



HAL
open science

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

Charlène Gémard, Thierry Aubin, Eliette Reboud, Francesco Bonadonna

► **To cite this version:**

Charlène Gémard, Thierry Aubin, Eliette Reboud, Francesco Bonadonna. Call rate, fundamental frequency, and syntax determine male-call attractiveness in blue petrels *Halobaena caerulea*. Behavioral Ecology and Sociobiology, 2021, 75 (3), 10.1007/s00265-021-02989-3 . hal-03146426

HAL Id: hal-03146426

<https://hal.science/hal-03146426>

Submitted on 31 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

[Click here to view linked References](#)

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

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

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

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

6 Orsay, France.

7 *Corresponding author: C. Gémard (charlene.gemard@cefe.cnrs.fr) (<https://orcid.org/0000-0002-8019-5842>)

8

9 **Abstract**

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

25 **Significance statement**

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

34 **Keywords** Vocal communication, sexual signal, attractiveness, mate choice, seabird, blue petrel

35 **Compliance with ethical standards**

36 **Funding**

37 The study was financially supported by the French polar institute Paul Emile Victor (IPEV) This work
38 was carried out under the IPEV research program no. 354 ETHOTAAF.

39 **Conflicts**

40 The authors declare that they have no conflict of interests.

41 **Ethics approval**

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

48 **Consent to participate**

49 This article does not contain any studies involving human participants performed by any of the
50 authors.

51 **Consent for publication**

52 All authors have approved the submitted version; and have agreed both to be personally accountable for
53 the author’s own contributions and to ensure that questions related to the accuracy or integrity of any
54 part of the work, even ones in which the author was not personally involved, are appropriately
55 investigated, resolved, and the resolution documented in the literature.

56 **Availability of data and material**

57 The dataset generated and analysed during the current study is available in supplementary material.

58 **Code availability**

59 Not applicable

60 **Authors' contributions**

61 All authors made substantial contributions to conception of experiment, analysis and interpretation of
62 data, and critical review of the manuscript. Charlène Gémard, Francesco Bonadonna and Thierry Aubin
63 contributed to the study conception and design. Charlène Gémard and Francesco Bonadonna performed
64 material preparation and data collection. Charlène Gémard and Eliette L. Reboud analysed the data. The
65 first draft of the manuscript was written by Charlène Gémard and all authors commented on previous
66 versions of the manuscript. All authors read and approved the final manuscript. **Acknowledgments**

67 We are very grateful to the French polar institute Paul Emile Victor (IPEV) which financially and
68 logistically supported our work. We thank Jessica Graham who improved the English of this manuscript,
69 and Guilhem Battistella and Jean-Yves Barnagaud for their precious help on the field.

70

71 **Introduction**

72 In animal species, mating is not random and the probability of mating with a given individual
73 of the opposite sex increases with some behaviour patterns (Halliday 1983). According to theoretical
74 and empirical studies, in many species, both males and females should profit from being choosy when
75 selecting their mating partner (Courtiol et al. 2016). To do so, they rely on attractive signals that inform
76 them about the signaller's qualities (Smith 1991). Although sexual signals are often multimodal, the
77 implication of vocal signals in mate choice have been well documented in many taxa. Male vocalizations
78 attract potential mates in insects (Walker 1957), fish (Amorim et al. 2006), frogs (Ryan 1980), bats
79 (Knornschild et al. 2017), songbirds (Mountjoy & Lemon 1991), and non-songbirds (Gibson 1989;
80 Martín-Vivaldi et al. 1999).

81 To highlight the influence of vocal signals in mate choice, two criteria have to be respected: (i)
82 males/females must show a preference for certain acoustic parameters of calls/songs when these are
83 presented in the absence of the caller/singer, and (ii) the same acoustic parameters correlate with the
84 caller/singer's mating success in natural conditions (Searcy & Andersson 1986). Well-known examples
85 of attractive acoustic parameters in birds and mammals are a low fundamental frequency (F0 or pitch),
86 a high vocalizing rate, long vocalizations, and vocalizations consisting in many elements (for a review:
87 Nowicki & Searcy 2004). These parameters reflect some overall qualities, such as morphological
88 characteristics (e.g. body size: Ballentine et al. 2004; Ballentine 2009; Byers et al. 2016; Favaro et al.
89 2017; Kriesell et al. 2018; bill morphology: Christensen et al. 2006), endurance, and fighting abilities
90 (McComb 1991). These parameters are also related to breeding success in natural conditions (Chastel et
91 al. 1995; Salton et al. 2015).

92 Most of our knowledge on vocal signal implication in mate choice focuses on songbirds.
93 Comparatively, non-songbirds, such as seabirds, have been poorly documented, although mate choice
94 is crucial in these species due to their particular breeding ecology (for a review see Bried & Jouventin
95 2002). Seabirds have distinct feeding and nesting areas: they feed at sea, while they breed on land. This
96 implies obligatory bi-parental care and cooperation between mates during the whole breeding cycle.
97 Burrowing petrels (Procellariiforms) are colonial seabirds breeding in self-dug burrows on coastal grass

98 slops (Warham 1990), to which they show a high fidelity year after year (Bried & Jouventin 2002). They
99 form lifelong monogamous pairs, and divorces and extra-pair copulations are rare (Jouventin & Mougin
100 1981; Warham 1990, 1996; Quillfeldt et al. 2012). Pairs lay a single egg per year with no possibility of
101 replacement clutch in case of failure and partners alternate several-day fasting periods in the burrow and
102 feeding trips at sea to restore energy (Warham 1990). Parental investment is thus high and parental care
103 is based on parents' cooperation and synchrony. In addition, with respect to species that can change
104 partner at each breeding, correcting possibly wrong choices, these petrels are lifelong faithful to the
105 mate. Consequently, choosing the wrong partner will affect the lifelong fitness more drastically than in
106 other species.

107 Bachelor petrel males actively call at night from their burrow while females fly calling over the
108 colony. This behaviour may be considered intriguing as calling in the colony exposes petrels to
109 predators, especially the brown skua (*Stercorarius antarcticus*) which uses the sexual calls of petrels to
110 locate and catch them (Mougeot & Bretagnolle 2000b). Blue petrels, *Halobaena caerulea*, and prions
111 *Pachyptila sp* are among their preys. Therefore, considering the high predation cost associated with their
112 production, vocal signals should play a major role in mate choice. After hearing a male call, females can
113 land close to the sound source, then enter the caller's burrow where they may start to perform extensive
114 duets (Storey 1984). It suggests that vocal signals are essential in mate choice, although it has not been
115 experimentally tested. Additional signals may be involved, such as olfactory signals to gather genetic
116 information (e.g. MHC) from the potential mate (Leclaire et al. 2017). After pairing mates are silent and
117 would rather use olfactory signals to find their burrow when returning to the colony at night (Bonadonna
118 & Nevitt 2004; Bonadonna & Sanz-Aguilar 2012; Leclaire et al. 2017). Females visit several males for
119 a couple of years before pairing (Bretagnolle 1996), suggesting that the mate choice by females is active,
120 and that male calls attract and/or stimulate potential mates (Bretagnolle 1990; Warham 1990).

