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Published on: 10 Feb 2020 - Ethology (John Wiley & Sons, Ltd)

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Lucie Desmedt, Isabelle George, Aïcha Mohamed Benkada, Maxime Hervé, Thierry Aubin, et al.. Maternal presence influences vocal development in the Japanese quail (*Coturnix c. japonica*). *Ethology*, Wiley, 2020, 126 (5), pp.553-562. <10.1111/eth.13007>. <hal-02474536>

Authors' pre-print

Editor's version available at the following:

<https://doi.org/10.1111/eth.13007>



1 **Short title:** Maternal influences on calls in quail

2 **Title:** Maternal presence influences vocal development in the Japanese quail (*Coturnix c.*
3 *japonica*)

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16

17 **Acknowledgments**

18 We are grateful to Emmanuel De Margerie for his contribution in writing the Matlab routine and we
19 would like to thank Céline Nicolle for the animal care.

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26 **Abstract**

27 Social influences on vocal development of young birds have been widely studied in oscine songbirds
28 who learn to sing by vocal imitation of conspecifics, mainly male adults. In contrast, vocal
29 development of non-vocal learners such as *Galliformes* is considered as being under strong genetic
30 influence and independent of the social environment. In this study, we investigated the role of the
31 mother on the vocal development of young Japanese quail (*Coturnix coturnix japonica*). We compared
32 the vocal development of mothered and non-mothered chicks during the first 21 days of life. We
33 analysed the structural changes of two vocalisations: a) the rally call, emitted during long distance
34 communication and in stressful situations, b) the contact call, emitted during short distance
35 communication when chicks are in visual and/or auditory contact with congeners. We showed that
36 temporal and spectral structures of the two types of calls changed during development and differed
37 between mothered and non-mothered chicks. These results demonstrate that maternal presence
38 influences the vocal development of the young in the Japanese quail. Even if the adaptive value of
39 such changes was not assessed, these results highlight that plasticity of vocalisations in species
40 considered as non-vocal learners has been underestimated.

41 **Keywords:** mother, vocal learning, vocalisations, precocial bird

42

43 **INTRODUCTION**

44 Vocal learning is the ability to imitate sounds from the acoustic environment. This prerequisite to
45 language development in humans is a rare trait in the animal kingdom. In birds, it has been described
46 in oscine songbirds, parrots and hummingbirds (Baptista & Petrinovich, 1984; Thorpe, 1958). For
47 example, in several species of oscine songbirds, young individuals learn to sing by imitating
48 conspecifics, mainly adults. An absence of auditory models leads to the production of impoverished or
49 abnormal songs (*Passeriformes*: Peter Marler, Mundinger, Waser, & Lutjen, 1972, Price, 1979;
50 *Psittaciformes*: Brittan-Powell, Dooling, & Farabaugh, 1997; *Apodiformes*: Jarvis, 2004). Early
51 maternal effects of call exposure studied in Superb Fairy-wren (*Malurus cyaneus*) embryos were

52 found to shape the learned begging call at hatch, which was demonstrated with cross-fostering
53 experiments (Colombelli-Négrel et al., 2012) and with *in ovo* measurement of response to calls and
54 song (Colombelli-Négrel, Hauber, & Kleindorfer, 2014; Colombelli-Négrel & Kleindorfer, 2017;
55 Kleindorfer, Evans, Hauber, & Colombelli-Négrel, 2018).

56 In the so-called non-vocal learner bird species, experiments of auditory deprivation showed little or no
57 effects on the ontogeny of vocalisations (*Galliformes*: Konishi, 1963; *Columbiformes*: Nottebohm &
58 Nottebohm, 1971; *Passeriformes*: Kroodsma & Konishi, 1991). This led to the conclusion that
59 vocalisations of non-vocal learners are under strong genetic influence.

60 However, several studies have reported vocal changes in both juvenile and adult birds of non-vocal
61 learner species. In adults, temporal and spectral variations in calls' structure has been observed in the
62 male loons *Gavia immer* after a change of territory (*Gaviiformes*: Walcott, Mager, & Piper, 2006), and
63 across seasons in the Gray Partridge *Perdrix perdrix* (*Galliformes*: Rotella & Ratti, 1988). Vocal
64 changes during vocal development have also been described in the Pied avocet *Recurvirostra avosetta*
65 (*Charadriiformes*: Adret, 2012), the Japanese quail *Coturnix coturnix japonica* (*Galliformes*:
66 Derégnaucourt, Saar, & Gahr, 2009; Guyomarc'h & Guyomarc'h, 1996), the Collared dove
67 *Streptopelia Decaocto* (*Columbiformes*: Ballintijn & Ten Cate, 1997) and the Grey crowned crane
68 *Balearica regulorum gibbericeps* (*Gruiformes*: Budde, 2001). To our knowledge, no study has explored
69 the social influences on vocal development in young birds of a non-vocal learner species. However, it
70 has recently demonstrated that the vocalisations of marmoset infants (*Callithrix jacchus*), non-human
71 primates traditionally considered as non-vocal learner species, are sensitive to parental feedback
72 (Takahashi et al., 2015).

73 Many studies based on a maternal deprivation paradigm in quails have already highlighted the non-
74 genetic role of the mother on the young's social motivation (Bertin & Richard-Yris, 2005), emotivity
75 (Pittet, Le Bot, Houdelier, Richard-Yris, & Lumineau, 2013), spatial skills (de Margerie et al., 2013)
76 and rhythmicity (Formanek, Richard-Yris, Houdelier, & Lumineau, 2009). In our study, we did not
77 examine vocal similarity between mother and chicks, but we aim to explore the maternal influences on
78 vocal development in chicks of the Japanese quail, a species traditionally considered as a non-vocal

79 learner. In this species, parental care after laying is exclusively carried out by the mother over a
80 relatively short period of time (Orcutt & Orcutt, 1976). Maternal behaviour can be easily induced via
81 an adoption procedure, avoiding genetic influences (Richard-Yris, Michel, & Bertin, 2005). Given the
82 behavioural plasticity of chicks, we thus expected to find maternal influences on vocal development
83 too. We also tested the possible existence of a horizontal transmission of vocalizations between chicks
84 raised in a same pair. Indeed, young could influence each other regardless of the presence or the
85 absence of the mother. In order to test this hypothesis we explored chicks' acoustic similarity.

