



HAL
open science

Individual signature in the most common and context-independent call of the Rook (*Corvus frugilegus*)

Benjamin Benti, Charlotte Curé, Valerie Dufour

► To cite this version:

Benjamin Benti, Charlotte Curé, Valerie Dufour. Individual signature in the most common and context-independent call of the Rook (*Corvus frugilegus*). *Wilson journal of ornithology*, 2019, 131 (2), pp.373-381. <10.1676/18-41>. <hal-02395415>

HAL Id: hal-02395415

<https://hal.science/hal-02395415v1>

Submitted on 11 Dec 2020

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.



HAL Authorization

The Wilson Journal of Ornithology

Individual signature in the most common and context-independent call of the Rook (*Corvus frugilegus*) --Manuscript Draft--

Manuscript Number:	wilsonjo-D-18-00041R1
Full Title:	Individual signature in the most common and context-independent call of the Rook (<i>Corvus frugilegus</i>)
Short Title:	Individual vocal signature in the Rook
Article Type:	Short Communication
Keywords:	corvids, DFA, individuality coding, PIC, Rook, vocal signature
Corresponding Author:	Benjamin Benti Universite de Strasbourg Strasbourg, FRANCE
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universite de Strasbourg
Corresponding Author's Secondary Institution:	
First Author:	Benjamin Benti
First Author Secondary Information:	
Order of Authors:	Benjamin Benti Charlotte Curé Valérie Dufour
Order of Authors Secondary Information:	
Abstract:	<p>The ability to recognize other individuals (e.g. mates, neighbors, and offspring) is crucial to process relationships between group members in social species. For bird species with limited use of visual information, like species living in colonies or dense environments, the acoustic channel provides a long distance and fast mean to effectively convey identity-related information. The Rook (<i>Corvus frugilegus</i>) is a monogamous species, and one of the most social corvids, living in highly cohesive groups within colonies of hundreds to thousands of individuals. However, despite being a highly vocal species, only few studies focused on its acoustic communication skills, investigating mostly its vocal repertoire and kin recognition in fledglings. Among the vocal repertoire of the Rook, the "caw" is the most common sound type. It is emitted independently in various contexts and is often considered as a "presenting" vocalization, serving as to introduce the identity of the emitter bird to the assembly. In this study, we investigated the potential individual signature of the caw. To do so, we recorded the caws of 5 semi-captive males Rooks and conducted acoustic analyses on both the frequency and time domains. A discriminant function and a potential for individuality coding analyses revealed the existence of a clear individual signature (mean \pm SD: 75 \pm 10% of correct classification), which was mainly supported by the caw duration and distribution of energy in the low frequency part of the spectrum. We discuss the potential variability of individuality coding across behavioral contexts and social affinities that needs further work.</p>

RRH: Short Communications

LRH: Benti et al.

Individual signature in the most common and context-independent call of the Rook (*Corvus frugilegus*)

Benjamin Benti^{1,2,3,4,6}, Charlotte Curé^{3,5}, and Valérie Dufour^{4,5}

¹ Department of Biology, École Normale Supérieure de Lyon, 46, allée d'Italie 69364 Lyon Cedex 07 (France)

² Current address: University of Strasbourg, 4, rue Blaise Pascal CS90032 F-67081 Strasbourg Cedex (France)

³ Current address: Cerema-Ifsttar, UMRAE, Laboratory of Strasbourg, Acoustics group, 11, rue Jean Mentelin 67035 Strasbourg Cedex 2 (France)

⁴ Current address: CNRS, Délégation Alsace, MOY1000, Cognitive and social ethology team, 23, rue du Loess 67200 Strasbourg (France)

⁵ These authors contributed equally to this work

⁶ Corresponding author: benjamin.benti@etu.unistra.fr

1

Abstract

2 The ability to recognize other individuals (*e.g.* mates, neighbors, and offspring) is crucial to
3 process relationships between group members in social species. For bird species with limited
4 use of visual information, like species living in colonies or dense environments, the acoustic
5 channel provides a long distance and fast mean to effectively convey identity-related
6 information. The Rook (*Corvus frugilegus*) is a monogamous species, and one of the most
7 social corvids, living in highly cohesive groups within colonies of hundreds to thousands of
8 individuals. However, despite being a highly vocal species, only few studies focused on its

9 acoustic communication skills, investigating mostly its vocal repertoire and kin recognition in
10 fledglings. Among the vocal repertoire of the Rook, the “caw” is the most common sound
11 type. It is emitted independently in various contexts and is often considered as a “presenting”
12 vocalization, serving as to introduce the identity of the emitter bird to the assembly. In this
13 study, we investigated the potential individual signature of the caw. To do so, we recorded
14 the caws of 5 semi-captive males Rooks and conducted acoustic analyses on both the
15 frequency and time domains. A discriminant function and a potential for individuality coding
16 analyses revealed the existence of a clear individual signature (mean \pm SD: 75 \pm 10% of
17 correct classification), which was mainly supported by the caw duration and distribution of
18 energy in the low frequency part of the spectrum. We discuss the potential variability of
19 individuality coding across behavioral contexts and social affinities that needs further work.