121 It has been shown recently that male calls carry information about the caller's morphological
122 characteristics, such as wing morphology, body size and bill shape (e.g. blue petrels: Gémard et al. 2019;
123 Genevois & Bretagnolle 1994; Antarctic prions *Pachyptila desolata*: Gémard et al. 2019). Big males
124 with a long, thin bill produce high-pitched calls consisting of many syllables. Males with long and thin
125 wings produce fast calls (high syllable rate). These morphological characteristics are linked to male

126 overall qualities and reproductive success: for instance, bill morphology is related to filter-feeding
127 efficiency (Klages & Cooper 1992), wing morphology to foraging behaviour (Weimerskirch et al. 1995)
128 and body condition to reproductive success (Chastel et al. 1995).

129 Females landing on the ground after hearing a male call is seemingly the first step of the mate
130 choice process in burrowing petrels described in literature (Bretagnolle 1996; Brooke 2004; Warham
131 1990; Warham 1996). Despite the seeming implication of vocal signals in mate choice, vocal
132 communication in burrowing petrels has been poorly studied so far, likely due to constraints associated
133 with fieldwork in remote locations and their particular breeding ecology (nocturnal and burrowing
134 habits). Although the suggestion that acoustic parameters of male calls reflect qualities and mating
135 success, the hypothesis that females actually show a preference for these parameters has never been
136 tested and thus we do not know if calls are signals in mate choice. Here, we proposed to test this
137 hypothesis by assessing whether females are actually attracted by male calls, and more precisely by
138 certain acoustic parameters of these calls.

139 We experimentally tested by playback experiments with modified calls: (i) the role of male calls
140 in mate attraction, and (ii) the role of certain acoustic parameters of male calls in mate choice. Among
141 burrowing petrels, the blue petrel is a good candidate to assess this question because it is highly vocal
142 and suffers from a high predation pressure (more than 70% of the brown skua diet: Montcorps et al.
143 1998). Based on our previous study on the informative content of blue petrels' calls (Gémard et al.
144 2019), we hypothesized that females should be attracted by males producing long calls with many
145 syllables and a high syllable rate. According to the handicap theory (Zahavi 1975; Zahavi 1977), females
146 may also be attracted by males that take large risks of predation, for instance by calling at a high call
147 rate and/or producing long calls as shown in other species (Johnstone 1995; Zuk & Kolluru 1998).

148 **Material and methods**

149 **Study area**

150 We conducted the fieldwork on a small island of the Kerguelen Archipelago (Ile Verte:
151 49°510'S, 70°050'E), southern Indian Ocean. In blue petrels *H. caerulea*, bachelor males and females
152 are vocally active and actively prospecting for a mate in the colony, at night, throughout the breeding

153 season (Warham 1996), although the daily activity in the colony is dependant of the moon phase and
154 clouds cover (Mougeot & Bretagnolle 2000a). We thus conducted the fieldwork during the birds'
155 incubation period, from November 27th to December 27th 2018.

156 **Studied species**

157 In blue petrels, callers are mainly bachelor males and females, although breeders call when they
158 are vocally challenged by a conspecific, likely to defend their burrow (Warham 1996). Their calls consist
159 of a repetition of distinct phrases, themselves composed of indivisible elements called syllables
160 (Bretagnolle 1996; Catchpole & Slater 2008). There are four types of syllable (mentioned as A, B, C,
161 D, in their order of appearance), distinguishable by the shape of their frequency modulations. Syllable
162 C is repeated between two and twelve times depending on the individuals (Fig. 1).

163 **Playback procedure**

164 We tested the attractiveness of five acoustic parameters related to morphological characteristics
165 in blue petrels: call rate, call duration, energy spectrum, number of syllables per phrase, and syllable
166 rate (Gémard et al. 2019). To do so, we used a two-choice playback experiment consisting in
167 broadcasting two versions (high or low) of a representative call of males, from inside two artificial
168 burrows at the same time. The two representative calls were calls for which syntax, temporal parameters
169 and frequencies are close to the mean values of the population, based on measurements of 38 acoustic
170 parameters presented (Appendix 1). Playbacks were emitted using a Sony NWE393B connected to a
171 JBL Flip 4 speaker (frequency response: 60 Hz- 12000 Hz \pm 5 dB). The volume occupied by the speaker
172 is close to the volume occupied by a blue petrel (about 0.7 L). Playbacks were broadcast during the most
173 intense vocal activity (10:00 pm to 3:00 am, unpublished data) at a natural amplitude (mean \pm SD: 66 \pm
174 9 dB, measured at the entrance of burrows with decibel-meter on 115 spontaneous calls from 24 bachelor
175 males in the studied population) and a natural call rate (a call every 40 s, unpublished data from 21
176 bachelor males in the studied population), except when we specifically tested the call rate attractiveness.

177 Signals to broadcast were synthetized using the signal processing software Avisoft–SASLab Pro
178 v 5.2.11 (Specht 2017). To obtain dyads of experimental signals, a single call (or exemplar) was recorded
179 from two male individuals (hereafter call1 and call2). Call1 and call2 were chosen, among calls recorded

180 in 2017, to have the mean parameters observed in the studied population (i.e. a call for which length,
181 number and structure of syllables are close to the mean values of the population). To create dyads, we
182 modified each of the two calls by decreasing and increasing a selected acoustic parameter, letting the
183 other parameters unchanged. This gave us dyads of stimuli for each parameter: a low-parameter-call and
184 a high-parameter-call (Table 1). To avoid extreme values and bias related to supra stimulus, we
185 increased/decreased the selected acoustic parameter in the natural range previously observed in the
186 studied colony (Appendix 1). Considering five acoustic parameters, we obtained five dyads for call1
187 and five dyads for call2.

188 We repetitively broadcast the experimental signals from inside an unoccupied artificial-burrow
189 chamber of the same size (volume about 4.8 L) to limit biases of sound propagation caused by volume
190 differences. Artificial burrows were installed during the previous breeding season in the colony (2017).
191 They consisted in a chamber made of a clay pot diameter 30 cm upside down, a 66-centimetre tunnel
192 made of two end-to-end half fired-clay wine rack, and a 30-centimetre PVC pipe diameter 125 mm
193 above the chamber to easily reach the birds and/or the egg. They were buried at a depth of 40 cm and
194 covered by the existing vegetation. A wooden board and a stone recovered the hole above the chamber,
195 as the other monitored burrows of the colony (see Appendix 2 for pictures). During the 2018 breeding
196 season, 75% of artificial burrows installed in 2017 were occupied by breeding petrels.

