1998) l'ont joliment dit, la communication est « *la colle maintenant les sociétés animales* » car elle est le fondement de nombreux comportements sociaux chez la majorité des espèces. Les pétrels fouisseurs offrent une excellente opportunité d'étudier la communication vocale dans un environnement qui, de prime abord, semble désavantageux. En effet, ces oiseaux marins se regroupent au cours de la saison de reproduction en denses colonies. En dépit des turbulences climatiques (ex. vents violents), des interférences vocales liées à la présence d'autres oiseaux et de la présence de prédateurs qui chassent à l'ouïe, les vocalisations sont à la base des interactions sociales. Durant mon doctorat, je me suis intéressée à deux espèces de pétrels fouisseurs phylogénétiquement proches : le pétrel bleu *Halobaena caerulea* et le prion de la Désolation *Pachyptila desolata*, tous deux connus pour leurs capacités olfactives développées. En dépit des contraintes environnementales, de la pression de prédation et la possibilité de communiquer via des signaux olfactifs, la communication vocale devrait procurer des bénéfices jusqu'alors méconnus. A l'aide d'expériences de repasse et d'attractivité menées sur un site de reproduction des oiseaux à Kerguelen, mon objectif a été d'étudier les déterminismes et implications des cris des mâles dans le choix de partenaire des femelles. Les résultats de la présente thèse soulignent : (i) la stratégie de codage de l'information statique (morphologie et identité individuelle) et dynamique (motivation) au niveau des caractéristiques spectrales et temporelles des cris de mâles ; (ii) en quoi la détectabilité du cri et surtout l'information contenue influencent le choix du partenaire par les femelles : et (iii) le rôle joué par le terrier dans la propagation du cri et le choix du partenaire par les femelles. Les deux espèces étudiées ici montrent des similarités dans leurs stratégies vocales et de codage de l'information, ce qui suggère que les mêmes contraintes environnementales sur la communication longue distance ont modifié les signaux de manière similaire. Ces résultats enrichissent nos connaissances sur la manière dont les oiseaux nichant en terriers, très peu étudiés, communiquent dans un environnement contraignant.

Mots-clés: communication vocale, choix de partenaire, codage de l'information, oiseaux marins, pétrels