20 Key words: corvids, DFA, individuality coding, PIC, Rook, vocal signature.

21 Intra-specific communication is involved in most vital functions of animals’ life and can be
22 supported by one or usually more sensory channels (Witzany 2014). In birds, the visual and
23 the acoustic channels are the two main sensory modalities used to communicate (Marler and
24 Slabbekoorn 2004). When visual information is scarce or unavailable, acoustic signals can
25 support the most reliable cues to effectively convey information (Curé et al. 2009). This can
26 be the case in monomorphic species for which individuals share similar body size and feather
27 coloration, or in particular ecological conditions such as in dark or crowded environments
28 (*e.g.* forest habitats, bird colonies) as well as in constraining social environments (*e.g.* highly
29 mobile species where animals need to communicate at distance). Bird vocalizations are
30 associated to a range of social interactions. For example, bird songs can be used in a breeding
31 context to attract a sexual partner and repel potential competitors (Kroodsma and Byers
32 1991), and in Chicks, begging calls are produced to solicit parents for feeding (Klenova
33 2015). Moreover, bird sounds can be functionally referential, *i.e.* provide information about a

34 particular element of the environment, such as the alarm call that can signal the presence and
35 identity of a predator (Suzuki 2015). Last but not least, one of the most important messages
36 conveyed by bird acoustic signals is information about the sender identity (*e.g.* its species,
37 gender, age, hierarchical status, and individual identity), facilitating recognition at different
38 levels (Curé et al. 2009). Because individual recognition can be involved in many aspects of
39 social life, it has been extensively studied in highly social species.

40 This is particularly true in birds, where individual vocal signature has been shown to
41 support recognition at various levels such as in mate-mate, parent-offspring recognition (Curé
42 et al. 2009), or in neighbor-stranger discrimination (Briefer et al. 2009). The ability to
43 recognize individuals can be crucial for intra-group cohesion in species living in densely
44 populated societies, like in seabird colonies for which the risk of confusion between
45 individuals is high. In complex social societies (*e.g.* in corvid species), animals also need to
46 discriminate among individuals in order to continuously maintain group cohesion and
47 especially during reunion with their group members in fission-fusion societies. In this regard,
48 corvids (*e.g.* crows, ravens, magpies, and jays) provides a good framework to address the
49 potential of individual signaling in their vocalizations. Corvid species are monogamous and
50 some species live in social groups (Clayton and Emery 2007) with a level of complexity in
51 their societies that has often been compared to those of highly social mammals (Emery and
52 Clayton 2004). Corvids are highly vocal species, thus likely to rely on acoustics as their
53 primary sensory modality to communicate and convey information regarding individual
54 identity. The ability to vocally identify an individual was demonstrated in juvenile Rooks
55 (*Corvus frugilegus*) which can discriminate between siblings' and non-siblings' calls
56 (Røskaft and Epsmark 1984), in Jungle Crows (*Corvus macrorhynchos*) which can
57 differentiate among the calls of familiar conspecifics (Kondo et al. 2010), and in Common
58 Ravens (*Corvus corax*) which can discriminate among food calls from familiar and

59 unfamiliar conspecifics (Szipl et al. 2015). Moreover, acoustic analyses of corvid calls
60 revealed a multi parametric individual signature supported by both temporal and frequency
61 domain variables, which birds could potentially use to recognize their congeners (Kondo et
62 al. 2010, Mates et al. 2015).

63 Compared to the other species of the genus *Corvus*, the Rook has been poorly studied
64 in respect to its vocal repertoire and the potential for individuality coding in its vocalizations.
65 Yet, the Rook is one of the most social corvid species (Clayton and Emery 2007), living all
66 year long in highly cohesive groups that can temporarily merge with others (Boucherie et al.
67 2016). Mated pairs do not establish into territories and remain in a social group, which
68 requires particularly reliable vocal signatures ensuring recognition between mates and among
69 group members. To our knowledge, the only work conducted on the Rook vocal repertoire is
70 the one from Røskaft and Espmark (1982), who described 13 distinct calls and 7 apparent
71 context-dependent usages of the same call, the “caw”. Among those contexts, males caw
72 during the breeding season, once they return and get perched near their nest. Since females
73 mostly remain in the nests during incubation and males continuously move away and towards
74 the nest to bring food to their partner, this caw could be crucial for the male to announce its
75 presence to the mate or other group members throughout the breeding season (Røskaft and
76 Espmark 1982).

77 Some studies investigated vocal individual signatures in context-specific calls of
78 corvids, such as calls produced in a feeding context to attract conspecifics to a food source or
79 to secure access to the food by repelling other birds (Boeckle et al. 2012), but there was no
80 such acoustic analysis demonstrating the use of individual signatures in broadly used and
81 context-independent calls. Here, we performed an acoustic analysis to investigate the
82 potential for individuality coding in the most produced Rook call type, the caw, for which we
83 suspected a role in recognition with other group members over a broad range of contexts. To

84 do so, we recorded the caws of 5 male Rooks reared in semi-captivity and assessed potential
85 inter-individual differences among a range of acoustic parameters measured in the frequency
86 and time domains.