197 To control the nest effect, we used two randomly selected burrow twosome successively:
198 twosome “A” (made of burrows Aa and Ab), then burrow twosome “B” (made of burrows Ba and Bb).
199 The two burrows of a twosome were at least five meters apart and had different orientation to avoid the
200 influence of sound propagation from a burrow to the other burrow. Each dyad of call1 was tested twice
201 the burrow twosome A: one night the low-parameter-call was in burrow Aa and the high-parameter-call
202 in the burrow Ab, the next night the reverse situation with the same dyad. Each dyad of call2 was then
203 tested twice the burrow twosome B following the same scheme described above.

204 We equipped each burrow with two infrared phototrap (Bushnell Nature View Essential HD
205 Camera) to record female behaviours at proximity of the tested burrows (Fig. 2, Appendix 3). We placed
206 phototrap 50 cm above the ground on wooden sticks at equidistance of the burrow entrance. We
207 oriented phototrap toward the burrow entrance. We used phototrap in video mode with both automatic

208 detection (i.e. one-minute record after movement detection) and “Field Scan” option (i.e. automatic one-
209 minute record every five minutes).

210 Videos were analysed by a blind-to-the-experiment student with VLC media player 2.1.5
211 Rincewind. In several burrowing-petrel species, bachelor females use a two-step approach: first flying
212 and landing close to the sound source, then listening to calls until they reach the source by walking
213 (Storey 1984). Here, for each night and each burrow, we counted the number of females flying close to
214 the burrow and the number of females on the ground. We calculated the total time each female spent on
215 the ground. To limit the risk of considering breeders shifting and transient individuals, we only
216 considered individuals flying at a maximum distance of five meters from the burrow entrance, and
217 individuals showing exploration behaviours on the ground, e.g. calling, walking, moving head in the
218 direction of the burrow (Appendix 4).

219 **Data analyses**

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

222 We used three distinct models to compare the attractiveness of the increased parameter and the
223 decreased for each five acoustic parameters: one for the number of females flying close to the burrow,
224 one for the number of females on the ground close to the burrow, and one for the time females spent on
225 the ground. To model the number of females flying as a function of the covariates, a Negative Binomial
226 General Linear Model (NB GLM) with a with a log link function was used. NB GLM is appropriate for
227 count and over-dispersed data. To model the number of females on the ground as a function of the
228 covariates, a Poisson GLM with a log link function was used. Poisson distribution is typically used for
229 count data. To model the time females spent on the ground as a function of the covariates, a Linear
230 Model from the *lme4* R package (Bates et al. 2015) was used. The “total time” variable was previously
231 log-transformed to normalize its distribution. The three models included the following categorical
232 variables as fixed effects: burrow twosome (A or B), and the interaction between acoustic parameter and
233 condition (low or high). Model assumptions were verified by plotting residuals versus fitted values
234 (Appendices 7, 8, and 9). For each of the three selected models, we created a contrast matrix based on

235 Tuckey contrasts with a Bonferroni-Holm correction method for multiple testing. We did not compare
236 the attractiveness of parameters between each other.

237 **Results**

238 **Number of Females Flying**

239 Model assumptions were verified (dispersion parameter = 1.02: residuals in Appendix 7).
240 Results showed significant differences between the maximum and the minimum in two acoustic
241 parameters (Table 2). More specifically, a high call rate attracted more flying females than a low call
242 rate (estimate (SE) = 2.12 (0.90), $z = 2.35$, $p < 0.05$: Table 2). High-pitched calls attracted more flying
243 females than low-pitched calls (estimate (SE) = 1.94 (0.89), $z = 2.18$, $p < 0.05$: Table 2). Based on the
244 model parameters, calls with phrases made of few syllables might also be more attractive than calls with
245 phrases of many syllables, although the relationship is not significant (estimate (SE) = -1.94 (1.03), $z =$
246 -1.88 , $p = 0.06$: Table 2, Fig. 3). Burrow twosome A was significantly more attractive than burrow
247 twosome B (estimate (SE) = -2.06 (0.42), $z = -4.9$, $p < 10^{-6}$).

248 **Number of Females on the Ground**

249 Model assumptions were verified (dispersion parameter = 4.12: residuals in Appendix 8).
250 Results show that a high call rate significantly attracted more females on the ground than a low call rate
251 (estimate (SE) = 1.22 (0.51), $z = 2.41$, $p < 0.05$: Table 3, Fig. 4). Burrow twosome A was significantly
252 more attractive than burrow twosome B (estimate (SE) = -0.47 (0.18), $z = -2.61$, $p < 0.01$).

253 **Duration of Females' Exploratory Behaviour on the Ground**

254 Model assumptions were verified (residuals in Appendix 9). Results show that the time females
255 spend on the ground was not significantly influenced by the five acoustic parameters tested ($F_{10-81} =$
256 1.27 , $p = 0.26$, $r^2 = 0.03$: Table 4, Fig. 5). The time females spent on the ground was not significantly
257 different between the two burrow twosomes (estimate (SE) = -0.47 (0.30), $z = -1.60$, $p = 0.11$).

258 Petrels' calls played-back also attracted brown skuas (N=17), especially when we tested the call
259 duration. We observed that short calls attracted more skuas than long calls (Appendix 5).

260 **Discussion**

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

268 Results show that male calls attracted potential mates, even in absence of the caller. Similar
269 results have been found in many taxa, including non-songbirds such as sage grouse and hoopoes
270 (Gibson 1989; Martín-Vivaldi et al. 1999). Blue petrel females are attracted by vocal signals, even in
271 absence of olfactory signals. Previous studies have assessed that olfactory signals contain genetic
272 information about the signaller, and that they are likely to influence mate choice (Bonadonna & Nevitt
273 2004; Bonadonna & Sanz-Aguilar 2012; Leclaire et al. 2017). We thus hypothesize that both vocal and
274 olfactory signals may influence mate choice but with a different timing: first, male calls may attract
275 flying females, then olfactory signals may play a role when females land and/or when both male and
276 female are in the burrow.

277 Results suggest that males calling with a high rate attract more flying females and more females
278 on the ground. Similar results have been found in mammals and birds (McComb 1991; Riebel 2009).
279 One possible explanation would be that males producing many frequent calls are easier to locate in dense
280 and noisy colonies (up to two burrows per m²: Brothers 1984) because the repetition of calls helps the
281 female walking on the ground to locate the source of emission (Storey 1984). Producing redundant vocal
282 signals is a communication strategy in response of misdetection and/or misclassification in noisy
283 environment (“cocktail-party effect”: Cherry 1957). It has been well documented in seabirds, especially
284 penguins (Aubin & Jouventin 1998; Jouventin et al. 1999; Lengagne et al. 1999). A high call rate is also
285 an indicator of sexual motivation in many birds, including burrowing petrels (Catchpole & Slater 2008;
286 Gémard et al. *in prep*; Searcy & Beecher, 2009). Nonetheless, bachelor petrels face a high predation
287 pressure and a high call rate also increases the risk of being detected by predators (Mougeot &
288 Bretagnolle 2000b). The handicap principle states that good-quality males take larger risks than other

289 males to produce sexual signal (Zahavi 1975, 1977). Based on this theory, we could hypothesize for the
290 blue petrels too that females are preferentially attracted by males that produce frequent calls, and thereby
291 are more exposed to predation.