86

87 **MATERIALS & METHODS**

88

89 *Ethical note*

90

91 All experiments were approved by the departmental direction of veterinary services (Ille-et-Vilaine,
92 France, permit number 005283) and were performed in accordance with the European Communities
93 Council Directive of 22th September 2010 (2010/63/EU). The breeding procedure was approved by
94 the regional ethics committee (agreement number: R-2011-SLU-02).

95

96 *Subjects and maintenance condition*

97

98 The birds (adults and chicks) used in this study were Japanese quail (*Coturnix c. japonica*) of a broiler
99 line. They were provided by an industrial farm (Les cailles de Chanteloup, Corps-Nuds, France).

100 Three weeks before the start of the experiment, 20 adult females (4.5 months old) were placed in
101 individual metal cages (52 x 40 x 35 cm) equipped with a feeder and a drinking trough. Opaque walls
102 prevented any visual contact between individuals.

103 The chicks came from eggs artificially incubated (Brinsea, OVA-Easy Advance Series II) in the
104 laboratory during 17 days. After hatching, chicks were weighed and identified with a coloured and
105 numbered ring on each leg. Then, groups of 20 individuals were placed in large cages (94 × 46 × 30
106 cm) equipped with a heater ($37 \pm 1^\circ\text{C}$), a feeder and a drinking trough. On the evening of the hatching
107 day (D1), chicks were moved in a mothering room and randomly assigned to an experimental group:
108 mothered (M-group) or non-mothered (NM-group). The mothered chicks (20 pairs) were raised by an
109 adoptive mother, while the non-mothered chicks (15 pairs) were kept with a heating lamp. The chicks
110 within each pair were not genetically related.

111 All the birds were in the same room, but pairs of chicks could not see each other. Food and water were
112 provided *ad libitum* throughout the duration of the experiment. The mothering room was kept at 22 ± 1
113 °C, with LD 10:14 cycle.

114 As quail chicks cannot be sexed by visual inspection before they are four weeks old (Baer, Lansford,
115 & Cheng, 2015), chicks were randomly attributed to one of each group without knowing their sex. Sex
116 was determined after the end of the experiment when the birds were 4 weeks old. However, the sex
117 ratio did not differ between the mothered (10 females and 20 males) and the non-mothered (17 females
118 and 13 males) group (Chi-square test: $X^2 = 2.42$, $df = 1$, $P = 0.12$).

119 The mothered and the non-mothered chicks' growth (body mass) differed during development (LMM
120 Wald test, *groups x days*: $X^2 = 6.0146$, $df = 1$, $P = 0.01419$), with faster growth for the non-mothered
121 chicks (Means and standard errors are presented in Table. S1). This result is in agreement with
122 previous studies (Pittet et al., 2013).

123

124 *Experimental procedure*

125

126 *Maternal induction*

127

128 The procedure used in this study was previously described and has demonstrated that tactile and vocal
129 stimulations between the female and the young at night favour the emergence of maternal behaviour
130 (Richard-Yris et al., 2005).

131 Three days before the induction of the maternal behaviour, a rearing box (19 × 19 × 19 cm) was
132 introduced in every cage of the mothering room. On the day of hatching, each female was locked in
133 the rearing box one hour before the end of the photoperiod. Two one-day old chicks were then placed
134 with each female and stayed there overnight. The chicks of the non-mothered group were also placed
135 in pairs in a rearing box equipped with a heating lamp.

136 The boxes were opened the next morning to check the expression of maternal behaviour by females.
137 Mothers with rejection or aggressive behaviours toward the chicks (n = 5) were excluded from the
138 study. After exclusion, mothered and non-mothered groups were both composed of 30 chicks.

139 Mothers and heating lamps were removed from the cages on the evening of the 11th day, at the age at
140 which the chicks disperse in the wild (Mills, Crawford, Domjan, & Faure, 1997; Orcutt & Orcutt,
141 1976). Pairs of chicks stayed in their respective cages until the end of the experiment (D21).

142

143 *Recording of vocalisations*

144 The vocalisations of the chicks were recorded every day between D3 and D21 of life. Due to a
145 technical problem, the vocalisations of D9 were not recorded.

146 Each day of recording, 2 chicks of the same pair were removed carefully from their life cage,
147 transported together to the recording room, and placed individually in a wooden cage (82 x 61 x 36
148 cm). The cages were placed in 2 sound-attenuating rooms (190 x 93 x 243 cm).

149 After 3.5 min of recording in social isolation, the two chicks were brought together in a third empty
150 cage (90 x 48 x 53 cm), also placed in a sound-attenuating room. The two chicks were placed on
151 opposite side of the cage. Two wire separations (43 x 27 cm, separated by 17 cm) prevented tactile
152 contacts between them, while allowing visual and vocal interactions. This separation allowed us to

153 then distinguish the calls emitted by the 2 chicks. The vocal interactions during this stage were
154 recorded for 3.5 min. The chicks were then brought back together in their life cage.

155 These two experimental situations made it possible to record two types of vocalisations, rally calls and
156 contacts calls.

157 The order in which every pair of chicks was recorded was randomised each day.

158 Vocalisations were recorded using the Sound Analysis Pro (SAP) software (Tchernichovski, Lints,
159 Derégnaucourt, Cimenser, & Mitra, 2004). The program was run on a PC equipped with an AudioBox
160 PreSonus 1818VSL interface (sampling frequency: 44.1 kHz) connected with omnidirectional
161 microphones (AKG C417PP, frequency response 30 Hz – 20 kHz \pm 5dB). One microphone was
162 positioned in the centre of the cage used for the social isolation phase (at 30 cm from the floor) and
163 two microphones were positioned on each side of the cage used for the reunion phase (at 16 cm from
164 the floor).

165

166 *Sound analysis*

167

168 Acoustic analyses were made with SAP signal processing software (Tchernichovski et al., 2004), and
169 the similarity analyses with the ANA software (Richard, 1991).

170

171 *Calls structure*

172 Good quality calls (no overlapping with noise due to the bird movements in the cage or with calls from
173 the other chick during the reunion phase) were selected by visual inspection of spectrograms.

174 During the isolation phase, we sampled the first thirty vocalisations emitted by each individual for
175 each day of recording. After an auditory and visual inspection of the spectrogram, each vocalisation
176 was classified according to already published descriptions of the vocal repertoire of the Japanese quail
177 (Guyomarc'h & Guyomarc'h, 1996). We focused our analysis on the rally calls (Fig. 1A), which are
178 vocalisations of strong social value and further emitted by chicks when losing visual contact with

179 conspecifics. Rally calls represented 90% of the sampled calls (sampled calls, n = 30276; rally calls, n
180 = 27464).