87 **Methods**

88 **Study animals and acoustic recordings**

89 We obtained acoustic recordings from 5 semi-captive male adult Rooks housed in an outdoor
90 aviary (17 x 9 x 3.6 m) with 7 other birds (3 males and 4 females). All 5 birds (named B, K,
91 N, O, and T) were fledglings fallen from the nest in 2005-2006 and hand-reared together in
92 the aviary since. K and O were each involved in a pair with a female. T was paired with a
93 male. B and N were single, but B was part of a triad including K and its female. It took part in
94 nest building and would sometimes attempt copulation with K's female. The 5 birds could be
95 clearly identified based on individual distinctive features (colored ring on each leg). We
96 recorded dominance status and level of affinity between individuals (see Boucherie et al.
97 2016 for more information on group history and inter-individual relationships). The aviary
98 was equipped with several wooden perches and located in a quiet green space of the campus
99 of Strasbourg University (France). Birds were fed once a day and could access water and
100 food *ad libitum*.

101 We recorded the calls and associated behavioral context during the breeding periods
102 (Feb to May) of 2014 and 2015, using a Sennheiser ME67 directional microphone (frequency
103 response: 50-20,000 Hz +/- 2.5 dB) and a Zoom H4 recorder (sampling frequency: 48 kHz).
104 We performed two 30 to 90 min recording sessions every week, randomly distributed
105 between 08:00 h and 18:00 h (local time). Before each session, the experimenter sat quietly
106 outside the aviary for about 15 min without moving before starting the recording and
107 behavioral data collection, thus ensuring that the recorded vocalizations were not triggered by

108 experimenter arrival. During each session, the observer was directly entering data about the
109 time, sender identity, and behavioral context of the sound production; using Prim8 software
110 (McDonalds and Johnson 2014) and an Android tablet.

111 **Acoustic analysis**

112 The caw of the Rook sounds “harsh” to the human ear. It has a roughly 1-2 kHz frequency
113 band with no clear harmonics, a heterogeneous repartition of the energy spectrum, and lasts
114 0.2 to 0.7 s (Røskaft and Espmark 1982). For the analysis, we selected the caws that showed
115 no overlap with other bird’s vocalizations or any noise in the environmental surroundings.
116 Rooks can produce structurally similar caws with or without clear functional contexts (duets,
117 before feeding a female, in response to another Rook’s vocalization, *etc.*). We only focused
118 on the caws emitted spontaneously outside a functional recognizable context, when the male
119 was perched on its own, thus avoiding the detection of any acoustic signature related to the
120 caws’ context of emission. Moreover, because energy features can vary depending on sound
121 propagation constraints, only the caw that were recorded at a maximum range of 8 m and
122 without obstacles between the emitter and the microphone were selected for analysis.

123 The selected caws were filtered with a high-pass band filter at 300 Hz in order to
124 remove background noise. Five acoustic features were measured in both time and frequency
125 domains. The duration of the caws was measured on the amplitude envelope (Fig. 1). For
126 most analyzed caws, there were no clear visible harmonics throughout the total call length
127 and the fundamental frequency was difficult to determine. The average minimum frequency
128 (F_{\min}) was measured from the power spectrum as the first detected spectral peak (Hanning
129 window, FFT length: 2048, threshold for spectral peak detection: -15 dB). To assess
130 parameters related to the energy distribution, the frequency of maximal amplitude (FMA),

131 and the frequency at the upper limit of the first and second quartiles of energy (abbreviated
132 F_{25} and F_{50} , respectively) were measured on the power spectrum (Fig. 1).

133 Acoustic analyses were performed using the “Seewave” package (Sueur et al. 2008)
134 in R software v.3.4.1 (R Core Team 2017).

135 **Assessment of caw individual signatures**

136 In order to assess whether sender identity can be assigned based on acoustic features, a
137 discriminant function analysis (DFA) was conducted on measured acoustic parameters. DFA
138 requires similar group sizes, the absence of correlation between variables, and a normal
139 distribution of variables within the groups. We achieved the homogeneity of group sizes by
140 selecting similar numbers of calls for each individual at random. N produced fewer high
141 quality caw calls than the other individuals and was the deciding factor in choosing the
142 number of calls per individuals. We selected 15 high quality caw calls for B, K, O, and T, and
143 12 such calls for N. We performed a principal component analysis (PCA) and removed
144 correlated variables from the dataset to ensure the absence of correlation between acoustic
145 features. We ran the DFA on the resulting uncorrelated variables instead of the PCA
146 components, in order to ease the interpretation of further results (Curé et al. 2009). We did
147 not necessarily met the normality criterion (Shapiro-Wilk test), but still performed the DFA
148 given the robustness of the procedure.

149 A DFA was considered successful at assigning sender identity to the caws when more
150 than 70% of the calls were attributed to the actual emitter. We validated the DFA through a
151 jack-knife procedure; one by one, we removed the samples from the dataset, ran a DFA, and
152 checked if the missing call was correctly sorted when it didn't account for the linear
153 discriminants (LD).