292 Our results also indicate that females are preferentially attracted by high-pitched calls when they
293 fly over the colony. Although low frequencies are less attenuated by distance and environmental
294 constrained (Marten et al. 1977), they are attenuated by the ground effect (Marten & Marler 1977;
295 Morton 1975), and some species are sensitive to high frequencies. A possibility is thus that calls higher
296 in frequency might make the emitter easier to locate (Dooling 1982; Klump 2000; Park & Dooling
297 1991), but so far little is known about how call frequency affects the ability of petrels to localize calls.
298 Another possibility is that high-pitched calls indicate males of good-quality, as shown in many taxa,
299 including tortoises (Galeotti et al. 2004), passerines (Cardoso et al. 2012), and mammals (Reby et al.
300 2010). In blue petrels, fundamental frequency may be related to bill morphology and body size: big
301 males with a long, thin bill produce high-pitched calls (Gémard et al. 2019). In these filter-feeding
302 seabirds, bill morphology may influence feeding efficiency (Klages & Cooper 1992), and consequently
303 the reproductive success.

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

314 Broadcast signals, regardless of the tested acoustic parameter, had no influence on the time
315 attracted females spend on the ground, at the proximity of the burrow. In burrowing petrels, females
316 vocalize towards the sound source (male in the burrow) when they are on the ground, and then walk

317 following female-directed calls produced by males until they find the burrow entrance (Storey 1984). In
318 blue petrels, males produce female-directed calls characterized by frequency and temporal modulations
319 that may indicate their sexual motivation (Gémard et al. *in prep*). Olfactory signals may also be involved
320 in sexual signalling because previous studies have shown burrows have a chemical signature
321 (Bonadonna et al. 2001; Bonadonna et al. 2004), and individuals have a body odour containing genetic
322 information (Bonadonna & Nevitt 2004; Bonadonna & Sanz-Aguilar 2012; Leclaire et al. 2017). Thus,
323 we hypothesize that a necessary exchange of vocal and/or olfactory signals might take place before the
324 female enters the burrow. In our experiments, we used a repetitive playback in an artificial burrow, so
325 that we could not interactively reply in an appropriate way to a female close to the burrow, and no odours
326 were emitted. In absence of these vocal and olfactory stimuli, and considering the predation risks
327 (Mougeot & Bretagnolle 2000b), females may fly rapidly away independently of the nature of the
328 modified call emitted.

329 Results show that we recorded more females flying and, on the ground, when we tested the first
330 burrow twosome (A) than when we tested the second twosome (B), likely because the number of
331 bachelor males and females decreases over the breeding season, even though they are still active.
332 Nonetheless, variations and significance of the attractiveness of the tested acoustic parameters were
333 consistent between the two burrow twosomes.

334 Blue petrels are the main prey of the brown skua *Stercorarius antarcticus*, representing more
335 than 70% of its diet (Mougeot & Bretagnolle 2000b; Mougeot et al. 1998). We observed that skuas were
336 more attracted by short calls than long calls. However, this result should be interpreted with caution due
337 to the small total number of observations. Although we know that brown skuas use prey calls to locate
338 them (Mougeot & Bretagnolle 2000b), there is no evidence so far that skuas select preys based on their
339 call parameters.

340 To sum up, we showed for the first time in a burrowing petrel that males' calls are sexual signals,
341 and that calls with certain acoustic characteristics are attractive to females. More precisely, females
342 flying over the colony are more attracted by males producing high-pitched calls and calling at a high
343 rate. Flying females might also be attracted preferentially by calls consisting in few-syllable phrases
344 rather than many-syllable phrases. These acoustic parameters are related to male bill morphology and

345 may thus be linked to male qualities, such as feeding efficiency. Another explanation is that males
346 producing high-pitched calls at a high call rate may be easier to locate. Females are also attracted by
347 short calls with few syllables, which make the caller less conspicuous. It might indicate a trade-off
348 between predation avoidance and conspicuous sexual advertisement to attract potential mates in the
349 hubbub of the colony. The time spent by females exploring on the ground might be influenced by
350 additional signals, such as a vocal response from the male, olfactory signals, or both.

351 **References**

- 352 Amorim MCP (2006) Diversity of Sound Production in Fish. *Diversity* 1:71–105
- 353 Aubin T, Jouventin P (1998) Cocktail-party effect in king penguin colonies. *Proc R Soc B Biol Sci* 265:1665–
354 1673. <https://doi.org/10.1098/rspb.1998.0486>
- 355 Ballentine B (2009) The ability to perform physically challenging songs predicts age and size in male swamp
356 sparrows, *Melospiza georgiana*. *Anim Behav* 77:973–978. <https://doi.org/10.1016/j.anbehav.2008.12.027>
- 357 Ballentine B, Hyman J, Nowicki S (2004) Vocal performance influences female response to male bird song: an
358 experimental test. *Behav Ecol* 15:163–168. <https://doi.org/10.1093/beheco/arg090>
- 359 Bates D, Maechler M, Bolker B, Walker S (2015) lme4: Linear mixed-effects models using Eigen and S4. 1–23
- 360 Bonadonna F, Nevitt GA (2004) Partner-specific odor recognition in an Antarctic seabird. *Science* (80-)
361 306:835. <https://doi.org/10.1126/science.1103001>
- 362 Bonadonna F, Sanz-Aguilar A (2012) Kin recognition and inbreeding avoidance in wild birds: The first evidence
363 for individual kin-related odour recognition. *Anim Behav* 84:509–513.
364 <https://doi.org/10.1016/j.anbehav.2012.06.014>
- 365 Bonadonna F, Spaggiari J, Weimerskirch H (2001) Could osmotaxis explain the ability of blue petrels to return
366 to their burrows at night? *J Exp Biol* 204:1485–1489
- 367 Bonadonna F, Villafane M, Bajzak C, Jouventin P (2004) Recognition of burrow's olfactory signature in blue
368 petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark. *Anim Behav* 67:893–898.
369 <https://doi.org/10.1016/j.anbehav.2003.08.013>
- 370 Bretagnolle V (1990) Behavioural affinities of the blue petrel *Halobaena caerulea*. *Ibis* (Lond 1859) 132:102–
371 105. <https://doi.org/10.1111/j.1474-919X.1990.tb01020.x>
- 372 Bretagnolle V (1996) Acoustic communication in a group of nonpasserine birds, the petrels. In: Kroodsma DE,
373 Miller EH (eds) *Ecology and Evolution of Acoustic Communication in Birds*, Cornell Un. New York, pp