181 For the reunion phase, we focused our analysis on contact calls, one of the main vocalisations
182 expressed during social interactions (Fig. 1B). Calls from the microphone on the left side of the cage
183 (n = 1336 calls) were manually selected from a visual inspection of the spectrogram to define the
184 beginning to the end of each call. A routine on Matlab was then used to automatically sample the same
185 calls in the recordings coming from the microphone placed on the right side of the cage. By comparing
186 the amplitude of the sampled calls on the two channels, each vocalisation could be attributed to one of
187 the individual chicks.

188 We used the SAP software to extract automatically the duration, the mean frequency, the Wiener
189 entropy and the frequency modulation (FM) of the rally calls. For the contact calls, the maximal
190 frequency and the minimal frequency were measured by clicking on the sonogram using SAP. These
191 values were used to measure the frequency bandwidth (see Table. 1 for parameters detail).

192

193 *Similarity analyses*

194 In order to explore the influence of maternal deprivation on the intra-pair (chicks raised in the same
195 life cage) and inter-pair (chicks raised in different life cage, but of the same group M or NM) acoustic
196 similarity, one contact call was selected randomly for each chick and each day from D3 to D21. A
197 total of 381 contact calls were used for this analysis. Nevertheless, for some individuals we have not
198 always been able to select a call per day because no contact calls were emitted during the recording.

199 We used a similarity index that has been used successfully in other species (birds: Adret-Hausberger,
200 1983; cetaceans: Miller & Bain, 2000; primates: Lemasson, Gautier, & Hausberger, 2003), using ANA
201 software (Richard, 1991). For each pairwise comparison, the program compared the frequency contour
202 of the sonograms and automatically looked for the best superposition along the frequency and duration
203 axes providing a ratio of 'overlap' between both contours.

204 Thus, for each day of development and each chicks, we calculated an intra-pair similarity index and an
205 inter-pair similarity index. Inter-pair similarity index corresponded to the average of inter-pair values
206 obtained between individuals of the same sex and raised in the same pair composition (pair of same-
207 sex chicks or not). For example, for a mothered male raised in a mixed pair (with a female), we
208 calculated the average of similarity index obtained between this male and all the other mothered males
209 raised in a mixed pair. This approach made it possible to obtain inter-pair similarity indices
210 independent of sex effects.

211

212 *Statistical analysis*

213

214 Statistical analyses were performed using the software R v.3.5.1 (R Core Team, 2016).

215 To test the influence of mothering on the acoustic parameters of chicks' calls we used Wald tests
216 applied on a linear mixed model (functions `lmer` from package *lme4* Bates, Mächler, Bolker, &
217 Walker, 2014 and `Anova()` from package *car* Fox & Weisberg, 2010). When the residuals did not
218 respect the conditions of application of the model, data were transformed with the square root
219 function. The fixed factors were the experimental group (mothered or non-mothered), the day of
220 recording (from D3 to D21; with scale function of R) and the sex of the individual. The random
221 factors were birds and pairs identity, and the pair composition.

222 We analysed the similarity scores using Wald tests applied on a generalised linear mixed model with a
223 logit link and a binomial distribution (functions `glmmPQL` from package *MASS* Ripley et al., 2018 and
224 `Anova()` as above). Fixed effects included experimental groups (mothered or non-mothered), the day
225 of recording (from D3 to D21), the sex of the individual and the comparison level (intra- or inter-pair).
226 Bird's identity and the pair composition were included as random factors.

227 All models included second-order interaction terms. The model estimates are presented in Table. S2,
228 and the slopes estimates in Table. S3. The threshold of significance was 0.05.

229

230 **RESULTS**

231

232 *Developmental changes of rally calls*

233

234 Both temporal and frequency parameters of rally calls changed significantly during development. We
235 observed a decrease of call duration and mean frequency with time, and an increase of frequency
236 modulation and Wiener entropy, for both mothered and non-mothered chicks (Fig. 2; Table. 2, LMM:
237 *postnatal day*; see Fig. S1 for individual curves).

238 We observed significant developmental differences between mothered and non-mothered chicks for
239 the four acoustic parameters (Table. 2, LMM: *group*postnatal day*). Overall, the development of the
240 rally calls was faster in the mothered chicks than in the non-mothered ones (Table. S3, steeper slopes
241 for the 4 acoustic parameters; Table. 2, LMM: *group*postnatal day*). The differences between rally
242 calls' structure of mothered and non-mothered chicks were not the same during and after the
243 mothering period. During the mothering period (first eleven days of life), the mothered chicks
244 produced higher-pitched calls with a lower Wiener entropy (Fig. 2C and 2D). After mothering ended,
245 differences in mean frequency disappeared but mothered chicks emitted shorter calls, with a higher
246 FM and Wiener entropy (Fig. 2A, 2B and 2D).

247 We also observed differences between females and males (Fig. S2; Table. 2, LMM: *sex*postnatal day*
248 and *sex*), independently of the experimental group (Table. 2, LMM: *group*sex*). Females produced
249 rally calls with a higher FM and a higher mean frequency than males' calls. Moreover, whereas the
250 call duration of females increased along development, the duration of males' calls decreased. Females'
251 calls also showed a slower decrease for the mean frequency (Table. S3).

252

253 *Developmental changes of contact calls*

254

255 The acoustic structure of contact calls also changed significantly during development, with an overall
256 decrease in duration, in maximum frequency and in frequency bandwidth (Table. 2, LMM: *postnatal*
257 *day*).

258 We observed significant developmental differences between mothered and non-mothered chicks
259 (Table. 2, LMM: *group*postnatal day*). During the mothering period, the two groups differed in
260 frequency bandwidth and maximum frequency (Fig. 3B and 3C). Mothered chicks produced contact
261 calls with a lower maximal frequency and a narrower frequency bandwidth than the non-mothered
262 chicks (Table. 2, LMM: *group*postnatal day*). After separation (D12), only the duration differed
263 between the two groups, with shorter contact calls in mothered chicks (Fig. 3A).

264 Overall, mothered chicks' calls showed a faster development of the temporal parameters (Table. S3,
265 steeper slope) and a slower development of frequency parameters (Table. S3, lower slope) than non-
266 mothered chicks' calls (Table. 2, LMM: *group*postnatal day*).

267 We found differences in the development of females' and males' contact calls (Fig. S3; Table. 2,
268 LMM: *sex*postnatal day*), independently of the experimental group (Table. 2, LMM: *group*sex*).
269 Frequency parameters and call duration decreased slower in females than in males (Table. S3).

270

271 *Acoustic similarity between contact calls of chicks' pairs*

272

273 There was no interaction between the experimental group and the age (Table. 2, GLMM:
274 *group*postnatal day*) and between the experimental group and the comparison level (inter- and intra-
275 similarity; Table. 2, GLMM: *group*comparison level*). We did not find any effect of mothering on
276 vocal similarity (Table. 2, GLMM: *group*).

277 However, there was a significant difference between inter- and intra- pair similarity with the stage of
278 development (Table. 2, GLMM: *comparison level*postnatal day*). Intra-pair similarity was always

279 greater than inter-pair similarity but it decreased along development whereas inter-pair similarity
280 remained stable (Fig. 3D; Table. S3).

281 The sex of the chicks also had an influence on the changes in the similarity index with development
282 (Fig. S3; Table. 2, GLMM: *sex*postnatal day*). There was a decrease in the similarity index of the
283 males while the similarity index of females remained stable (Table. S3). Sex did not interact with the
284 experimental group (Table. 2, GLMM: *group*sex*), nor with the comparison level (Table. 2, GLMM:
285 *comparison level*sex*).

286

287 **DISCUSSION**

288

289 Our results highlight the role of social interactions on the vocal development of Japanese quails. The
290 differences in acoustic structures observed between mothered and non-mothered chicks demonstrate
291 that the presence of the mother influences the vocal development of its young. This finding challenges
292 the idea that in birds traditionally classified as non-vocal learners, vocal development of young is
293 independent of the auditory and social environments.

294 It is very likely that the mother induced vocal changes through both short- and long-term influences on
295 the behavioural phenotype of her young. In Japanese quail, mothered birds are more sensitive to social
296 separation at young age (Bertin & Richard-Yris, 2005) and adulthood (Pittet et al., 2013). Thus, the
297 context of social isolation in our study may have led to an increased level of stress in mothered chicks.
298 Since stressful situations have been shown to be accompanied by spectral changes in calls of many
299 mammals (Briefer, 2012; Zhang & Ghazanfar, 2016) and more recently in a bird species (Perez et al.,
300 2012), an increased level of stress may explain the production of rally calls higher in frequency and
301 with a lower Wiener Entropy in mothered chicks during the mothering period. In *Galliform* species,
302 social isolation is accompanied by the production of rally calls (Guyomarc'h & Guyomarc'h, 1996)
303 but our study is the first one to explore the existence of structural variations in these calls in response
304 to a stressful situation. Vocal changes related to emotional states may be due to physiological changes

305 or the release of hormones such as glucocorticoids (Perez et al., 2016; Ritters, 2012). Other hormones
306 such as testosterone have also been shown to influence the vocalisation pattern in *Galliformes* (Beani,
307 Briganti, Campanella, & LUPO, 2000; P. Marler, Kreith, & Willis, 1962).

308 The emotional and motivational state of the birds during the reunion phase is more complex to
309 explain. Indeed, the impossibility of any physical contact between the two chicks might have induced
310 a state of frustration or emotional confusion. Previous studies have shown that motherless chicks are
311 less socially motivated and more aggressive (Bertin & Richard-Yris, 2005). Thus, in our study,
312 production of high-frequency calls by non-mothered chicks could be associated with a higher
313 emotional state (higher level of stress) following in the same way the structural motivational code
314 conceptualised by Morton (Morton, 1982) for bird vocalisations. Indeed, if, for the non-mothered
315 chicks, the reunion was complete (because they met their unique life partner), for the mothered chicks
316 it was partial only because they met their same-age congener but not their mother. Maybe in the case
317 of a complete reunion, mothered chicks would produce high-frequency calls. Moreover, in addition to
318 the acute context-related stress during recordings, maternal deprivation may have created a chronic
319 stress that influenced the developmental trajectory of non-mothered chicks' vocalisations. Additional
320 experiments including video recordings and physiological measurements would be required to
321 document the influence of the emotional state on the acoustic structure of quail's vocalisations.

322 The mother, by her presence, could also influence the growth of her chicks, and thus the maturation of
323 their vocal apparatus. Several studies have demonstrated a negative correlation between body size and
324 vocal frequency (e.g. Chabert et al., 2015; Patel, Mulder, & Cardoso, 2010). In our study, we found
325 that the mothered chicks had slower growth than the non-mothered chicks. These results could explain
326 the production of higher-frequency calls at the beginning of the development in the mothered chicks.
327 However, since the mothered chicks produced lower-frequency contact calls, the contact calls'
328 structure does not seem to support this hypothesis. A thorough monitoring of the growth during chick
329 development would be necessary to test whether some vocal changes could correlate with differences
330 in body mass or size.

331 Vocal differences observed in our study, between mothered and non-mothered chicks, may have a
332 functional aspect. Vocalisations can transmit information about the needs of young (Klenova, 2015;
333 Leonard & Horn, 2001) and they can affect maternal responses accordingly (Chabert et al., 2015;
334 Perez et al., 2016). Vocalisations of the mothered chicks are likely to be better adapted to the mother-
335 young interactions than those of the non-mothered chicks but playback experiments would be required
336 to test this hypothesis.

337 The mother could also influence the vocal development of her young through imitation like in
338 songbirds. Young oscines learn their songs by memorising and imitating those produced by
339 conspecific adults (Brainard & Doupe, 2002). Social isolation leads to the production of abnormal
340 songs in several oscine species (Chaiken, Gentner, & Hulse, 1997; Price, 1979). A comparative
341 analysis of the maternal and the juvenile vocalisations could be made to test this hypothesis.

342 Our results also suggest that a potential imitation could occur horizontally between the two chicks, in
343 both the mothered and the non-mothered groups. Indeed, the acoustic similarity index showed a
344 greater intra-pair similarity compared to the inter-pair similarity, regardless of the presence or absence
345 of the mother. Chicks from the same pair may have stimulated and imitated each other. In songbirds
346 like European starlings and zebra finches, young influence each other either in the absence or in
347 presence of a conspecific adult (Chaiken et al., 1997; Derégnaucourt & Gahr, 2013; Poirier et al.,
348 2004; Volman & Khanna, 1995). The decrease in intra-pair acoustical similarity during development
349 may reflect an individualisation of contact calls after separation from the mother.

350 In conclusion, our study shows, for the first time, non-genetic maternal influences on vocal
351 development in the Japanese quail, a bird species with a vocal repertoire composed of different calls
352 whose structure has been considered for a long time to be insensitive to social influences. In line with
353 recent research on vocal development in non-human primates (Lemasson, Ouattara, Petit, &
354 Zuberbühler, 2011; Takahashi et al., 2015), our study is a strong invitation to revisit the traditional
355 dichotomy between vocal learners and non-vocal learners species.

356

357 **Supplementary material**

358 Data related to this paper are available from the Dryad Digital Repository:
359 <https://doi.org/10.6084/m9.figshare.8241326.v1>. Codes for statistics are available from Dryad
360 Digital Repository: <https://doi.org/10.6084/m9.figshare.10321517.v1>.

361

362

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532 **Table 1. Description of the acoustic parameters used to compare the vocal development of**
533 **mothered and non-mothered chicks.**

Acoustic parameters	Description	Rally calls	Contact calls
Duration (ms)	Time from the beginning to the end of the call	✓	✓
Frequency modulation	Mean slope of the call frequency	✓	
Mean frequency (Hz)	Center of power distribution	✓	
Wiener entropy	Spectral flatness based on the ratio of geometric mean to arithmetic mean of the spectrum	✓	
Maximum frequency (Hz)	The highest frequency value in the call		✓
Frequency bandwidth (Hz)	Difference between the maximum and the minimum frequency		✓

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547 **Table 2. Statistical analysis of developmental changes for rally calls and contact calls.**

Acoustical parameter ~ Group+ Sex+ Postnatal day+ Postnatal day:Group+ Postnatal day:Sex+ Group:Sex+ (1|Bird ID)+(1|Pair ID)+(1|Pair composition)

Rally calls	Call duration			Frequency modulation			Mean frequency			Wiener entropy		
<i>Explanatory variables</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>
Group	2.37	1	0.12	2.06	1	0.15	2.46	1	0.12	0.37	1	0.54
Sex	0.67	1	0.41	5.82	1	0.02	5.75	1	0.02	1.4	1	0.24
Postnatal day	23.65	1	< 0.0001	10835.47	1	< 0.0001	28658.25	1	< 0.0001	4035.48	1	< 0.0001
Group*Postnatal day	27.68	1	< 0.0001	20.04	1	< 0.0001	88.24	1	< 0.0001	159.55	1	< 0.0001
Sex*Postnatal day	93.84	1	< 0.0001	0.14	1	0.71	72.75	1	< 0.0001	3.07	1	0.08
Group*Sex	0.07	1	0.79	0.14	1	0.71	0.05	1	0.82	0.04	1	0.83

Acoustical parameter ~ Group+ Sex+ Postnatal day+ Postnatal day:Group+ Postnatal day:Sex+ Group:Sex+ (1|Bird ID)+(1|Pair ID)+(1|Pair composition)

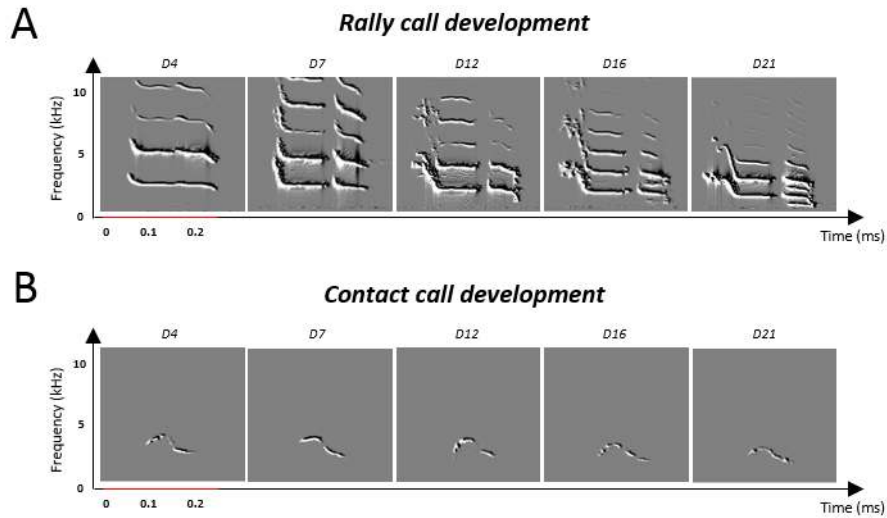
Contact calls	Call duration			Frequency bandwidth			Maximal frequency			Acoustical similarity		
<i>Explanatory variables</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>	χ^2	<i>df</i>	<i>p-value</i>
Group	1.27	1	0.26	2.15	1	0.14	0.24	1	0.62	2.03	1	0.15
Sex	2.85	1	0.09	3.28	1	0.07	0.08	1	0.77	1.35	1	0.24
Postnatal day	23.28	1	< 0.0001	51.42	1	< 0.0001	956.45	1	< 0.0001	14.92	1	0.0001
Comparison level	-	-	-	-	-	-	-	-	-	114.11	1	< 0.0001
Group*Postnatal day	12.53	1	0.0004	5.86	1	0.02	14.27	1	0.0002	1.91	1	0.17
Sex*Postnatal day	4.47	1	0.04	15.67	1	< 0.0001	6.72	1	0.01	7.47	1	0.006
Group*Sex	0.31	1	0.58	0.4	1	0.52	1.17	1	0.28	0.45	1	0.5
Comparison level*Postnatal day	-	-	-	-	-	-	-	-	-	5.79	1	0.02
Group*Comparison level	-	-	-	-	-	-	-	-	-	0.2	1	0.65
Sex*Comparison level	-	-	-	-	-	-	-	-	-	0.37	1	0.54

548 *Significant results (linear models, p < 0.05) are in bold. (-) for factors not included in the statistical*

549 *model.*

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Mothered chick



Non-Mothered chick

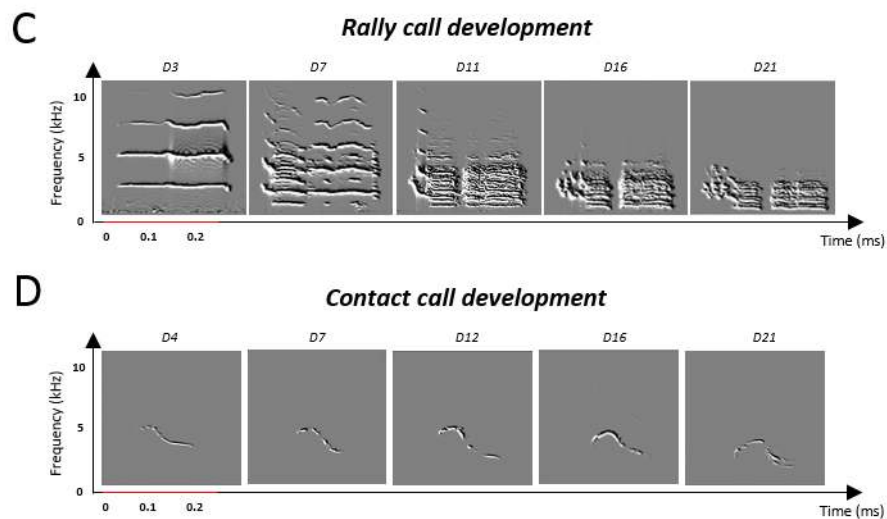
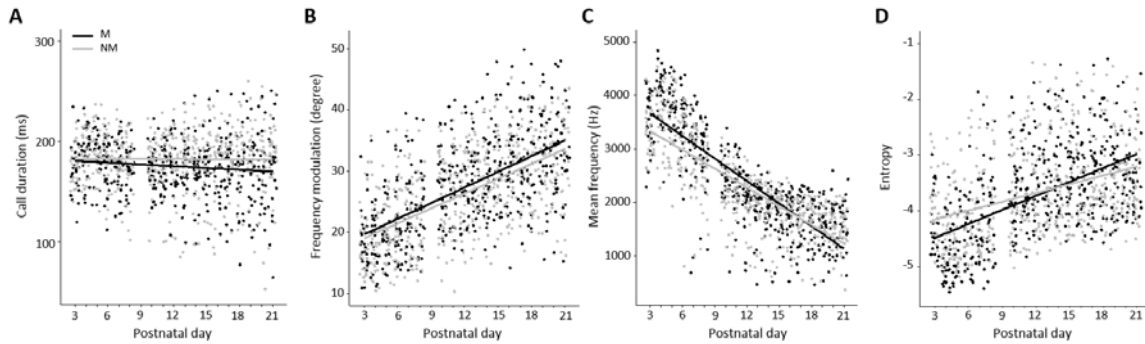


Figure 1. Vocal development on different days of the rally call (A, C) and the contact call (B, D) of a mothered and a non-mothered chick.

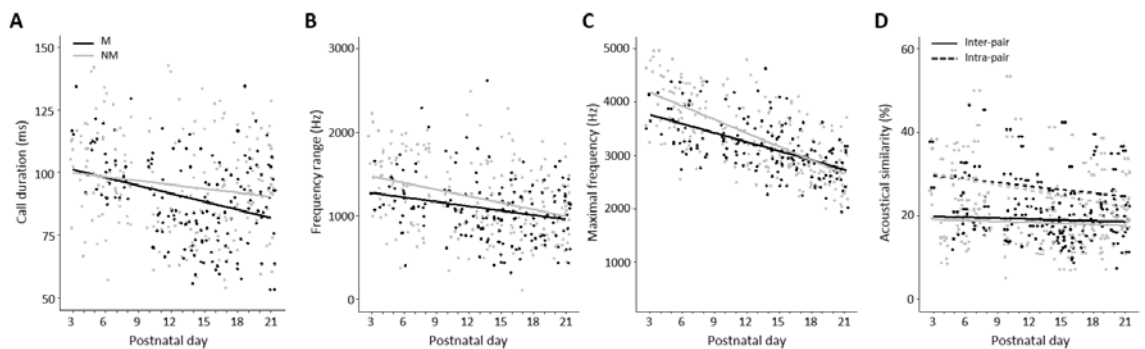
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552 **Figure 1. Vocal development on different days of the rally call (A) and the contact call (B) of a**
553 **mothered chick.**



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555 **Figure 2. (A-D) Acoustic changes of rally calls along the development of mothered (M) and non-**
 556 **mothered (NM) chicks, from postnatal day 3 to postnatal day 21. (A) Call duration (ms); (B)**
 557 **Frequency Modulation; (C) Mean frequency (Hz); (D) Wiener Entropy. Dots represent individual**
 558 **means for each day. Trend curves are linear regressions.**

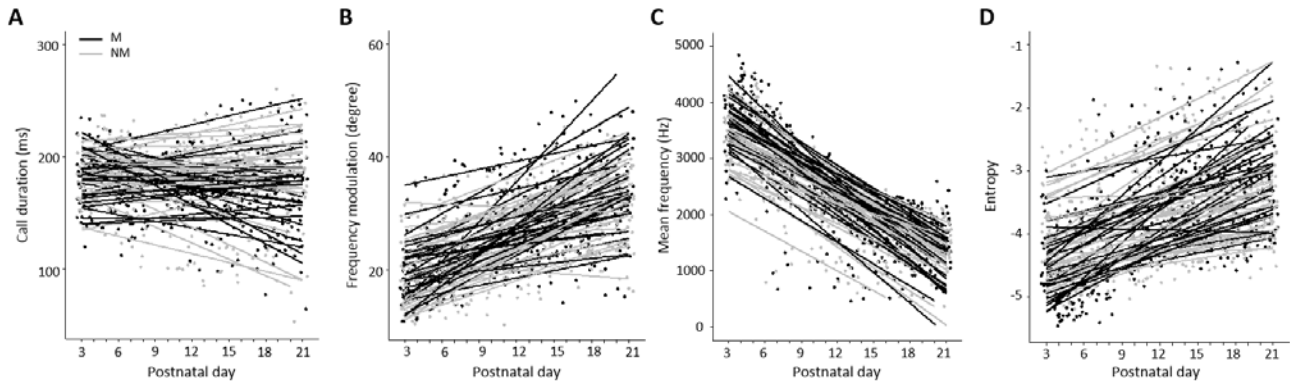


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560 **Figure 3. (A-C) Acoustic changes of contact calls during the development of mothered (M) and**
 561 **non-mothered (NM) chicks, from postnatal day 3 to postnatal day 21. (A) Call duration (ms); (B)**
 562 **Frequency bandwidth (Hz); (C) Maximal frequency (Hz). Dots represent individual means for each**
 563 **day. (D) Developmental changes of the percentage of intra- (dotted lines, filled dots) and inter-pair**
 564 **(full lines, open dots) acoustical similarity. Trend curves are linear regressions.**

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Supplementary methods

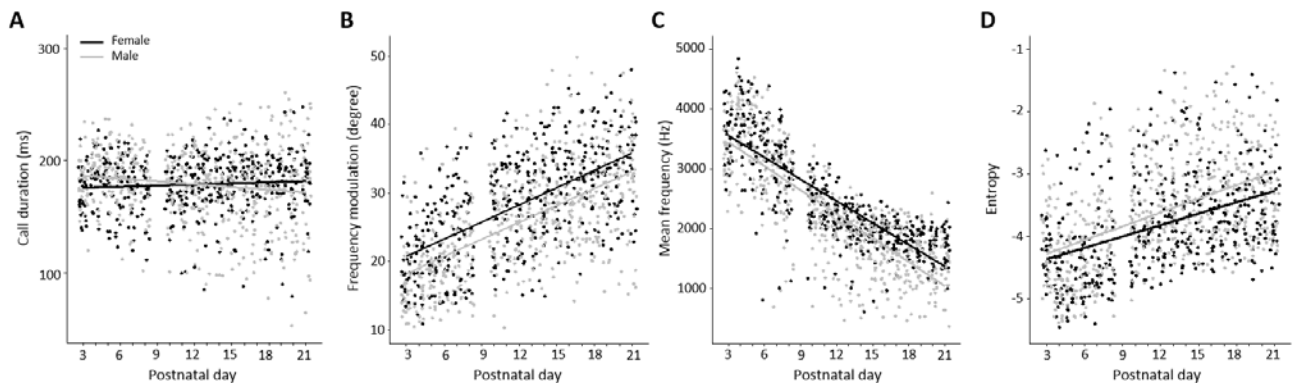


1 **Figure S1. (A-D) Acoustic changes of rally calls along the development of mothered (M) and non-**
2 **mothered (NM) chicks, from postnatal day 3 to postnatal day 21. (A) Call duration (ms); (B) Frequency**
3 **Modulation; (C) Mean frequency (Hz); (D) Wiener Entropy. Dots represent individual means for each**
4 **day. Trend curves are linear regressions by individuals.**

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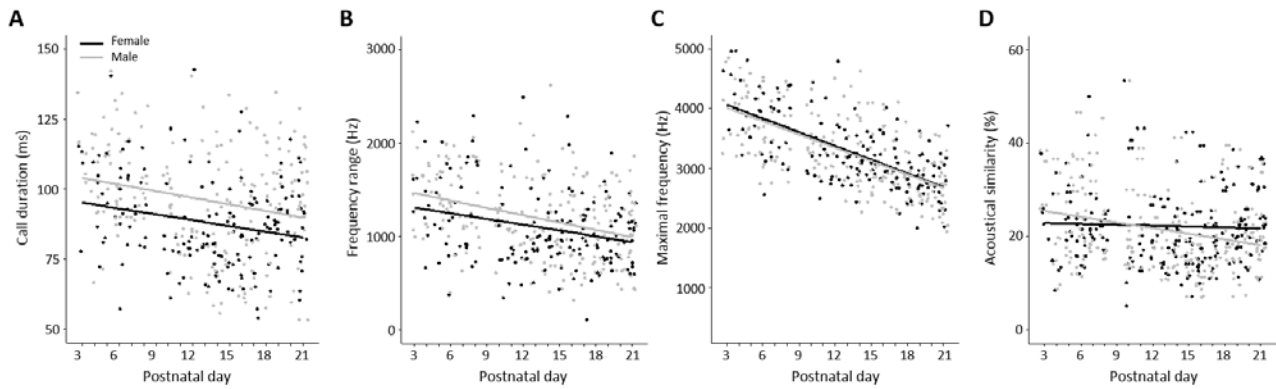
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8 **Figure S2. (A-D) Sex effects on the acoustical changes of rally calls during development, from**
9 **postnatal day 3 to postnatal day 21. (A) Call duration (ms); (B) Frequency Modulation; (C) Mean**
10 **frequency (Hz); (D) Wiener entropy. Dots represent individual means for each day. Trend curves are**
11 **linear regressions.**

12

Supplementary methods



13 **Figure S3.** (A-C) Sex effects on the acoustical changes of contact calls during development, from
 14 postnatal day 3 to postnatal day 21. (A) Call duration (ms); (B) Frequency bandwidth (Hz); (C) Maximal
 15 frequency (Hz). Dots represent individual means for each day. (D) Developmental changes of the
 16 percentage of intra- (dotted lines) and inter-pair (full lines) acoustical similarity. Trend curves are linear
 17 regressions.

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19

20 **Table S1.** Body weights (mean \pm standard error) of mothered and non-mothered chicks from D1 to
 21 **D25.**

	Mothered	Non-mothered
Postnatal days		
D1	10.44 \pm 0.1273	10.10 \pm 0.1194
D11	54.86 \pm 2.1350	63.40 \pm 1.5140
D18	108.87 \pm 3.2251	120.07 \pm 2.1490
D25	176.70 \pm 4.3211	187.04 \pm 2.9004

22

Supplementary methods

23 **Table S2. Influence of the mothering on the acoustical changes of the rally calls and the contact calls during chicks' vocal development.**

Acoustical parameter ~ Group+ Sex+ Postnatal day+ Postnatal day:Group+ Postnatal day:Sex+ Group:Sex+ (1 Bird ID)+ (1 Pair ID)+ (1 Pair composition)												
Rally calls	Call duration			Frequency modulation			Mean frequency (sqrt)			Wiener entropy		
<i>Fixed Effects</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>
(Intercept)	175.13	6.52	26.87	29.04	1.51	19.24	49.97	1.38	36.29	-3.85	0.17	-22.11
Group - NM	6.88	8.21	0.84	-1.28	1.86	-0.69	-2.16	1.75	-1.24	0.06	0.22	0.27
Sex - male	2.78	7.98	0.35	-2.51	1.81	-1.38	-3.01	1.64	-1.83	0.13	0.2	0.67
Postnatal day	0.04	0.45	0.1	4.94	0.09	54.06	-7.36	0.09	-84.68	0.45	0.01	37.48
Group - NM*Postnatal day	2.44	0.47	5.26	-0.42	0.09	-4.48	0.84	0.09	9.39	-0.16	0.01	-12.63
Sex - male*Postnatal day	-4.51	0.47	-9.69	0.04	0.1	0.37	-0.77	0.09	-8.53	0.02	0.01	1.75
Group - NM*Sex-male	2.97	11.02	0.27	-0.92	2.5	-0.37	0.52	2.26	0.23	0.06	0.28	0.21

Acoustical parameter ~ Group+ Sex+ Postnatal day+ Postnatal day:Group+ Postnatal day:Sex+ Group:Sex+ (1 Bird ID)+ (1 Pair ID)+ (1 Pair composition)												
Acoustical similarity ~ Group+ Sex+ Postnatal day+ Comparison level+ Postnatal day:Group+ Postnatal day:Sex+ Group:Sex+ Comparison level:Postnatal day+ Group:Comparison level+ Sex:Comparison level+ (1 Bird ID)+ (1 Pair ID)+ (1 Pair composition)												
Contact calls	Call duration			Frequency bandwidth			Maximal frequency			Acoustical similarity		
<i>Fixed Effects</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>
(Intercept)	86.99	4.14	21.03	978.58	107.03	9.14	3083.08	150.51	20.48	-1.61	0.16	-10.2
Group - NM	2.4	5.35	0.45	100.3	123.19	0.81	166.03	151.99	1.09	0.13	0.14	0.95
Sex - male	2.96	4.2	0.71	76.29	101.44	0.75	66.54	102.45	0.65	0.27	0.14	2.002
Postnatal day	-3.5	1.01	-3.46	11.75	24.62	0.48	-260.38	24.64	-10.57	0.01	0.009	1.44
Comparison level - intra	-	-	-	-	-	-	-	-	-	0.69	0.13	5.24
Group - NM*Postnatal day	3.59	1.01	3.54	-59.58	24.62	-2.42	-93.29	24.69	-3.78	-0.01	0.008	-1.37
Sex - male*Postnatal day	-2.04	0.97	-2.11	-93.09	23.5	-3.96	-60.98	23.52	-2.59	-0.01	0.007	-2.71
Group - NM*Sex-male	3.12	5.57	0.56	85.68	134.64	0.64	-146.47	135.21	-1.08	-0.06	0.09	-0.66
Comparison level - intra*Postnatal day	-	-	-	-	-	-	-	-	-	-0.02	0.007	-2.38
Group*Comparison level - intra pairs	-	-	-	-	-	-	-	-	-	-0.04	0.08	-0.44
Sex*Comparison level - intra pairs	-	-	-	-	-	-	-	-	-	-0.05	0.08	-0.6

24 *Linear mixed models were applied on acoustical parameters of both rally calls and contact calls (lmer function from lme4 R package). A generalized mixed*
 25 *model was applied on the similarity index of the contact calls (glmmPQL function from MASS R package). Results were obtained with the summary function*
 26 *of R.*

Supplementary methods

27 **Table S3. Influence of the mothering on the acoustical changes of the rally calls and the contact calls**
 28 **during chicks' vocal development. Slopes estimates for group, sex and comparison level's effects.**

	<i>Estimate</i>	<i>Std.Error</i>	<i>df</i>	<i>lower.CL</i>	<i>upper.CL</i>	<i>t.ratio</i>	<i>p-value</i>
Rally calls							
<i>Call duration</i>							
M	-0.4	0.06	27409.59	-0.52	-0.28	-6.63	< 0.0001
NM	0.04	0.06	27417.59	-0.07	0.16	0.75	0.45
Female	0.23	0.06	27412.76	0.11	0.35	3.76	0.0002
Male	-0.59	0.06	27414.62	-0.7	-0.48	-10.46	< 0.0001
<i>Frequency modulation</i>							
M	0.9	0.01	27408.1	0.88	0.93	73.16	< 0.0001
NM	0.83	0.01	27414.74	0.8	0.85	71.31	< 0.0001
Female	0.86	0.01	27410.71	0.84	0.89	69.11	< 0.0001
Male	0.87	0.01	27412.26	0.85	0.89	75.63	< 0.0001
<i>Mean frequency (sqrt)</i>							
M	-1.41	0.01	27408.45	-1.44	-1.39	-120.14	< 0.0001
NM	-1.26	0.01	27415.19	-1.28	-1.24	-114.06	< 0.0001
Female	-1.27	0.01	27411.34	-1.29	-1.24	-106.61	< 0.0001
Male	-1.41	0.01	27412.92	-1.43	-1.38	-128.61	< 0.0001
<i>Wiener entropy</i>							
M	0.09	0.002	27410.52	0.08	0.09	51.77	< 0.0001
NM	0.06	0.002	27418.42	0.05	0.06	36.41	< 0.0001
Female	0.07	0.002	27414.16	0.07	0.07	41.35	< 0.0001
Male	0.07	0.003	37416.03	0.07	0.08	47.54	< 0.0001
Contact calls							
<i>Call duration</i>							
M	-0.85	0.16	1328.01	-1.16	-0.54	-5.4	< 0.0001
NM	-0.18	0.11	1324.01	-0.39	0.04	-1.58	0.11
Female	-0.32	0.14	1318.21	-0.6	-0.04	-2.22	0.03
Male	-0.7	0.12	1328.49	-0.94	-0.47	-5.82	< 0.0001
<i>Frequency bandwidth</i>							
M	-6.53	3.82	1326.54	-14.01	0.96	-1.71	0.09
NM	-17.7	2.69	1325.59	-22.98	-12.43	-6.59	< 0.0001
Female	-3.38	3.51	1323.25	-10.26	3.49	-0.97	0.34
Male	-20.85	2.93	1327.58	-26.6	-15.09	-7.11	< 0.0001
<i>Maximal frequency</i>							
M	-54.56	3.83	1325.55	-62.07	-47.05	-14.26	< 0.0001
NM	-72.06	2.69	1318.85	-77.34	-66.78	-26.79	< 0.0001
Female	-57.59	3.5	1316.29	-64.46	-50.72	-16.45	< 0.0001
Male	-69.03	2.94	1324.89	-74.8	-63.26	-23.47	< 0.0001
<i>Acoustical similarity</i>							
M	-0.006	0.006	457	-0.02	0.006	-0.98	0.33
NM	-0.02	0.005	457	-0.03	-0.008	-3.66	0.0003
Female	-0.001	0.006	457	-0.01	0.01	-0.21	0.83
Male	-0.02	0.005	457	-0.03	-0.01	-4.37	< 0.0001
Inter-pair	-0.003	0.005	457	-0.01	0.008	-0.5	0.62
Intra-pair	-0.02	0.005	457	-0.03	-0.009	-3.74	0.0002

29
 30 *Linear mixed models were applied on acoustical parameters of both rally calls and contact calls (lmer*
 31 *function from lme4 R package). A generalized mixed model was applied on the similarity index of the*
 32 *contact calls (glmmPQL function from MASS R package). Results were obtained with the emtrends*
 33 *function of R (from emmeans package).*