154 Whenever the DFA successfully assigned sender identity to the calls (jack-knife-
155 validated), we investigated which parameters supported the individual vocal signature. We
156 calculated the potential for individuality coding (PIC) of each acoustic feature as follows
157 (Robinson et al. 1993):

$$158 \quad PIC = CV_b / \text{mean}(CV_i)$$

159 Where CV_b is the coefficient of inter-individual variation and CV_i are the coefficients of intra-
160 individual variation, both measured as:

$$161 \quad CV = 100 \left(1 + \frac{1}{4N} \right) \frac{SD}{\text{mean}}$$

162 Where N is the sample size, mean and SD the mean and standard deviation of the feature.

163 Parameters with a PIC higher than 1, *i.e.* with a within individual variation smaller than the
164 inter-individual variation, can be interpreted as individual-specific (Robinson et al. 1993,
165 Curé et al. 2009). We performed Kruskal-Wallis tests on these parameters to check whether
166 inter-individual differences confirmed the PIC value.

167 All statistical tests were conducted on R software v.3.4.1 (R Core Team 2017).
168 Package “MASS” (Venables and Ripley 2002) was used for the DFA and package “car” (Fox
169 and Weisberg 2011) for data visualization. Significance level was set at 0.05 for all tests.

170 **Results**

171 The PCA performed on all acoustic features detected that the F_{25} and the F_{50} were strongly
172 correlated. We chose to keep the F_{25} for further analyses, as low frequencies are less sensitive
173 than high frequencies to emitter-distance variation. We ran the DFA using the following
174 variables: duration of the call, FMA, F_{25} , and F_{\min} .

175 Visual inspection of the spectrograms showed some variation in the duration of the
176 calls between individuals. Inter-individual differences in energy parameters were more
177 difficult to detect visually (see Fig. 2 for an example spectrogram of each individual's caw).
178 The DFA applied to the calls of 5 male Rooks indicated a significant difference across
179 individuals (Wilk's $\lambda = 0.07524$, $F_{16, 196} = 16.33$, $P < 0.001$). The jack-knife validation
180 procedure classified on average 75% (mean \pm SD: $75 \pm 10\%$) of the calls correctly (Tab. 1).
181 The most identifiable caller was T with 87% of caws correctly sorted, and the least
182 identifiable was O with 60% of correct classification. Individuals B, K, and N showed
183 intermediate values, with respectively 73, 80, and 75% of caws correctly assigned (Fig. 3).
184 The DFA misclassified some caws within and between both pairs of individual N-O
185 (6 misclassifications) and B-K (3 misclassifications), whereas no other bird was mistaken for
186 T.

187 Only the first linear discriminant (LD) of the DFA had an eigenvalue superior to 1
188 and accounted for 75% of the inter-individual variation. The LD1 was mostly driven by the
189 F_{25} and the duration of the caws (Tab. 2).

190 The PIC values of the variables confirmed the DFA results. Indeed, the duration of the
191 caw, the F_{25} , and the F_{50} had a PIC higher than one, whereas the FMA and the F_{\min} had a PIC
192 inferior to 1 (Tab. 3). Inter-individual differences in call duration, F_{25} , and F_{50} were also
193 detected by Kruskal-Wallis test (Tab. 3).

194 Altogether, our results show that the distribution of energy in the low frequency part
195 of the spectrum and the duration of the caw were the main features underlying the individual
196 vocal signature of the Rook.

197 **Discussion**

198 In the present study, we conducted an acoustic analysis of the caws of 5 male Rooks and
199 showed that the individuals were distinctive based mainly on the duration and the low
200 frequency spectral energy distribution.

201 Our work highlighted the existence of an individual vocal signature in the caw call of
202 the Rook. However, further work is required to investigate whether Rooks are capable of
203 using such individual vocal signatures to recognize each other. Indeed, we focused on the
204 sender's side of individuality and showed that Rooks produced individually specific caw
205 calls. To test the ability of receiver Rooks to recognize this individual signature, we should
206 conduct playback experiments (Curé et al. 2016). We would need evidence that Rooks react
207 differently to the broadcasted calls of different individuals.

208 Compared to other studies in corvids, we used a limited number of acoustic
209 parameters (5 in our study) and we excluded measures of the fundamental frequency, which
210 could not be clearly identified given the noisy structure of the Rooks' caws. Kondo *et al.*
211 (2010) and Yorzinski *et al.* (2006), for instance, used respectively 24 and 20 measured
212 acoustic features in the caws of the Jungle Crows and of the American Crows (*Corvus*
213 *brachyrhynchos*). In both studies, individual call signature involved the duration and specific
214 frequency values measured on the fundamental frequency. Here, we showed that both spectral
215 energy distribution and duration parameters carried sufficient information to sort individuals,
216 making the individual signature a multi-parametric feature of the caw. Therefore, this coding
217 strategy based on different parameters appears to be a common mean in corvids and other
218 colonial birds to secure information transfer from the emitter to the receiver in the noisy
219 environment of the colony (Aubin and Jouventin 2002, Curé et al. 2009). As underlined by
220 Tibbets and Dale (2007), there are numerous potential benefits associated with sender
221 identity signaling. On one hand, it may reduce risks of inbreeding and aggressive interactions

222 with conspecifics. On the other hand, it may facilitate kin selection and decision making for
223 trade-offs such as between food competition and cooperation.