374 160–177

375 Bried J, Jouventin P (2001) Site and mate choice in seabirds: An evolutionary approach. In: *Biology of Marine*

376 *Birds*. pp 263–305

377 Brothers NP (1984) Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. *Wildl Res*

378 11:113–131. <https://doi.org/10.1071/WR9840113>

379 Brumm H, Zollinger SA (2013) Avian vocal production in noise. pp 187–227

380 Byers BE, Akresh ME, King DI (2016) Song and male quality in prairie warblers. *Ethology* 122:660–670.

381 <https://doi.org/10.1111/eth.12513>

382 Cardoso GC (2012) Paradoxical calls: the opposite signaling role of sound frequency across bird species. *Behav*

383 *Ecol* 23:237–241. <https://doi.org/10.1093/beheco/arr200>

384 Catchpole CK, Slater PJB (2008) *Bird song: biological themes and variations*

385 Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study

386 of three petrel species. *Ecology* 76:2240–2246. <https://doi.org/10.2307/1941698>

387 Cherry C (1957) On human communication; a review, a survey, and a criticism

388 Christensen R, Kleindorfer S, Robertson J (2006) Song is a reliable signal of bill morphology in Darwin’s small

389 tree finch *Camarhynchus parvulus*, and vocal performance predicts male pairing success. *J Avian Biol*

390 37:617–624. <https://doi.org/10.1111/j.0908-8857.2006.03684.x>

391 Courtiol A, Etienne L, Feron R, et al (2016) The evolution of mutual mate choice under direct benefits. *Am Nat*

392 188:521–538. <https://doi.org/10.1086/688658>

393 Dooling RJ (1982) Auditory perception in birds. In: Kroodsma D, Miller E (eds) *Acoustic Communication in*

394 *Birds*, Vol. 1. New York: Academic Press, pp 95–130

395 Favaro L, Gamba M, Gili C, Pessani D (2017) Acoustic correlates of body size and individual identity in banded

396 penguins. *PLoS One* 12:e0170001. <https://doi.org/10.1371/journal.pone.0170001>

397 Galeotti P, Sacchi R, Rosa DP, Fasola M (2005) Female preference for fast-rate, high-pitched calls in Hermann’s

398 tortoises *Testudo hermanni*. *Behav Ecol* 16:301–308. <https://doi.org/10.1093/beheco/arl165>

399 Gémard C, Aubin T, Bonadonna F (2019) Males’ calls carry information about individual identity and

400 morphological characteristics of the caller in burrowing petrels. *J Avian Biol* jav.02270.

401 <https://doi.org/10.1111/jav.02270>

402 Genevois F, Bretagnolle V (1994) Male blue petrels reveal their body mass when calling. *Ethol Ecol Evol*

403 6:377–383. <https://doi.org/10.1080/08927014.1994.9522988>

404 Gibson RM (1989) Field playback of male display attracts females in lek breeding sage grouse. *Behav Ecol*
405 *Sociobiol* 24:439–443. <https://doi.org/10.1007/BF00293273>

406 Halliday T (1983) The study of mate choice. In: P. Bateson (ed) *Mate choice*. Cambridge University Press,
407 Cambridge, pp 3–32

408 Jouventin P, Aubin T, Lengagne T (1999) Finding a parent in a king penguin colony: the acoustic system of
409 individual recognition. *Anim Behav* 57:1175–1183. <https://doi.org/10.1163/156853999501595>

410 Jouventin P, Mougin J-L (1981) Les stratégies adaptatives des oiseaux de mer. *Rev Ecol (Terre vie)* 35:217–249

411 Klages NTW, Cooper J (1992) Bill morphology and diet of a filter- feeding seabird: the broad- billed prion
412 *Pachyptila vittata* at South Atlantic Gough Island. *J Zool* 227:385–396. <https://doi.org/10.1111/j.1469->
413 [7998.1992.tb04401.x](https://doi.org/10.1111/j.1469-7998.1992.tb04401.x)

414 Klump GM (2000) Sound localization in birds. In: Dooling RJ, Fay RR, Popper AN (eds) *Comparative Hearing:*
415 *Birds and Reptiles*. Springer New York, pp 249–307

416 Knörnschild M, Blüml S, Steidl P, et al (2017) Bat songs as acoustic beacons - Male territorial songs attract
417 dispersing females. *Sci Rep* 7:1–11. <https://doi.org/10.1038/s41598-017-14434-5>

418 Kriesell HJ, Aubin T, Planas-Bielsa V, et al (2018) Sex identification in king penguins *Aptenodytes patagonicus*
419 through morphological and acoustic cues. *Ibis (Lond 1859)* 160:755–768.
420 <https://doi.org/10.1111/ibi.12577>

421 Leclaire S, Strandh M, Mardon J, et al (2017) Odour-based discrimination of similarity at the major
422 histocompatibility complex in birds. *Proc R Soc B Biol Sci* 284:2016–20466.
423 <https://doi.org/10.1098/rspb.2016.2466>

424 Lengagne T, Aubin T, Lauga J, Jouventin P (1999) How do king penguins (*Aptenodytes patagonicus*) apply the
425 mathematical theory of information to communicate in windy conditions? *Proc R Soc B Biol Sci*
426 266:1623–1628. <https://doi.org/10.1098/rspb.1999.0824>

427 Marten K, Quine D, Marler P (1977) Sound transmission and its significance for animal vocalization. *Behav*
428 *Ecol Sociobiol* 2:291–302. <https://doi.org/10.1007/BF00299741>

429 Martín-Vivaldi M, Palomino JJ, Soler M (2000) Attraction of hoopoe *Upupa epops* females and males by means
430 of song playback in the field: influence of strophe length. *J Avian Biol* 31:351–359.
431 <https://doi.org/10.1034/j.1600-048X.2000.310311.x>

432 Martín-Vivaldi M, Palomino JJ, Soler M (1999) Function of song in the hoopoe *Upupa epops*. *Bird Study*
433 46:104–111. <https://doi.org/10.1080/00063659909461120>

434 Martín-Vivaldi M, Palomino JJ, Soler M (1998) Song structure in the hoopoe (*Upupa epops*) - Strophe length
435 reflects male condition. *J fur Ornithol* 139:287–296. <https://doi.org/10.1007/BF01653339>

436 McComb KE (1991) Female choice for high roaring rates in red deer, *Cervus elaphus*. *Anim Behav* 41:79–88.
437 [https://doi.org/10.1016/S0003-3472\(05\)80504-4](https://doi.org/10.1016/S0003-3472(05)80504-4)

438 Moncorps S, Chapuis JL, Haubreux D, Bretagnolle V (1998) Diet of the brown skua *Catharacta skua lönnbergi*
439 on the Kerguelen archipelago: comparisons between techniques and between islands. *Polar Biol* 19:9–16.
440 <https://doi.org/10.1007/s003000050210>

441 Morton ES (1975) Ecological Sources of Selection on Avian Sounds. *Am Nat* 109:17–34.
442 <https://doi.org/10.1086/282971>

443 Mougeot F, Bretagnolle V (2000a) Predation risk and moonlight avoidance in nocturnal seabirds. *J Avian Biol*
444 31:376–386. <https://doi.org/10.1034/j.1600-048X.2000.310314.x>

445 Mougeot F, Bretagnolle V (2000b) Predation as a cost of sexual communication in nocturnal seabirds: an
446 experimental approach using acoustic signals. *Anim Behav* 60:647–656.
447 <https://doi.org/10.1006/anbe.2000.1491>

448 Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown skua (*Catharacta*
449 *skua lönnbergi*) at Mayes Island, Kerguelen. *J Zool* 244:429–438.
450 <https://doi.org/10.1017/S0952836998003136>

451 Mountjoy DJ, Lemon RE (1991) Song as an attractant for male and female European starlings, and the influence
452 of song complexity on their response. *Behav Ecol Sociobiol* 28:97–100.
453 <https://doi.org/10.1007/BF00180986>

454 Park TJ, Dooling RJ (1991) Sound localization in small birds: absolute localization in azimuth. *J Comp Psychol*
455 105:125–133. <https://doi.org/10.1037/0735-7036.105.2.125>

456 Quillfeldt P, Masello JF, Segelbacher G (2012) Extra-pair paternity in seabirds: a review and case study of thin-
457 billed prions *Pachyptila belcheri*. *J Ornithol* 153:367–373. <https://doi.org/10.1007/s10336-011-0751-9>

458 Reby D, Charlton BD, Locatelli Y, McComb K (2010) Oestrous red deer hinds prefer male roars with higher
459 fundamental frequencies. *Proc R Soc B Biol Sci* 277:2747–2753. <https://doi.org/10.1098/rspb.2010.0467>

460 Riebel K (2009) Song and female mate choice in zebra finches: A review. In: *Advances in the Study of*
461 *Behavior*, 1st edn. Elsevier Inc., pp 197–238

462 Ryan MJ (1980) Female mate choice in a neotropical frog. *Science* (80-) 209:523–525.
463 <https://doi.org/10.1126/science.209.4455.523>

464 Salton M, Saraux C, Dann P, Chiaradia A (2015) Carry-over body mass effect from winter to breeding in a
465 resident seabird, the little penguin. *R Soc Open Sci* 2:140390–140390. <https://doi.org/10.1098/rsos.140390>

466 Schreiber EA, Burger J (eds) (2001) *Biology of Marine Birds*. CRC Press, Boca Raton, London, New York,
467 Washington DC

468 Searcy WA, Andersson M (1986) Sexual selection and the evolution of song. *Annu Rev Ecol Syst* 17:507–533.
469 <https://doi.org/10.1146/annurev.es.17.110186.002451>

470 Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. *Anim Behav* 78:1281–1292.
471 <https://doi.org/10.1016/j.anbehav.2009.08.011>

472 Smith JM (1991) Theories of sexual selection. *Trends Ecol Evol* 6:146–151. [https://doi.org/10.1016/0169-5347\(91\)90055-3](https://doi.org/10.1016/0169-5347(91)90055-3)

474 Specht R (2002) Avisoft-saslab pro: sound analysis and synthesis laboratory. Berlin

475 Storey AE (1984) Function of Manx shearwater calls in mate attraction. *Behaviour* 89:73–89

476 Walling, Cheves; Rabinowitz R (1957) *Studies on the acoustical behavior and taxonomy of the tree crickets*
477 (Orthoptera: Oecanthinae) of the eastern United States. The Ohio States University

478 Warham J (1990) *The petrels: their ecology and breeding systems*. London

479 Warham J (1996) Behaviour and vocalizations of Procellariidae, Hydrobatidae and Pelecooididae. In: *The*
480 *Behaviour, Population Biology and Physiology of the Petrels*. Elsevier

481 Weimerskirch H, Chastel O, Ackermann L (1995) Adjustment of parental effort to manipulated foraging ability
482 in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav Ecol Sociobiol* 36:11–16.
483 <https://doi.org/10.1007/BF00175723>

484 Zahavi A (1977) The cost of honesty. Further remarks on the handicap principle. *J Theor Biol* 67:603–605.
485 [https://doi.org/10.1016/0022-5193\(77\)90061-3](https://doi.org/10.1016/0022-5193(77)90061-3)

486 Zahavi A (1975) Mate selection — A selection for a handicap. *J Theor Biol* 53:205–214.
487 [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)

488 Zuk M, Kolluru GR (1998) Exploitation of Sexual Signals by Predators and Parasitoids. *Q Rev Biol* 73:415–438.
489 <https://doi.org/10.1086/420412>

490

491 **FIGURE CAPTIONS**

492 **Fig. 1** Spectrogram (top) and oscillogram (bottom) of a two-phrase call of a male blue petrel *Halobaena caerulea*.

493 Letters from A to D represent the four syllable types constituting a phrase.

494 **Fig. 2** Experimental installation on the field. Grey triangles represent the field of view of each phototrap.

495 **Fig. 3** Number of blue petrel females flying at a maximum distance of five meters from the burrow where

496 modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow

497 twosome where we broadcast a stimuli dyad

498 **Fig. 4** Number of blue petrel females showing exploratory behaviours on the ground at proximity of the burrow

499 where modified calls of male blue petrel were broadcast (in percentage). Lines link the two burrows of a burrow

500 twosome where we broadcast a stimuli dyad

501 **Fig. 5** Time spent by blue petrel females showing exploratory behaviours on the ground, at proximity of the

502 burrow where modified calls of male blue petrel were broadcast

Fig. 1

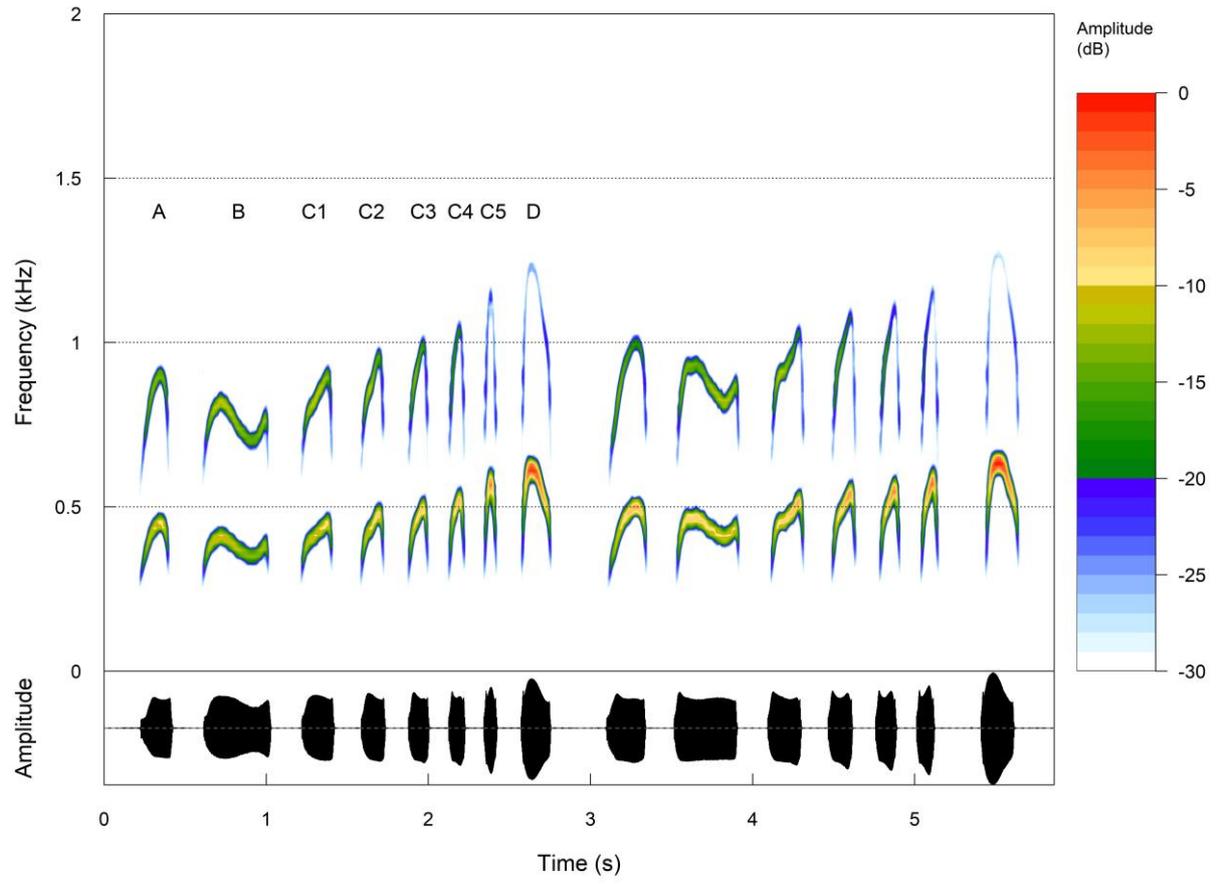


Fig. 2

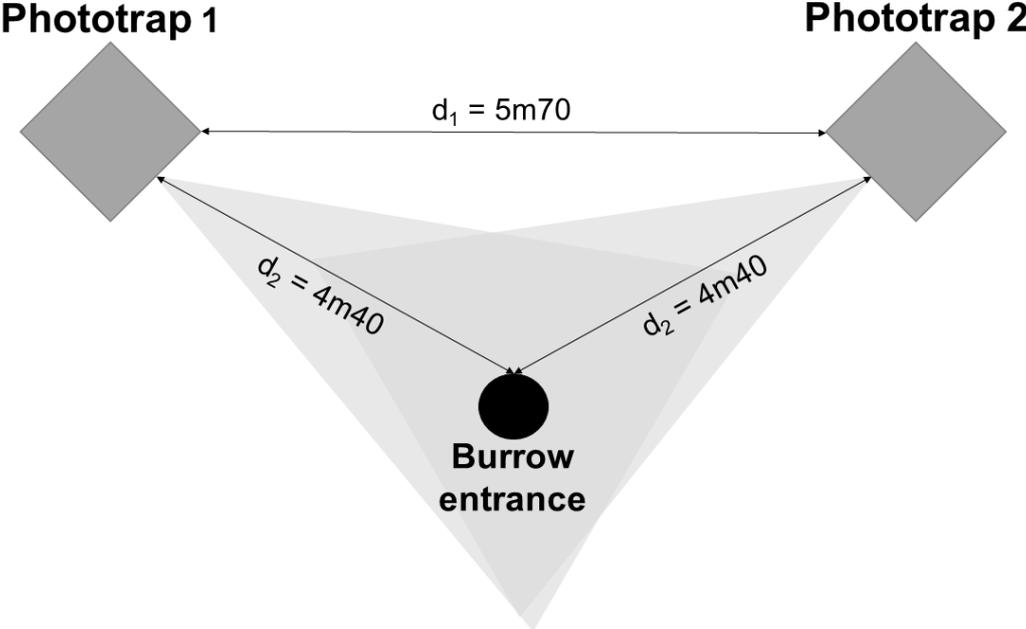


Fig. 3

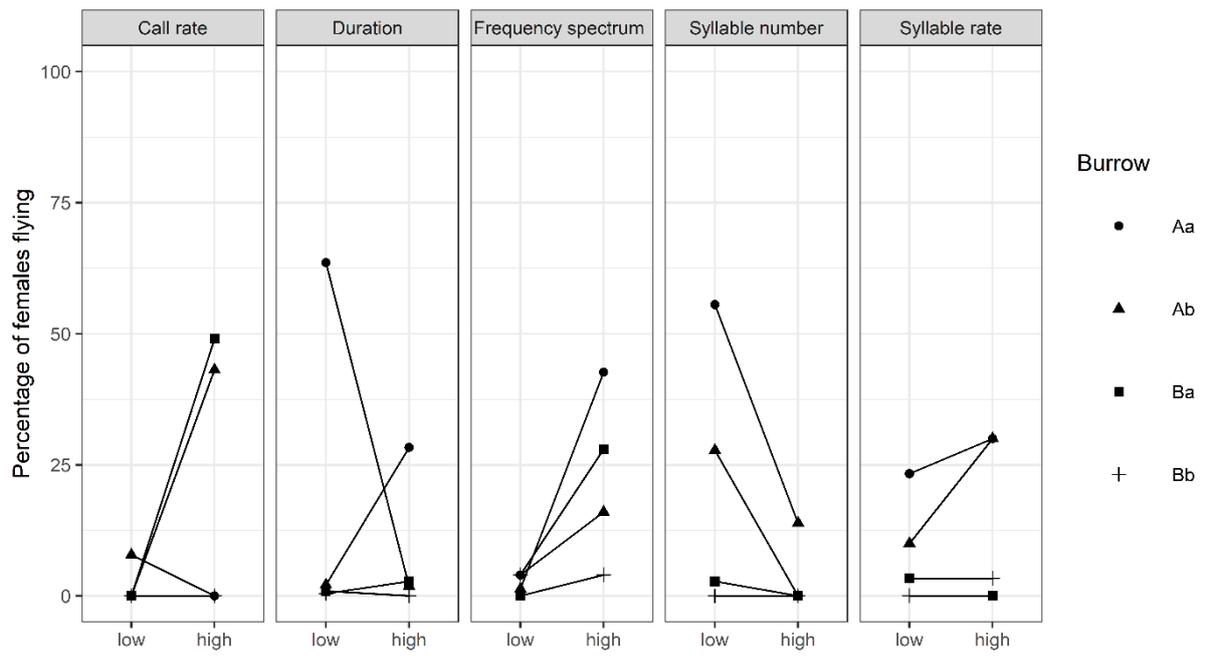


Fig. 4

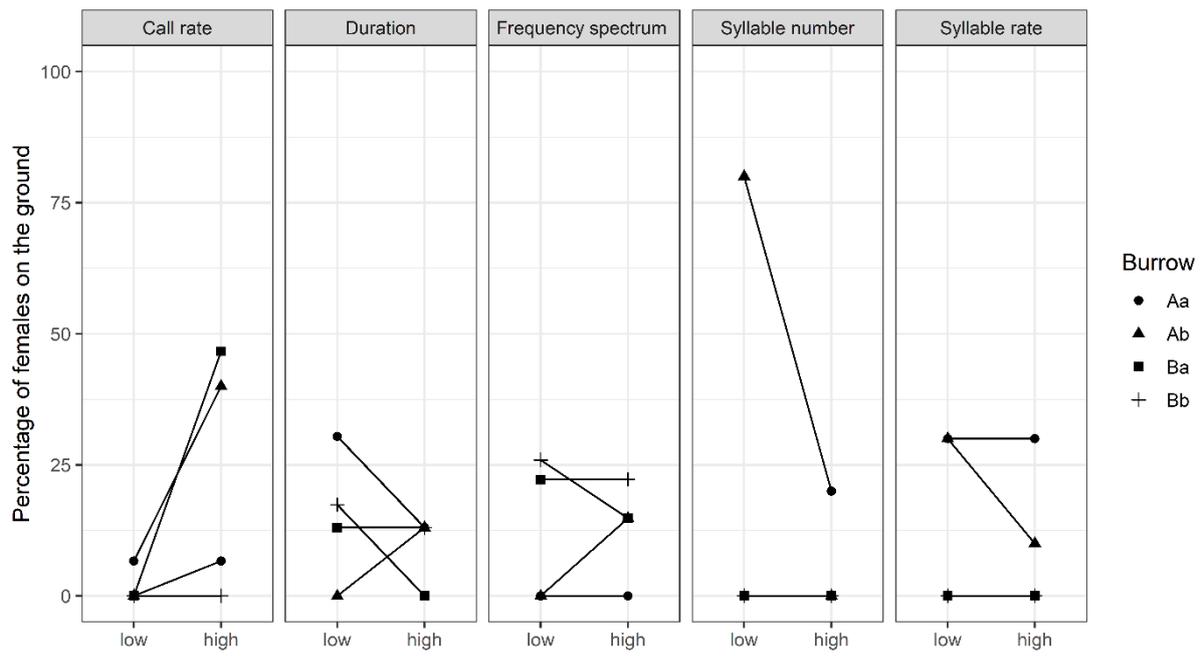


Fig. 5

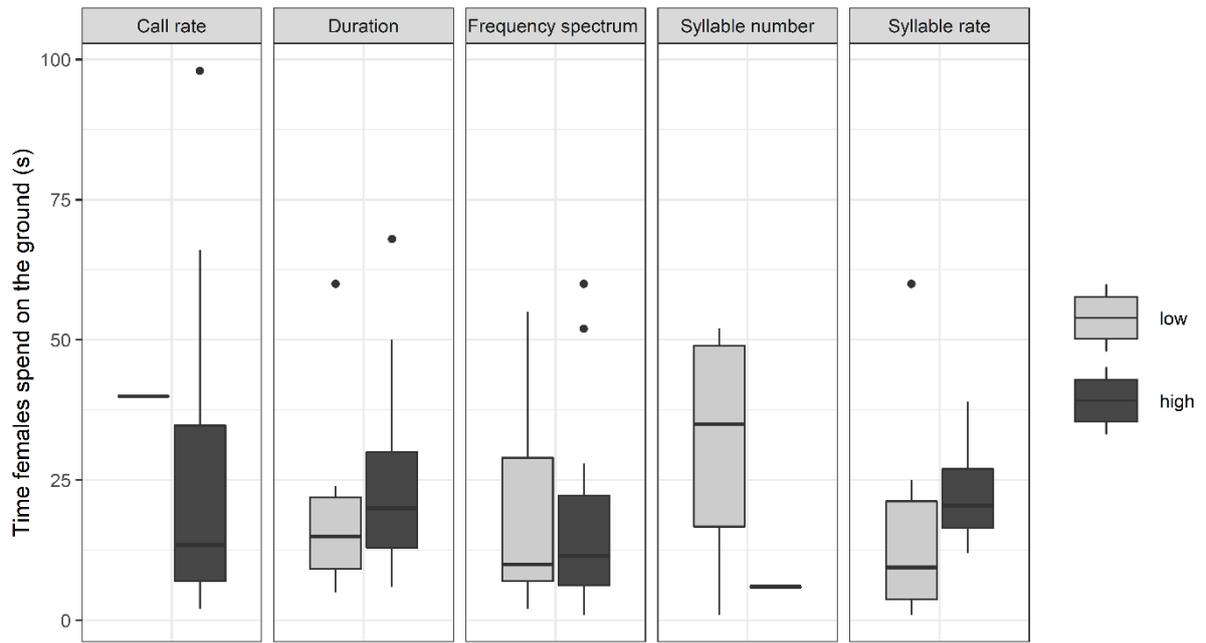


Table 1 Dyads of experiment signals broadcast to test the attractiveness of different acoustic traits

Acoustic trait	Low	High
Call rate	1 call/3 min	1 call/30 sec
Call duration	2 phrases	8 phrases
Call energy spectrum	-50 Hz	+50 Hz
Number of syllables per phrase	2 syllables C	6 syllables C
Syllable rate	-50% inter-syllable silence	+50% inter-syllable silence

Table 2 NB GLM contrasts between high-trait-call and the low-trait-call for each acoustic trait. Significant contrasts ($*p < 0.05$) are in bold

Acoustic traits	Estimate	SE	z value	p value	
Call rate	2.12	0.90	2.35	0.02	*
Duration	-0.25	0.84	-0.30	0.77	
Energy spectrum	1.94	0.89	2.18	0.03	*
Number of syllables	-1.94	1.03	-1.88	0.06	.
Syllable rate	0.24	0.98	0.24	0.81	

Table 3 GLM contrasts between high-trait-call and the low-trait-call for each acoustic trait. Significant contrasts ($*p < 0.05$) are in bold

Acoustic traits	Estimate	SE	z value	p value	
Call rate	1.22	0.51	2.41	0.02	*
Duration	-0.46	0.31	-1.49	0.14	
Energy spectrum	0.18	0.35	0.52	0.60	
Number of syllables	-1.79	1.08	-1.66	0.10	
Syllable rate	-0.34	0.41	-0.81	0.42	

Table 4 Linear Model contrasts between the high-trait-call and the low-trait-call for each acoustic trait. Significant contrasts ($*p < 0.05$) are in bold

Acoustic traits	Estimate	SE	t value	p value
Call rate	-1.04	0.66	-1.71	0.09
Duration	0.15	0.46	0.32	0.75
Energy spectrum	-0.18	0.39	-0.46	0.65
Number of syllables	-0.94	1.18	-0.79	0.43
Syllable rate	0.53	0.60	0.88	0.38