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Sexual and intrapopulation variation in the territorial calls of the Blue Petrel (Halobaena caerulea) on Diego Ramírez Island, Chile

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Abstract

Bioacoustics enables the non-invasive study of animal communication and has proven to be a useful tool in avian systematics and conservation. Within the order Procellariiformes, calls are particularly relevant given the nocturnal and philopatric behaviour of its members, and because females vocalize as much as males. We analysed the territorial calls of the Blue Petrel *Halobaena caerulea* on Diego Ramírez Island, the main breeding site of the species, aiming to characterize calls by sex and individual and to assess intrapopulation variation. From recordings of nesting individuals, we measured five acoustic parameters per element (low frequency, high frequency, delta frequency, delta time, and peak frequency), as well as the number of elements per vocalization. Females produced calls with a greater number of elements (10–18) than males (5–9). Accounting for the hierarchical structure of the data (elements nested within calls and individuals) using linear mixed models, delta time consistently differentiated the sexes; delta frequency showed only a marginal difference; and high, low, and peak frequency did not differ significantly between sexes. Coefficients of variation indicated that low frequency, high frequency, and delta frequency are the most individually conserved characters. In males, discriminant analysis correctly classified 65% of calls to their individual of origin through cross-validation, and PERMANOVA confirmed that individual identity explains 65% of the acoustic variation, supporting the existence of an individual vocal signature and of intrapopulation variation in this species.

Introduction

Bioacoustics is the science in which biology and acoustics converge to investigate, non-invasively, the production and reception of biological sound, as well as the means by which information is transmitted acoustically and propagated through the environment (Pedroza et al. 2016; Buxton et al. 2018; Brownlie et al. 2020). The discipline has developed markedly since the second half of the twentieth century, owing to the availability of technical means capable of storing and analysing sounds (Tubaro 1999; Snaddon et al. 2012; Tegeler et al. 2012; Vallee 2017). Its applications relate to the systematics, conservation and management of wild bird populations (Teixeira et al. 2019), with the use of calls being especially prominent in the diagnosis of new species and the study of their systematic relationships (Sangster et al. 2013; Avendaño et al. 2015; Albornoz et al. 2017, 2018; Prawiradilaga et al. 2017; Krabbe et al. 2020). Bioacoustics also provides powerful, low-cost techniques for monitoring biodiversity in remote areas, even allowing relative population densities to be estimated (Tubaro 1999; Pedroza et al. 2016; Teixeira et al. 2019).

Most interactions among animals involve some form of communication; in birds, calls convey information about the characteristics of the emitting individual, both to conspecifics and to individuals of other species (Dhondt and Lambrechts 1992; Font and Carazo 2009; Magrath et al. 2015). Vocal signals have been widely studied in Passeriformes within the framework of sexual selection and the dual-function hypothesis, which holds that songs serve two purposes: attracting mates and deterring rivals (Kroodsma and Byers 1991; Gémard et al. 2019), and that individual differences in phenotypic quality translate into differences in the structure of vocal signals (Rowe and Houle 1996; Gémard et al. 2019). In

songbirds, song learning derives from the parents, so that they show greater geographic variation without associated genotypic change (Baker and Cunningham 1985; Lachlan and Servedio 2004; López 2020). By contrast, in species with a larger innate component in their calls (non-passerines and suboscines), a single call type is maintained across large geographic extents, and differentiation may reflect genotypic variants, which are even used in the systematic classification of these groups (Tubaro 1999; Araya 2010; López 2020).

Within the order Procellariiformes, the study of calls is particularly interesting for four reasons. First, its members breed on islands in remote oceans, which provides natural geographic isolation. Second, both adults and juveniles are highly philopatric (Weimerskirch et al. 1985; Thibault 1993; Bretagnolle and Genevois 1997). Third, females vocalize as much as males, which allows variation in female calls to be investigated—a trait scarcely studied in birds (Bretagnolle and Genevois 1997; Riebel et al. 2019). Fourth, many species in this order are nocturnal, so that the information conveyed through calls is highly relevant, given that they depend solely on acoustic signals during courtship (Mougeot and Bretagnolle 2000).