224 In American Crows though, individual discrimination was less clear when several
225 contexts for cawing were considered (Mates et al. 2015), but could be still achieved with 65%
226 of success when focusing on alarm calls only (Yorzinski et al. 2006). The authors
227 acknowledged that the acoustic structure of the caws could show variability (in duration for
228 example) depending on the context of emission. In crows, different contexts can elicit the
229 production of similar types of calls, with potential differences in the temporal structure of call
230 emission, such as in the amplitude or in the repetition rate of the caws.

231 In our study, we deliberately focused on caws produced spontaneously with no clear
232 functional context to avoid any variability depending on a particular context of emission and
233 showed a clear individual signature. Given the diversity of contexts in which the caw can be
234 used in Rooks, further investigation is needed to assess whether a contextual signature exists
235 in the caw. Individuals might also differ based on other aspects of their vocal production: like
236 American Crows, they may differ in the temporal pattern of successive cawing (Thompson
237 1969, Richards and Thompson 1978). They may also have a characteristic repertoire of calls.
238 Indeed, although the caw was the most common vocalization produced by the Rooks we
239 studied, it was not as frequently produced by all the birds of the aviary and could even be
240 absent of the repertoire. During the breeding season, the females' most frequent call was the
241 begging call. Caw calls from females occurred but were too few, and their quality was too
242 low (e.g. overlap within group calling events) to include females in the analysis. Thus, apart
243 from the 5 males studied here, we could not gather enough caws of good quality from the
244 other individuals of the aviary to integrate them in the analysis. Further studies should
245 investigate whether similar individual signature also exists in the caw of the female Rook,
246 and whether birds that do not produce the caw have an equivalent call type.

247 Interestingly, while the caws of each bird differed sufficiently from one another to
248 allow individual identification, some individuals' caws were more alike than others (B-K and
249 O-N). None of these birds are genetically related, but B is a close affiliate to K (together with
250 K's mate they form a triad, Boucherie et al. 2016). O and N have shown high tolerance
251 toward each other for years, as they build their respective nests in contact to each other's
252 during the breeding season. Our sample size was too small to conclude further on the acoustic
253 similarities of caws among birds according to their social affinities, but this was demonstrated
254 in another study on Ravens (Enggist-Dueblin and Pfister 2002) showing acoustic similarities
255 within pair and affiliates. Moreover, acoustic resemblances or shared elements between
256 neighbors' vocal repertoire might be used as a group signature to discriminate neighbors from
257 strangers in order to engage conflict only towards non-familiar individuals (Mackin 2005,
258 Briefer et al. 2013). In our study, all birds were breeding in the same aviary (and so they were
259 all familiar to each other), which is not adapted to elucidate this question. As other corvids,
260 Rooks are territorial breeders and are surrounded by other nesting birds of the colony, making
261 the task to find their nest and partner back challenging. On the other hand, acoustic
262 distinction between neighbors might help to identify more easily one's partner from
263 neighbors and to avoid nest confusion. An optimal balance between acoustic similarities and
264 differences with neighbors should allow birds to discriminate neighbors from strangers and to
265 identify their partners from proximate neighbors. Further studies exploring the degree of
266 similarity of the vocal repertoire and acoustic features of the Rook's calls according to natal
267 influences, late adulthood relationships, and physical distance with other breeders (neighbors
268 versus strangers) are needed to explore these questions.

269 **Aknowledgments**

270 We would like to thank the students who took part in data collection and analysis: T Boelhy,
271 V Jourdain, C Laubu, C Lausecker, E Meaux, and C Schmitt. We are grateful to R Gayet for
272 his review of the manuscript.

273 **Literature Cited**

274 Aubin T, Jouventin P. 2002. Localisation of an acoustic signal in a noisy environment: the
275 display call of the King Penguin *Aptenodytes patagonicus*. *Journal of Experimental*
276 *Biology*. 205: 3793–3798.

277 Boeckle M, Spizl G, Bugnyar T. 2012. Who wants food? Individual characteristics in Raven
278 yells. *Animal Behaviour*. 84(5): 1123–1130.

279 Boucherie PH, Mariette MM, Bret C, Dufour B. 2016. Bonding beyond the pair in a
280 monogamous bird: impact on social structure in adult Rooks (*Corvus frugilegus*).
281 *Behaviour*. 153(8): 897–925.

282 Briefer E, Aubin T, Rybak F. 2009. Response to displaced neighbours in a territorial songbird
283 with a large repertoire. *Naturwissenschaften*. 96: 1067.

284 Briefer E, Rybak F, Aubin T. 2013. The role of shared phrases in skylark song: true syntax or
285 simple auditory object? *Animal Behaviour*. 86: 1131–1137.

286 Clayton NS, Emery NJ. 2007. The social life of corvids. *Current Biology*. 17(16): R652–
287 R656.

288 Curé C, Aubin T, Mathevon N. 2009. Acoustic divergence between two sympatric nocturnal
289 burrowing petrels: the Yelkouan and the Cory's shearwaters. *Biological Journal of the*
290 *Linnean Society*. 96: 115–134.

- 291 Curé C, Mathevon M, Aubin T. 2016. Mate vocal recognition in the Scopoli's shearwater
292 *Calonectris diomedea*: do females and males share the same acoustic code?
293 *Behavioural Processes* 128: 96-102
- 294 Emery NJ, Clayton NS. 2004. The mentality of crows: convergent evolution of intelligence in
295 corvids and apes. *Science*. 306(5703): 1903–1907.
- 296 Enggist-Dueblin P, Pfister U. 2002. Cultural transmission of vocalizations in Ravens, *Corvus*
297 *corax*. *Animal Behaviour*. 64(6): 831–841.
- 298 Fox J, Weisberg S. 2011. An R companion to applied regression. 2nd. Thousand Oaks (CA):
299 Sage.
- 300 Klenova AV. 2015. Chick begging calls reflect degree of hunger in three Auk species
301 (Chaladriiformes: Alcidae). *PLoS ONE*. 10(11): e0140151
- 302 Kondo N, Izawa EI, Watanabe S. 2010. Perceptual mechanism for vocal individual
303 recognition in Jungle Crows (*Corvus macrorhynchos*): contact call signature and
304 discrimination. *Behaviour*. 147(8): 1051–1072.
- 305 Kroodsma DE, Byers BE. 1991. The function(s) of bird song. *Integrative and Comparative*
306 *Biology*. 31(2): 318–328.
- 307 Mackin WA. 2005. Neighbour-stranger discrimination in Audubon's shearwater (*Puffinus l.*
308 *herminieri*) explained by a 'real enemy' effect. *Behavioral Ecology and*
309 *Sociobiology*. 59:326–332.
- 310 Marler P, Slabbekoorn H. 2004. Nature's music. The science of birdsong. San Diego (CA):
311 Academic Press/Elsevier.

312 Mates EA, Tarter RR, Ha JC, Clark AB, McGowan KJ. 2015. Acoustic profiling in a
313 complexly social species, the American Crow: caws encode information on caller sex,
314 identity and behavioural context. *Bioacoustics*. 24(1): 63–80.

315 McDonald M, Johnson S. 2014. “There’s an app for that”: a new program for the collection
316 of behavioural field data. *Animal Behaviour*. 95: 81–87.

317 R Core Team. 2017. R: a language and environment for statistical computing. Vienna
318 (Austria): R Foundation for Statistical Computing.

319 Richards DB, Thompson NS. 1978. Critical properties of the assembly call of the common
320 American Crow. *Behavior*. 64: 3–4.

321 Robinson P, Aubin T, Brémond JC. 1993. Individuality in the voice of the Emperor Penguin
322 *Aptenodytes forsteri*: adaptation to a noisy environment. *Ethology*. 94(4): 279–290.

323 Røskaft E, Espmark Y. 1982. Vocal communication by the Rook *Corvus frugilegus* during
324 the breeding season. *Scandinavian Journal of Ornithology*. 13(1): 38–46.

325 Røskaft E, Espmark Y. 1984. Sibling recognition in the Rook (*Corvus frugilegus*).
326 *Behavioural Processes*. 9:223–223.

327 Sueur J, Aubin T, Simonis C. 2008. Seewave: a free modular tool for sound analysis and
328 synthesis. *Bioacoustics*. 18: 213–226.

329 Suzuki TN. 2015. Assessment of predation risk through referential communication in
330 incubating birds. *Scientific reports*. 5:10239

331 Szípl G, Boeckle M, Wascher CAF, Spreafico M, Bugnyar T. 2015. With whom to dine?
332 Ravens’ responses to food-associated calls depend on individual characteristics of the
333 caller. *Animal Behaviour*. 99: 33–42.

334 Thompson NS. 1969. Individual identification and temporal patterning in the cawing of
335 Common Crows. *Communications in Behavioural Biology*. 4: 29–33.

336 Tibbets EA, Dale J. 2007. Individual recognition: it is good to be different. *Trends in Ecology*
337 *and Evolution*. 22(10): 529–537.

338 Venables WN, Ripley BD. 2002. *Modern Applied Statistics with S*. 4th. New York (NY):
339 Springer.

340 Witzany G. 2014. *Biocommunication of animals*. Dordrecht (Netherlands): Springer.

341 Yorzinski JL, Vehrencamp SL, McGowan KJ, Clark AB. 2006. The inflected alarm caw of
342 the American Crow: differences in acoustic structure among individuals and sexes.
343 *The Condor*. 108(3): 518–529.

344 **Figure captions**

345 Figure 1: Acoustic variables measured in a male caw of the Rook. Spectrogram (top panel) of
346 the caw along with the indication of the relative amplitude (grey scale). Amplitude envelope
347 (middle panel) showing the measure of the caw duration. Power spectrum of the caw (bottom
348 panel) showing the detected spectral peaks: the regular cross indicates the F_{\min} and the bold
349 cross indicates the FMA. F_{25} and F_{50} were measured from the power spectrum and
350 correspond to the frequency values below which the spectrum contains respectively 25 and
351 50% of the total energy.