In petrels, these acoustic signals are typically used by males seeking a mate: when perceived by females they elicit approach and, subsequently, a duet between both individuals (James 1985; Bretagnolle and Lequette 1990; Bretagnolle and Genevois 1997). Calling behaviour is therefore of primary importance for pair formation and mate choice (Bretagnolle and Genevois 1997), which is consistent with the behaviour of the Blue Petrel Halobaena caerulea (Genevois and Bretagnolle 1994; Bretagnolle and Genevois 1997).

The Blue Petrel *H. caerulea* (Gmelin, 1789) belongs to the family Procellariidae and is a pelagic bird with a circumpolar subantarctic distribution. It nests on seven island groups of the Southern Ocean; in Chile, colonies occur in the Cape Horn archipelago, Ildefonso Island and the Diego Ramírez archipelago, the latter being the main breeding site worldwide, holding approximately 80% of the global population (~ 1,350,000 pairs) and standing out as one of the few subantarctic groups free of introduced predators (Clark et al. 1992; Lawton et al. 2006; Scofield and Reyes-Arriagada 2013; Dilley et al. 2017; Vaneiro-Ramírez 2018). Its vocalization becomes very frequent at dusk, both in flight and from burrows, and has been described as a “kuk-kuk-kuk coo-coo”, similar to the cooing of doves (Murphy and Jaques 1936). Using bioacoustic tools, we analysed the territorial calls of *H. caerulea* with the aims of: (a) characterizing calls at the individual level and by sex, and (b) determining whether vocal variation exists among individuals of the Diego Ramírez Island population.

Materials and methods

Territorial calls

We assembled a database of our own recordings (N = 37) from different individuals of *H. caerulea* recorded on Diego Ramírez Island (56°30'00" S, 68°43'60" W) during the breeding season (egg stage) of 2011. Each recording was made at a different nest, so that each is associated with a given individual.

Calls were recorded with a Zoom H4n recorder and a Sennheiser ME66/K6 condenser microphone. All recordings were made in WAV format, at 24 bits and a sampling rate of 44.1 kHz.

Analysis of calls

Fine-scale measurements and sonograms (i.e. graphical representations of frequency as a function of time) were obtained with Raven Pro 1.4 (Bioacoustics Research Program 2011), using default spectrogram parameters (window type: Hann; window size: 256 samples = 5.33 ms; 3-dB filter bandwidth: 270 Hz; time grid overlap: 50%; hop size: 128 samples = 2.67 ms; frequency grid DFT: 256 samples; grid spacing: 188 Hz). A band-pass filter was applied to remove noise outside the frequency range of *H. caerulea* calls. In each sonogram we measured five parameters per element: low frequency (Hz), high frequency (Hz), delta frequency (delta frequency = high frequency − low frequency, Hz), delta time (s) and peak frequency (Hz). We additionally recorded the number of elements in each call. The identification of sex in territorial calls was based on information from Bretagnolle & Genevois (1997).

Data analysis

All statistical analyses were performed in R v.4.3 (R Core Team 2024). One element (of 477) was excluded from analyses of minimum frequency and delta frequency because of a spectrogram measurement artifact (0 Hz reading; see Results). For each acoustic parameter we calculated descriptive statistics (mean, standard deviation, minimum, maximum and coefficient of variation) by sex, at the element level. Because elements are nested within calls, which are in turn nested within individuals, comparisons of each characteristic between sexes were made with linear mixed models fitted to the element-level data, with call nested within individual included as random intercepts (package lme4; Bates et al. 2015); the significance of sex was assessed by likelihood-ratio test, and response variables were log-transformed when this improved residual normality. As a nonparametric check that does not rely on distributional assumptions, we additionally compared sexes using the Mann–Whitney test on individual-level means (one value per individual, averaged across its calls and elements; 18 males, 8 females). The number of elements per call was compared using a generalized linear mixed model (Poisson family) with individual as a random intercept, and, as a check, a Mann–Whitney test on individual-level means.

To evaluate variation in calls at the individual level we used the coefficient of variation (Fitzsimmons et al. 2008). We calculated within-individual (CVa) and among-individual (CVb) coefficients of variation and, from these, the ratio CVw = CVb / CVa. The value of CVw > 1.0 indicates that a variable is more variable among individuals than within a single individual, which has been suggested as a signal of individual identity (Fitzsimmons et al. 2008).

For the following tests, the unit of analysis was the individual call (replicate), summarized as the mean value of each acoustic parameter across its elements. To quantitatively assess the potential for individual identity in calls, we performed a linear discriminant analysis (LDA) on the five acoustic

parameters, restricted to males with at least three recorded calls (nine individuals, 46 calls). Classification performance was estimated by leave-one-out cross-validation, and the accuracy obtained was contrasted against the rate expected by chance (proportional assignment) using a binomial test. Additionally, we assessed whether among-individual variation exceeded within-individual variation using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on the Euclidean distance matrix of the standardized parameters, considering males with at least two calls (eleven individuals, 50 calls) and using 999 permutations; the assumption of homogeneity of multivariate dispersions was verified with the betadisper test. Finally, as a descriptive ordination technique, we performed a principal component analysis (PCA) by sex, in order to identify the acoustic characters contributing most to the observed variation. Because the parameters are expressed in different units (Hz and seconds), the PCA was computed on standardized variables (correlation matrix). As an exploratory rather than inferential analysis, the PCA requires no assumptions of normality or homoscedasticity. Multivariate analyses were run with the package vegan (Oksanen et al. 2022) and the discriminant analysis with the package MASS (Venables and Ripley 2002).

Results

Female calls had a greater number of elements, ranging between 10 and 18 elements (mean = 12.6 ± 2.8; n = 8 calls; Fig. 2), in contrast to males, which had between 5 and 9 elements (mean = 6.6 ± 0.9; n = 57 calls; Fig. 2). This difference was statistically significant (Mann–Whitney, $P < 0.001$). Descriptive statistics for the five acoustic parameters by sex are summarized in Table 1.

Table 1
Descriptive statistics of the five acoustic parameters measured in the territorial calls of male and female *Halobaena caerulea* on Diego Ramírez Island. Values are mean ± standard deviation (SD); n = number of elements. CV coefficient of variation.

Parameter	Sex	Mean ± SD	Min	Max	CV (%)
Low frequency (Hz)	Male	163.6 ± 62.0	34.6	449.3	37.9
	Female	205.6 ± 152.1	34.6	929.6	74.0
High frequency (Hz)	Male	1834.2 ± 605.0	622.1	5253.3	33.0
	Female	1338.9 ± 376.8	855.3	2661.2	28.1
Delta frequency (Hz)	Male	1671.3 ± 609.7	464.3	5080.5	36.5
	Female	1141.2 ± 453.0	366.6	2592.1	39.7
Delta time (s)	Male	0.21 ± 0.12	0.05	0.62	54.8
	Female	0.11 ± 0.11	0.03	0.70	94.6
Peak frequency (Hz)	Male	640.5 ± 178.1	258.4	1033.6	27.8
	Female	645.6 ± 186.6	172.3	861.3	28.9

Accounting for the nested structure of the data (elements within calls within individuals) with linear mixed models, delta time differed significantly between sexes ($\chi^2 = 22.26$, df = 1, $P < 0.001$), and delta frequency differed only marginally ($\chi^2 = 4.32$, df = 1, $P = 0.038$). High frequency did not differ significantly once this structure was accounted for ($\chi^2 = 3.49$, df = 1, $P = 0.062$), nor did low frequency ($\chi^2 = 0.33$, df = 1, $P = 0.566$) or peak frequency ($\chi^2 = 0.18$, df = 1, $P = 0.669$). A nonparametric check comparing individual-level means (Mann–Whitney, 18 males, 8 females) gave a consistent pattern for all five parameters (delta time: $P = 0.004$; delta frequency: $P = 0.049$; high frequency: $P = 0.063$; low frequency: $P = 0.760$; peak frequency: $P = 0.637$; Fig. 1).

The CVw values allowed the most conserved call characteristics to be identified. In both sexes, low frequency, high frequency and delta frequency showed CVw > 1.0, indicating greater variability among individuals than within a single individual; these characteristics would therefore be the most useful for identification at the individual level. By contrast, delta time showed CVw < 1.0 in both sexes (Table 2).

Table 2
Within-individual (CVa) and among-individual (CVb) coefficients of variation and their ratio (CVw = CVb/CVa) for each acoustic parameter in male and female *Halobaena caerulea*. CVw > 1 suggests individual identity.

Parameter	**Sex**	**CVa**	**CVb**	**CVw**
Low frequency (Hz)	Male	29.04	33.16	1.14
	Female	32.87	69.27	2.11
High frequency (Hz)	Male	16.26	41.61	2.56
	Female	8.83	30.71	3.48
Delta frequency (Hz)	Male	18.31	45.79	2.50
	Female	11.61	43.27	3.73
Delta time (s)	Male	57.51	13.77	0.24
	Female	66.42	59.14	0.89
Peak frequency (Hz)	Male	16.74	24.15	1.44
	Female	20.23	23.66	1.17

The linear discriminant analysis, applied to the nine males with at least three calls, correctly classified 65.2% of calls to their individual of origin through cross-validation, a rate 4.2 times higher than expected by chance (15.6%) and statistically significant (binomial test, 30 of 46 calls correct; $P < 0.001$). The first two discriminant axes accounted for 80.1% of the variation (LD1 = 53.4%; LD2 = 26.7%) and separated most individuals in discriminant space (Fig. 3; Table 3).

Table 3
Performance of the cross-validated linear discriminant analysis (LDA) for assigning calls to their individual of origin in male *Halobaena caerulea* with at least three recorded calls.

Parameter	Value
Individuals analysed	9
Calls analysed	46
Correct classification	65.2%
Expected by chance	15.6%
Improvement over chance	4.2×
Binomial test	$P < 0.001$
Variance LD1 + LD2	80.1%

Consistently, the PERMANOVA confirmed that individual identity explains a substantial and significant fraction of the total acoustic variation among males ($R^2 = 0.65$; $F = 7.31$; $P = 0.001$); that is, among-individual variation greatly exceeded within-individual variation. The betadisper test was not significant ($F = 1.59$; $P = 0.16$), indicating that multivariate dispersions were homogeneous among individuals and that the PERMANOVA result is not attributable to differences in dispersion.

The PCA summarized acoustic structure in few dimensions. In males, the first two components explained 72.3% of the variance (PC1 = 45.7%; PC2 = 26.6%); the first component was dominated by high frequency (loading = 0.63) and delta frequency (0.62), whereas low frequency and peak frequency mainly defined the second component (Online Resource 1). In females, the first two components accounted for 79.3% of the variance (PC1 = 50.0%; PC2 = 29.3%), with PC1 likewise dominated by delta frequency (0.63) and high frequency (0.59; Online Resource 2). These results agree with the coefficients of variation in identifying frequency variables as those with the greatest weight in individual call variation.

Discussion

The structure of *H. caerulea* territorial calls showed a greater number of elements in females (10–18) than in males (5–9), which is consistent with the results of Bretagnolle and Genevois (1997), who describe seven elements for males and eleven for females. When comparing call characteristics between sexes using models that account for the hierarchical structure of the data, delta time differed consistently between sexes, delta frequency differed only marginally, and high frequency, low frequency and peak frequency were similar between males and females. These sexual differences in spectral and temporal parameters are consistent with what has been documented in other Procellariiformes and colonial seabirds in North Atlantic shearwaters (*Puffinus* spp.), the sexes differ in five of seven parameters of the aerial call (Sangster et al. 2024), and in the Cape Gannet *Morus capensis*, a

monomorphic species, sexual signatures have been identified that even allow non-invasive sexing in the field (Bowmaker-Falconer et al. 2022). The fact that female *H. caerulea* produce calls with more elements contributes quantitative data on an aspect (female vocalization) historically under-represented in the ornithological literature (Riebel et al. 2019; Austin et al. 2021). High CVw values allow the most conserved characteristics of calls to be identified (Fitzsimmons et al. 2008). For *H. caerulea*, three characteristics (low frequency, high frequency and delta frequency) proved to be the most conserved, and could therefore be useful for identification at the individual level.

The discriminant analysis and PERMANOVA provide quantitative evidence reinforcing the existence of an individual vocal signature in male *H. caerulea*. The correct classification of 65% of calls to their individual of origin, well above chance, and the fact that individual identity explains 65% of the total acoustic variation indicates that calls carry sufficient information for individual identification, in agreement with what has been described for other burrowing petrels (Gémard et al. 2019). That frequency variables (high frequency and delta frequency) are consistently, across the coefficient of variation, the PCA and the discriminant axes, the most contributing to this differentiation suggests that these characters constitute the acoustic basis of individual recognition in the species. These traits, linked to vocal tract morphology, tend to be more stable within individuals and therefore more informative about the emitter's identity (Fitzsimmons et al. 2008). Our results are directly comparable with those of Sun et al. (2023), who, using linear discriminant analysis with leave-one-out cross-validation (the same approach used here), confirmed individual vocal signatures in the Manx Shearwater *Puffinus puffinus*, a species that, like *H. caerulea*, must recognize and locate its mate among thousands of conspecifics calling simultaneously in the darkness of dense colonies. The classification accuracy we obtained (65%) is consistent with the magnitude reported for burrowing petrels, given the potential for individual coding (Gémard et al. 2019), and supports the view that vocal individuality is a widespread trait in Procellariiformes despite the apparent stereotypy of their genetically determined calls (Gémard et al. 2021a).

The development of differences in vocalization among individuals and between sexes of *H. caerulea* may be related to the habitat and nocturnal behaviour of the species. According to Tobias et al. (2016), among the multiple hypotheses on the function of song is the influence of habitat; in places where visual signals are ineffective, members of a pair or group may maintain contact through acoustic signals. In *H. caerulea*, females, which are especially selective and whose mate choice may take several years, are more attracted to high-pitched calls with a high emission rate (Gémard et al. 2021b), lending functional relevance to the frequency variables that, in our study, proved most informative for individual identity. The intrapopulation variation documented here, together with the marked philopatry of the species, is consistent with the patterns of fine-scale structuring described in other highly philopatric petrels (Danckwerts et al. 2021).

Taken together, our results support the existence of intrapopulation variation in the calls of individuals of both sexes in the *H. caerulea* population of Diego Ramírez Island. The call characteristic that most consistently differentiates males from females is delta time, with delta frequency showing only a

marginal difference. Finally, the existence of an individual vocal signature and of intrapopulation variation in *H. caerulea* opens opportunities for passive acoustic monitoring of this species, a tool increasingly used to census and estimate population parameters in nocturnal, hard-to-observe seabirds such as burrowing petrels (Linares et al. 2022; Bennett et al. 2025). Given that Diego Ramírez holds close to 80% of the world's population of the species, the development of non-invasive call-based methods is especially valuable for its conservation and long-term monitoring.

Declarations

Competing Interests:

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval:

This study was based exclusively on non-invasive acoustic recordings of free-living birds. No animals were captured, handled or manipulated, and therefore no approval from an animal ethics committee was required. Fieldwork was conducted in accordance with the legal requirements and guidelines for the study of wildlife in Chile.

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Author Contribution

CB and HVN conceived and designed the research. VR collected acoustic recordings in the field. CB, EMS and HVN analysed the data. CB and HVN wrote the first draft of the manuscript. All authors commented on previous versions and read and approved the final manuscript.

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Data availability:

The acoustic recordings and the dataset of acoustic measurements generated and analysed during the current study are available from the corresponding author on reasonable request.

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Figures

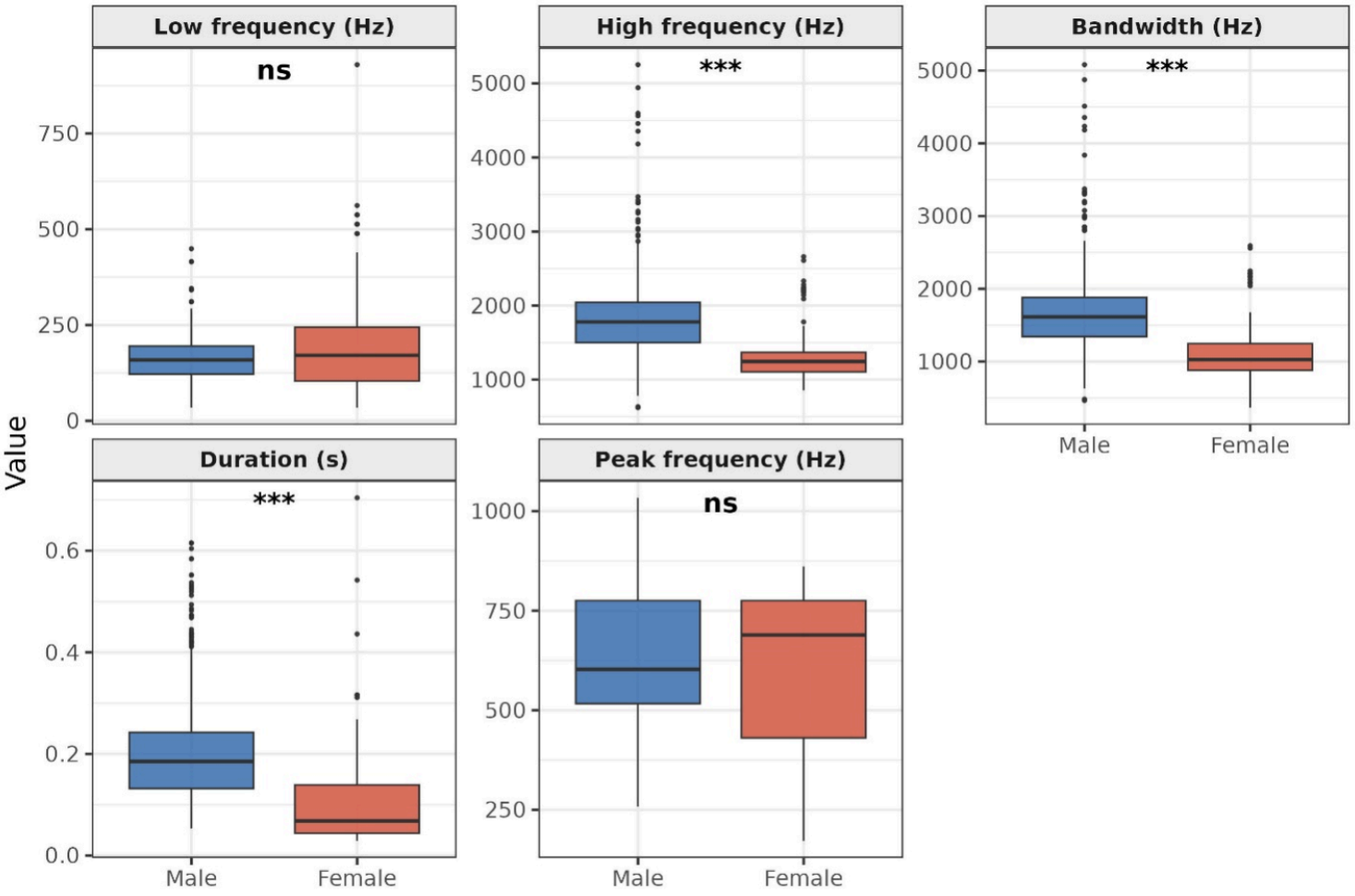


Figure 1

Comparison of the five acoustic parameters between male and female *Halobaena caerulea* on Diego Ramírez Island. Significance is based on linear mixed models accounting for the nested structure of the data (elements within calls within individuals) (*** P < 0.001; * P < 0.05; ns not significant).

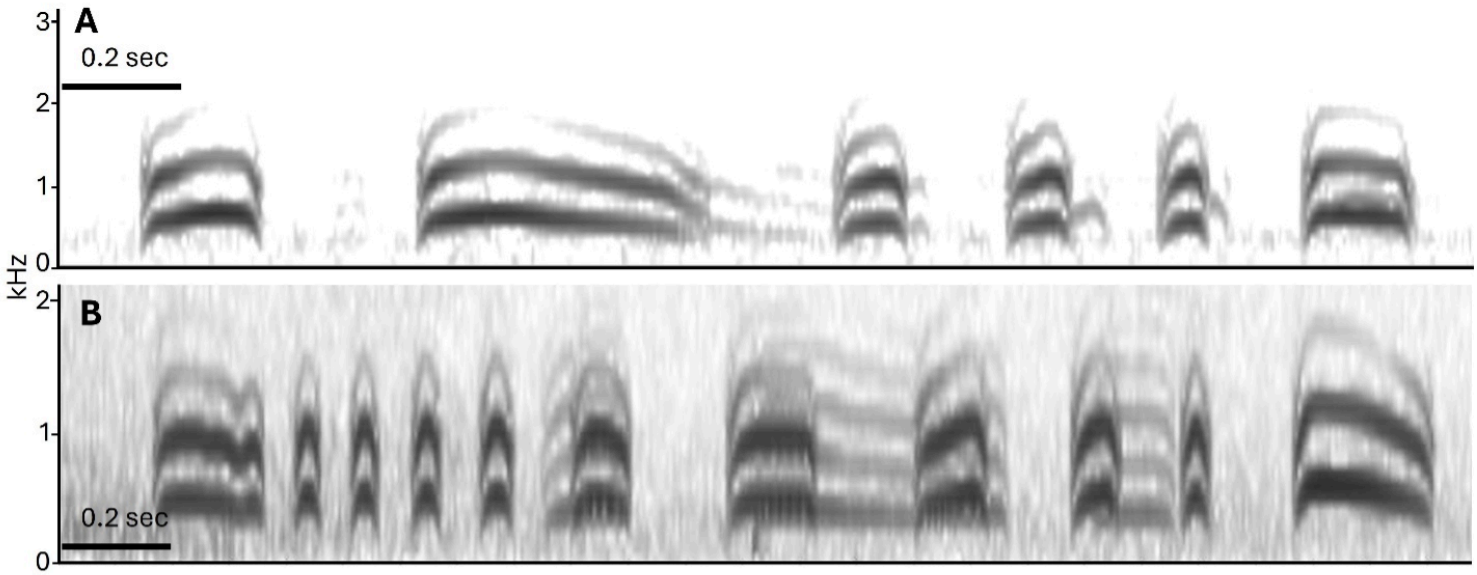


Figure 2

A) Sonogram of the territorial call of a male Blue Petrel (*Halobaena caerulea*) and B) territorial call of a female. Spectrogram obtained from a recording at 44.1 kHz, computed with a short-time Fourier transform (Hanning window, window length = 512 samples, overlap = 87%).

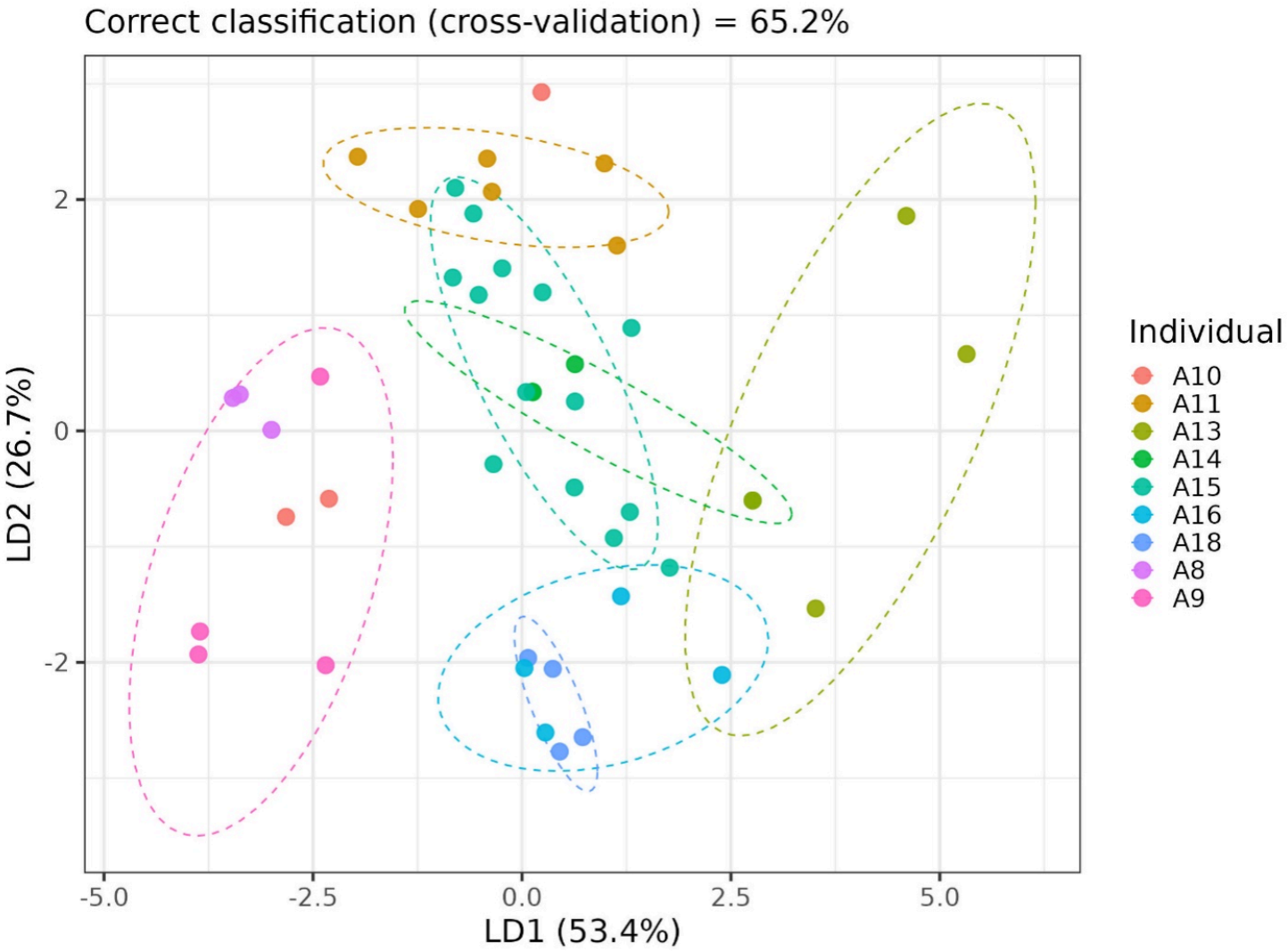


Figure 3

Linear discriminant analysis (LDA) ordination of calls from male *Halobaena caerulea* with at least three recorded calls. Each colour represents an individual; ellipses enclose 68% of the data. The percentage of correct classification corresponds to leave-one-out cross-validation.

Supplementary Files

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- SupplementaryInformation.docx