352 Figure 2: Spectrogram and indication of the relative amplitude (grey scale) of one example
353 caw of each individual B, K, N, O, and T (Hanning window, 2048 points, 25% overlap).

354 Figure 3: Visual representation of the DFA results. This graph represents the values of the
355 analyzed caws through the LD1 and LD2 (respectively on the x- and y-axis). The caws from

356 B are represented as squares, from K as circles, from N as triangles, from O as + crosses, and
357 from T as x crosses. Each individual is summarized by an ellipse with a different hatching,
358 which surrounds 70% of its calls.

359 Table 1: Results of the jack-knife-validated classification of the caws by the DFA.

DFA Class		B	K	N	O	T	Correct classification (%)
Real Class	B	11	2	2	0	0	73
	K	1	12	1	1	0	80
	N	1	0	9	2	0	75
	O	1	1	4	9	0	60
	T	1	1	0	0	13	87
						Total	75

360

361 Table 2: Results of the DFA applied on the caws and loadings of the 3 extracted LD. The
 362 LD1 was the only extracted component of the DFA with an eigenvalue >1 with duration and
 363 F₂₅ as the most representative variables (in bold).

Variable	Linear Discriminant		
	LD1	LD2	LD3
Duration	0.437722	0.592371	-0.399456
F ₂₅	-0.716319	0.327439	-0.616106
FMA	-0.098303	0.088232	-0.652831
F _{min}	-0.043263	-0.789367	-0.412623
Eigenvalue	4.35425	0.882161	0.318782
Variance explained (cumulative %)	78	94	100

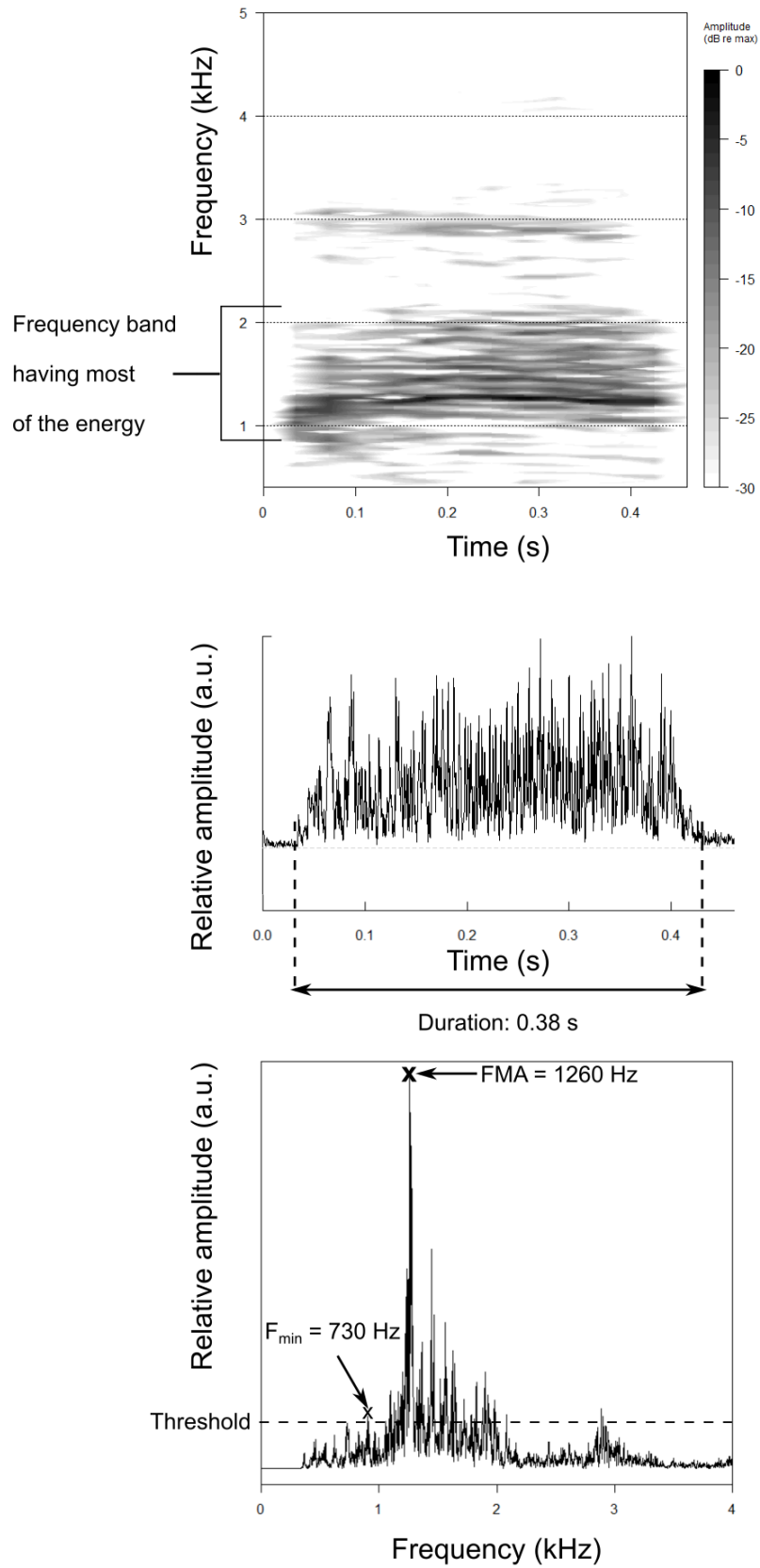
364

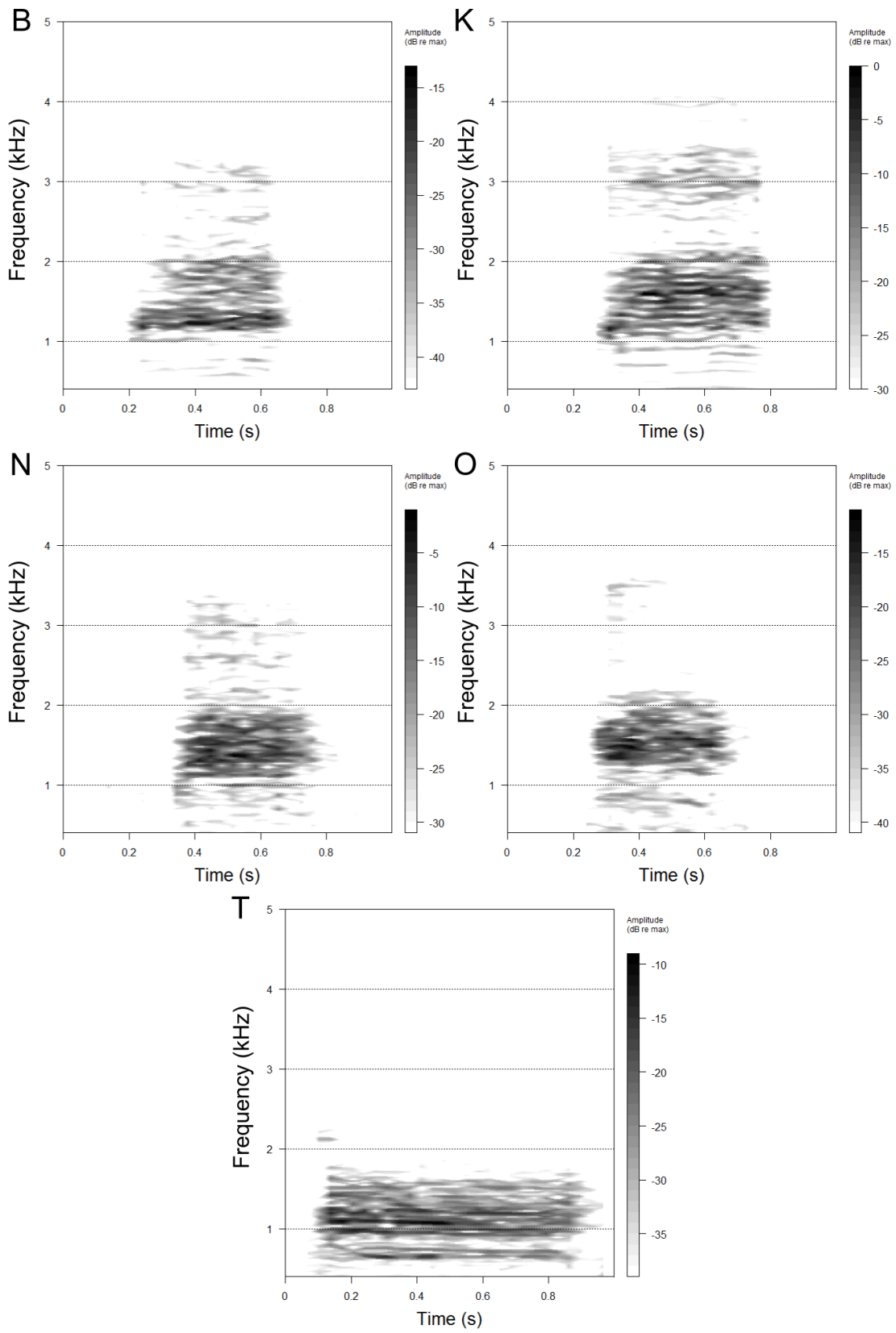
365 Table 3: PIC values and Kruskal-Wallis tests for all 5 measured acoustic parameters.
 366 *P*-values inferior to the significance threshold of 0.05 (in bold) indicate the parameters with a
 367 potential for individuality coding.

Variable	CV _i	CV _b	PIC	Kruskal-Wallis test <i>P</i> -value
Duration	8.918	13.346	1.497	<0.001
F ₂₅	3.460	6.339	1.832	<0.001
F ₅₀	5.420	8.348	1.540	<0.001
FMA	9.225	4.728	0.513	N/A
F _{min}	26.591	24.045	0.904	N/A

368

369 Figure 1:





372 Figure 3:

