HAL

archives-ouvertes.fr

Impact of group size and social composition on group vocal activity and acoustic network in a social songbird

Marie Fernandez, Clémentine Vignal, Hédi Soula

▶ To cite this version:

HAL Id: hal-01537565

https://hal.archives-ouvertes.fr/hal-01537565

Submitted on 27 Jun 2017

Impact of group size and social composition on group vocal activity and acoustic network in a social songbird

M.S.A. Fernandez [1,2], C. Vignal [1,] H.A. Soula[2,3]

[1] Univ Lyon, UJM-Saint-Etienne, CNRS, Neuro-PSI/ENES UMR9197, France

[2] EPI BEAGLE INRIA, Villeurbanne, France

[3] INSERM U1060 INSA, Villeurbanne, France

Correspondence:

M.S.A. Fernandez

marieferndez@gmail.com

1 **Abstract**

2

3 In social species individuals living in the same group may synchronize activities such as

4 movements, foraging or anti-predator vigilance. Synchronization of activities can also be observed

5 between partners especially during breeding and can be crucial for breeding success.

6 Vocalizations are behaviours that can be coordinated between individuals, but simultaneous

7 vocalizations in groups have most of the time been considered as a noise that does not bear any

8 information.

9 Indeed little is known about the structure and function of vocal communications involving a network

10 of individuals. How the individual vocal activity participates in the resulting communal sound, and

11 in return how the group influences individual vocal activity, are questions that remain to be studied.

12 Zebra finches are social monogamous songbirds that form lifelong pair-bonds. In the wild, zebra

13 finches are typically found in small groups, with the pair as the primary social unit, and gather in

14 'social' trees where both females and males produce vocalizations. Here we investigated in the

15 laboratory the influence of group size and composition on general vocal activity and synchrony, as

16 well as the influence of pair-bond and spatial location on finer characteristics of

17 dyads vocal interactions. We used a set-up that locked the birds at fixed spatial positions of our

18 choosing to control the proximity network and allowed us an individual tagging of most of the

19 vocalizations. We used an in-house software suite that automatically detects vocalizations from

20 hours of passive recording.

21 We show that zebra finches groups synchronize their general vocal activity with waves of collective

22 vocalizations, which depend both on the group size and composition. The acoustic network is

23 shaped by pair-bonds at different time scales. Birds preferentially vocalize closely in time

24 (synchrony) or directly after (turn-taking) their partner when it is present and then the nearest

25 neighbour when the partner is not available.

26 # Introduction

In social species, many activities are synchronized between individuals living in the same group. Group members maintain group cohesion during movements and foraging (Agetsuma, 1995; Beauchamp, 1992; Blanc & Thériez, 1998; Blanc, Thériez, & Brelurut, 1999; Boyd & Bandi, 2002; Chivers, 1974; Conradt, 1998; Côte, Schaefer, & Messier, 1997; Daan & Slopsema, 1978; Gillingham & Klein, 1992; Linnane, Brereton, & Giller, 2001; McMahon & Evans, 1992; Rasmussen, 1985; Rook & Huckle, 1995; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2001; Saino, Fasola, & Waiyaki, 1995; Schenkeveld & Ydenberg, 1985; Tayler, 1953; Tremblay & Cherel, 1999; Wilson, Wilson, & McQuaid, 1986). Individuals may also coordinate activities such as anti-predator vigilance and feeding (Gerkema & Verhulst, 1990; Kavanagh, 1978; Rook & Penning, 1991). Activities can also be synchronized between partners of a pair. Pairs in many long-term monogamous species show an increase in their breeding success over time, and this could be attributed to a better coordination of partners (Black & Hulme, 1996; Forslund & Pärt, 1995). Partners can also coordinate foraging activities, and can synchronize their nest visits to feed the chicks (Bebbington & Hatchwell, 2015; Lee, Kim, & Hatchwell, 2010; Mariette & Griffith, 2012, 2015; van Rooij & Griffith, 2013). When both partners incubate, their hatching success can increase by synchronizing foraging trips (Coulson, 1966; Davis, 1988) or coordinating incubation bouts (Spoon, Millam, & Owings, 2006).

Vocalizations are behaviours that can be coordinated between individuals. Territorial songbirds vocally compete by answering each other, sometimes matching their song-types and using song-overlap as a signal of escalation (Langemann, Tavares, Peake, & McGregor, 2000). Some monogamous birds use coordinated vocal duets for territory defense, mate guarding, pair-bond maintenance (Farabaugh, 1982; Hall, 2004) or parental care (Boucaud, Mariette, Villain, & Vignal, 2015; Elie et al., 2010). Some group vocal productions have also been identified as organized signals bearing messages, like the communal vocalizations of some social mammals that communicate on spacing (Bornean gibbons, *Hylobates muelleri*, (Mitani, 1984); wolves, *Canis*

53 *lupus,* (Harrington & Mech, 1979); (Frommolt, 1999)) or group size (female lions, *Leo leo,*

54 (McComb, Packer, & Pusey, 1994). But most of the time, group vocal productions have been

55 considered as by-products of individuals' simultaneous but not necessarily coordinated

56 vocalizations. For example, this noisy sound can result from the activity of up to thousands of

57 individuals in choruses of birds (Burt & Vehrencamp, 2005), insects (Greenfield, 1994), frogs (M.

58 E. Bates, Cropp, Gonchar, & Knowles, 2010; Jones, Jones, & Ratman, 2009; Marshall, 2003;

59 Simmons, Bates, & Knowles, 2009), as well as in fish communities (D'spain & Berger, 2004;

60 Locascio, 2004; Locascio & Mann, 2005; Mann, 2003), colonies of nesting birds (Adret-

61 Hausberger, 1982; Mathevon, 1997) or breeding marine mammals (Schusterman, 1978; Southall,

62 Schusterman, & Kastak, 2003). This sound resulting from a group of individuals vocalizing

63 simultaneously has mainly been viewed as a source of noise pollution constraining the pairwise

64 communications (Aubin & Jouventin, 1998; Gerhardt & Klump, 1988). But this group sound with no

65 clear identifiable message might bear information on the structure of the underlying social

66 network (McGregor & Horn, 2014).

67

68 Not much is known about the structures and functions of vocal communications involving a

69 network of individuals. More specifically, little is known about the dynamics of pairs and group

70 vocal exchanges at an individual-level resolution. How the individual vocal activity participates in

71 the resulting communal sound, and in return how the group influences individual vocal activity, are

72 questions that remain to be studied. Yet, we know that the group, as a communication network, is

73 composed of several signalers and receivers sharing the same active signaling space, which

74 implies that it can interfere with pairwise vocal exchanges. Eavesdropping is defined as extracting

75 information from signaling interactions while not being the main recipient, and seems to occur in

76 many species (McGregor & Dabelsteen, 1996). In birds for example, it has been shown that

77 eavesdroppers can respond to vocal exchanges even if they were not part of it initially (Mennill,

78 Ratcliffe, & Boag, 2002). Audience effects show that the presence of other conspecifics can

influence a sender's behavior (Doutrelant, McGregor, & Oliveira, 2001; Evans & Marler, 1994; Hector, Seyfarth, & Raleigh, 1989; Matos & McGregor, 2002; Plath, Blum, Schlupp, & Tiedemann, 2008). The communication behaviour of male zebra finches can be modified by the individuals that are listening, and by the nature of the social relationships between them (Vignal, Mathevon, & Mottin, 2004).

The zebra finch (*Taeniopygia guttata*) is a social species native to Australia and is monogamous. This songbird forms lifelong pair-bonds (Zann, 1996), and partners are inseparable even outside of the breeding season. In the wild, zebra finches are usually found in small groups, and the pair is the primary social unit (McGowan, Mariette, & Griffith, 2015). This species extensively uses acoustic communication during social interactions: groups gather in 'social' trees near watering points or feeding areas (Zann, 1996) in which they produce a background sound composed of calls and songs. Some studies have started to focus on vocal dynamics in this species (Elie, Soula, Mathevon, & Vignal, 2011; Fernandez, Mariette, Vignal, & Soula, 2016; Gill, Goymann, Ter Maat, & Gahr, 2015; Perez, Fernandez, Griffith, Vignal, & Soula, 2015; Villain, Fernandez, Bouchut, Soula, & Vignal, 2016). Because of the amount of accumulated knowledge on both behavioral and neurobiological aspects of its acoustic communication, the zebra finch is an interesting model to study communal vocalization and its relation to the social structure of the group.

Here we hypothesized that the organization of group vocal activity might reveal some aspects of group structure, such as group size and composition. Using the zebra finch as a study species, we investigated the impact of group size and composition on proxies of the group vocal activity and synchrony. We also tested the influence of pair-bonds and spatial location on finer characteristics of dyads vocal interactions. One common difficulty encountered when studying an acoustic network is to determine the identity of the caller and thus to obtain an individual tagging of vocalizations. Also, when we want to assess the acoustic network it might be relevant to control

105 the spatial proximity between individuals. To overcome both of these issues we used a set-up that

106 first locked the birds in a fixed spatial network of our choosing and allowed us an individual tagging

107 of all vocalizations. We used an in-house software suite that automatically detects vocalizations

108 from hours of passive recording. Our setup also allows for an automatic removal of non-

109 vocalizations (wings or cage noise) using classification.

110 We built groups of identical sex-ratio but that varied in group sizes and social structures

111 (percentage of paired / unpaired birds). We recorded these groups' vocal activity during several

112 hours on several days, and analyzed the vocal sequences resulting from these recordings.

Materials and Methods

Subjects and Housing Conditions

We used 88 adult zebra finches (*Taeniopygia guttata*) in this study: 44 males and 44 females. All birds came from our breeding colony. Before the experiment, unpaired males and unpaired females were housed with individuals of the same sex, and female-male pairs were housed separately in cages (all cages dimensions: 40 X 40 X 40 cm) equipped with perches and a pool for environmental enrichment. All birds were kept under the same environmental conditions: temperature between 24 and 26 °C, light conditions of 14:10 h light-dark, water, seeds and cuttlefish bones ad libitum and supplemented with salad once a week. As zebra finches are opportunistic breeders, all conditions were reunited for them to breed (water restriction is needed to be in non-breeding condition (Prior, Heimovics, & Soma, 2013). However they did not have access to nest material so they were not breeding at the time of the recording.

Recording Protocol

The experiment took place from March to May 2014 and from January to February 2015. The day before the experiment, each bird was moved from the rearing room to the experimental room (sound attenuating chamber, 2.22 m height x 1.76 m width x 2.28 m length, Silence Box model B, Tip Top Wood, France) and was placed in a cage (40 X 40 X 25). Microphones (Audio Technica AT803), connected to a recorder (zoom R16), were placed on top of each cage, above the head of the bird and facing downwards, which is the best position to minimize the variability in vocalization amplitude due to the orientation of the bird's head, and thus maximize vocalization detection (Brumm & Zollinger, 2011). On each recording day, we recorded vocal exchanges during a long period (three to six hours between 10 am and 4 pm).

138

Group Composition

140

We recorded 35 groups of different sizes (two, four, or eight individuals) and different social compositions (0%, 50%, or 100% of paired birds). Table 1 gives the number of recorded groups per group size and composition, as well as the number of repetitions for each group, and the total number of hours of recording for each combination. We organized the cages so that all birds can be in visual contact with each member of the group (Figure 1). We defined the distance between two birds as one if the two birds' cages were neighbour, two if the two birds' cages were separated by one cage, etc. Pair mates were always put in neighbouring cages to reduce stress. In 4-bird groups, two males were always located in diagonal and two females in diagonal. In 8-bird groups, the positions of males and females were defined at random.

150

Vocalization Extractions

Vocalizations were extracted from recordings using in-house softwares. These programs were written in python (www.python.org) by authors H.A.S. and M.S.A.F using open-source libraries. Briefly, vocalization detection consisted of a pipeline of five stages. The first process was a simple threshold-based sound detection based on a high-pass filtered energy envelope (1024 samples FFT; 441 Hz sampling; cut-off frequency: 500Hz). During the second stage, each event above the threshold was reconstructed in order to maintain an amplitude range of 90% compared to the maximum amplitude. Thus, each event was either lengthened or shortened to obtain the same amplitude range during the event. This technique allows a good estimate of a vocal event's duration. The third stage simply merged overlapping event segments. Together, the three first stages produced start, end, and duration values for each sound event detected in the recording. The accuracy of these three first steps was tested in (Elie et al., 2011).

163 The fourth stage removed double vocalizations - vocalizations produced by one bird and recorded

164 by its microphone but also recorded by the microphones of all other birds of the group - by using

165 energy and delay differences: to attribute a vocalization to a bird, our program detects

166 vocalizations for each microphone. Then we apply the following algorithm: for each vocalization A

167 (start=sA, end=eA) we look if other vocalizations were detected at the same period in other

168 microphones. If for a vocalization B (start = sB) we have sB>sA but sB<eA (B is starting after A but

169 is overlapping A) we look if the energy of vocalization B is higher than the energy of A. If this is the

170 case we keep both vocalizations. If not, we remove B (because B is likely to be A recorded in

171 another microphone). We do this for all vocalizations by eliminating them and/or associate them

172 with a track (hence a bird). Thus, when a vocalization was produced without overlap with another

173 vocalization, our program has a success rate of 100 % (see corresponding tests in supplementary

174 figure 1, a human listener would make more mistakes because the time delay between two

175 microphones is very low, i.e. few milliseconds). The main problem occurs when a vocalization B

176 overlaps a vocalization A (sB<eA), and when B is weaker on its microphone B than A is on the

177 microphone A. In that case our program considers that B is the same vocalization as A, and thus

178 the vocalization B is lost. We have quantified this type of error. The overlapping vocalizations

179 represent around 11% of the total number of vocalizations. We have a 46% error rate on

180 overlapping vocalizations, i.e. the software makes a mistake when attributing the overlapping

181 vocalizations in 46% of the cases (percentages computed over 1200 vocalizations over eight

182 randomly chosen groups). Thus the errors due to overlapping vocalizations increases the final

183 error rate by 5%.

184 This step effectively tagged uniquely each sound event to an individual. The fifth and last stage

185 removed cage or wings noises using a machine learning process. We trained a supervised

186 classifier using a data set composed of 4500 random extracted sounds from all of our data. Each

187 sound was classified by one expert (M.S.A.F.) as "vocalization" or "non- vocalization". The

188 classification was performed on the spectrogram of the sounds reduced to 50ms: the idea was to

189   reduce the quantity of information in term of time and frequency, and sample this information in

190   such a way that we got the same amount of information for each vocalization (short or long). The

191   spectrogram matrix was first reduced to the frequencies of interest – between 500Hz and 6kHz.

192   Then two cases appeared: if the vocalization duration was longer than 50 ms, we extracted 50 ms

193   in the middle of the sound event. If duration was lower than 50 ms, we padded with zero to obtain

194   a 50ms sound event with the relevant event in the middle. The spectrogram was then flattened to

195   obtain a one dimensional vector. We trained a Random Forest classifier (Breiman, 2001) using

196   1500 sounds as a training set. The validation set was composed of the remaining 3000 sounds.

197   This classifier had an overall rate of error below 10%.

198

199   Our vocalization extraction yielded over 1,730k vocalizations (840k for females and 890k for

200   males) over a total of 441 hours of recording. Supplementary Figures 2(a) and 2(b) show the

201   histograms of vocalization durations for all extracted vocalizations for each sex. These distributions

202   are composed of two modes that likely represent the two main types of vocalizations produced by

203   zebra finches in this context (Zann, 1996): distance calls i.e. the longer and louder calls given by

204   zebra finches, consisting of a harmonic series modulated in frequency as well as amplitude, and

205   tet or stack calls i.e. softer and shorter calls than distance calls, around 50ms (Zann, 1996). Song

206   syllables are also represented in this histogram because they could not be removed from the

207   dataset (see above). We estimated several parameters of the distribution using a sum of two

208   Gaussians:

$$P(d) \ = \ a \, N(\mu_1, \sigma_1^2) \ + \ (1-a) \, N(\mu_2, \sigma_2^2)$$

209   where $N(\mu, \sigma^2)$ is the normal Gaussian distribution with mean μ and variance σ^2. The fit was made

210   on the duration histogram (time step=10ms on 0-1s interval) with the least square method.

211   Note that individual song syllables (for males) are not discriminated in one category and can be of

212   any duration. Female and male short calls (tet or stack) have similar duration (first mode at 52 ms).

213 Consistent with the literature, distance calls are shorter in males (120 ms) compared to females

214 (149 ms) (Supplementary Table 1).

215 Because we were interested only in the dynamic of the vocal exchanges, we decided to pool all

216 vocalizations types together in the following analyses.

217

218 *Data Analysis*

219

220 We separated the analysis into four parts described below: general vocal activity and

221 vocalization rate autocorrelation (analysis of long-term vocal dynamics), and the dyads cross-

222 correlation and turn-taking transitions analysis (analysis of short-term vocal dynamics).

223

224 *General vocal activity*

225 We computed the main vocal activity metrics namely the number of vocalizations per time unit for

226 each individual. We also defined a burst as a period where the total vocal activity (for all individuals

227 in the group) was 10% higher than the average vocal activity (taken on the whole recording day).

228 To find the bursts we split the time into six minutes bins with an overlap of one minute. Thus, a

229 burst could not last less than 5min. We then analyzed the number of bursts per hour and the total

230 vocalizations rate in bursts only.

231

232 *Vocalization rate autocorrelation*

233 The vocalization rate autocorrelation gives information about the presence of cycles in the group

234 general vocal activity. For example, it could tell if the variation of vocalization rate presents

235 patterns over time, i.e. waves of collective vocalizations.

236   We split the time into 180s bins (3min) with an overlap of 90s (1min30) and counted the total

237   number of vocalizations in each bin. We then computed the autocorrelation AC(T) of this signal

238   with the following formula:

239    $ac(T) = mean[(S(t) - mean(S))(S(t+T) - mean(S))]$,

240   with the normalization step we have: $AC(T) = ac(T)/ac(0)$. t is the time bin number, S(t) is the total

241   number of vocalizations in the bin t, and T is the time lag value, between 0 and 80 min.

242   A peak at time T in the autocorrelation curve means that the vocalization rate activity presents a

243   cycle of duration T.

244

245   *Cross-correlation*

246   We assessed the vocal temporal synchrony between two birds by computing the cross-correlation

247   at T=500 ms. To do that we split the time into 500 ms bins, and each bird signal was one if the bird

248   vocalized within this period, and zero if not. We computed the cross-correlation (CC(T)) of the two

249   birds' signals with the following formula:

250    $cc = mean[(S_{bird1}(t) - mean(S_{bird1}))(S_{bird2}(t) - mean(S_{bird2}))]$,

251   with the normalization step we have: $CC(T) = cc(t) / (SD(S_{bird1})* SD(S_{bird2}))$

252   Where S_{bird1} and S_{bird2} the two birds vocal signals as functions of t (time).

253   For each day of recording we computed cross-correlations for all possible dyads of birds. Two

254   birds having a high cross-correlation value were two birds that were regularly vocalizing closely in

255   time together (within 500ms).

256   We compared cross-correlation between paired/unpaired and neighbour/non-neighbour birds.

257

258 *Turn-taking transitions probability*

259 In this analysis, we kept only the sequence of callers' identity (without temporal aspect), i.e. the

260 turn-taking. Vocal sequences were obtained with the caller's identity in their order of vocalizing

261 (e.g. ABCA was a sequence of four vocalizations, produced successively by the bird A, then bird

262 B, bird C and finally bird A). We compared the mean transition probabilities for each dyad of birds:

263 between bird A and bird B, the mean transition probability is (prob(A->B)+prob(B->A)) / 2. We

264 compared this measure between paired/unpaired and neighbour/non-neighbour birds.

265

266

267 ## *Statistics*

268 All statistical tests were performed using R software (R Core Team, 2014). Linear mixed models

269 were built with the lmer function ('lme4' R package (D. Bates, Maechler, Bolker, & Walker, 2014))

270 and generalized mixed models were built with the glmer function ('lme4' R package). Models

271 outputs from Anova ('car' library) and summary functions are presented.

272

273 *Model validation*

274 Before being interpreted each model was checked, paying particular attention to their residuals.

275 For models with Poisson family, overdispersion was tested, and if the model presented

276 overdispersion we used a negative binomial model. The model validity was also checked with the

277 plotresid function from the 'RVAideMemoire' package before interpreting the model results. When

278 possible, the variance of the data explained by the models was quantified and a conditional

279 coefficient of determination was calculated with 'r.squaredGLMM' function ('MuMIn' R package).

280

281 *Model selection*

282 We chose to build biologically relevant models and we kept the full model as recommended by

283 Forstmeier & Schielzeth (2011).

284 *Model estimates and confidence intervals*

285 When possible we added information about the quantification of the biological effect given by the

286 models. Confidence intervals were computed with the "confint.merMod" function of the lme4

287 package, with the Wald method.

288

289 *Vocal activity*

290   -   Number of vocalizations

291 We chose to use the number of vocalizations (NVoc) as the response variable (seen as a count)

292 and we added the recording duration (RecordingDuration) as an offset because all recordings did

293 not last the same time. It was not possible to test the interaction between the group size

294 (GroupSize) and the percentage of pairs in the group (PercentPair) because by definition we did

295 not have a complete crossover design. The other interactions were tested because they were

296 biologically relevant (BirdSex * GroupSize and BirdSex * PercentPair). As a bird could be recorded

297 in several groups, we added the random factor GroupID/BirdID (group identity / bird identity),

298 which took into account the group and the bird in the group. We also had repetitions of recording

299 for each group so we added the repetition number (RepetitionNb) as a random factor:

300 NVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair),

301   random=GroupID/BirdID, RepetitionNb

302

303 We used a negative binomial model as the model using a Poisson distribution presented over-

304 dispersion. The interaction between BirdSex and GroupSize was significant, so we separated the

305 dataset into three subsets (for the three group sizes).

306

307   -   Number of bursts: We counted the number of bursts and tested the influence of the group

308   size and percentage of pairs on this metric. We built a generalized Poisson model with the

309   recording duration as offset. As for the previous model, it was not possible to test the

310   interaction between the percentage of pairs and the group size because we did not have a

311   complete crossover design. The random factors were the group identity and the repetition

312   number.

313 NumberOfBurst ~ offset(log(RecordingDuration)) + GroupSize + PercentPair, random=GroupID,

314 RepetitionNb

315

316   -   Vocalization rate in bursts: We measured the overall vocalization rate in the bursts (for each

317   burst, the vocalization rate was the total number of vocalizations produced by all individuals

318   divided by the duration of this burst). We tested the influence of the group size and

319   percentage of pair. We built a mixed linear model, and as for the previous model, it was not

320   possible to test the interaction between the percentage of pairs and the group. The random

321   factors were the group identity and the repetition number.

322

323 VocRateBurst ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

324

325 Vocalizations *rate autocorrelation*

326 We looked at the difference in the time lag of vocalization rate autocorrelation between different

327 group compositions (0%, 50%, 100% of pairs). We detected the secondary maximum peak of each

328 curve from each recording session (the first peak is at 0). For that we used the function

329 'find_peaks_cwt' from the 'signal' python library. We built the following model for each group size:

330 AutocorrelationTimeLag ~ PercentPair random=GroupID, RepetitionNb.

331

332 *Cross-correlation*

333   We first build the following general model:

334   CrossCorr ~ GroupSize + PercentPair + Paired, random=GroupID, RepetitionNb, Bird1, Bird2.

335   Explanatory variables had different number of levels depending on group size: the distance

336   between two birds was always 1 for the 2-bird groups, it was either 1 or 2 for the 4-bird groups,

337   and it could be 1, 2, 3, or 4 for the 8-bird groups. Also, the percentage of pairs could only be tested

338   in the 4-bird and 8-bird groups. We thus decided to split the dataset into three sets (one for each

339   group size).

340   We built the following mixed linear models. The variable Paired was "yes" if the bird was paired

341   with another bird in the group, and "no" otherwise. The random factors were the group identity, the

342   repetition number, and the two birds' identities.

343

344   Group size=2: CrossCorr ~ Paired, random=GroupID, RepetitionNb, Bird1, Bird2.

345

346   Group size=4: We could not test the interaction between the Paired and Distance variables,

347   because pairs were always at a distance of 1. It was also not possible to test the interaction

348   between Paired and PercentPair because in groups with 100% of pairs, all birds were paired, and

349   the opposite in groups of 0% pairs.

350   CrossCorr ~ PercentPair + Paired + Distance + PercentPair:Distance,

351   random=GroupID, RepetitionNb, Bird1, Bird2.

352

353   Group size=8: The model structure was the same as for the 4-bird groups model above.

354   CrossCorr ~ PercentPair + Paired + Distance + PercentPair:Distance,

355   random=GroupID, RepetitionNb, Bird1, Bird2.

356

357   We build a second model that included only the data from distance = 1:

358   CrossCorr ~ PercentPair * Paired + SameSexDyad + SameSexDyad:Paired,

359 random=GroupID, RepetitionNb, Bird1, Bird2

360 The variable SameSexDyad is 'yes' if the corresponding dyad is two females of two males, and 'no'

361 if the corresponding dyad is one male and one female.

362

363

364 For the 8-bird groups, the interaction between PercentPair and Distance was significant. We

365 focused on groups with 50% and 100% of pairs in order to test the interaction between PercentPair

366 and Paired:

367 CrossCorr ~ PercentPair * Paired + Distance + PercentPair:Distance,

368 random=GroupID, RepetitionNb, Bird1, Bird2

369

370

371 *Turn-taking transitions probability*

372 We compared the mean transition probabilities between paired/unpaired and neighbours/non-

373 neighbours dyads of birds. As all pairs were set up as neighbours, we had only three possibilities

374 for each dyad of birds in a group with these parameters: UnPaired and NonNeighbour, UnPaired

375 and Neighbour, Paired and Neighbour. As the intrinsic random probability of jumping from a caller i

376 to a caller j depended on the group size (1/4 for 4-bird groups and 1/8 for 8-bird groups), we

377 studied separately the different group sizes. We had not enough data to compute this metrics on

378 the 2-bird groups. We used the following model for 4-bird and 8-bird groups:

379 MeanTransitionProba ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

380 with PairedNeighb a variable with the three possible levels: UnPaired and NonNeighbour,

381 UnPaired and Neighbour, Paired and Neighbour.

382

383

384 **Results**

Effect of Group Size and Composition on Long-Term Vocal Dynamics

Individual vocalization rate and burst vocalization rate increase with group size

The group size had an effect on the individual vocalization rate: each bird vocalized more when in a larger group. The individual vocalization rate in 8-bird groups was 1.57 times [1.09;2.27] higher than the individual vocalization rate in 2-bird groups. The individual vocalization rate in 4-bird groups was intermediate between the 2-bird and 8-bird groups, but the differences between the 8-bird vs 4-bird and 4-bird vs 2-bird groups were not significant (Figure 2a, Table 2).

The number of bursts was higher in large groups than in small groups. The number of bursts was 1.27 times [1.03;1.55] higher in 4-bird groups than in 2-bird groups, and 1.47 times [1.22;1.80] higher in 8-bird groups than in 2-bird groups (Figure 2b, Table 3). The overall vocalization rate in bursts was also higher when the group size increased (Figure 2c, Table 3).

Individual vocalization rate decreases when the percentage of pairs increases in the group.

In 8-bird groups, we found that the percentage of pairs had an effect on the individual vocalization rate: the individual vocalization rate was lower in groups composed of 100% of pairs than in groups composed of unpaired birds only. In 8-bird groups, the individual vocalization rate was 1.35 times [1.01;1.82] lower in 100% pairs groups than in 0% pairs groups (Figure 3a, Table 2).

Waves of collective vocalizations have shorter cycles in groups only including unpaired birds

407 A peak at time T on the autocorrelation curve means that the vocalization rate activity presents a

408 cycle of duration T. Groups' compositions (0%, 50%, 100% of pairs) were compared at different

409 time lag T (Figure 3b for 8-bird groups, Table 4).

410 In 8-bird groups, the vocalization rate autocorrelation in 0% pairs groups presented a peak at

411 around 36min +/- 13min (mean +/- sd). In 50% pairs groups, the peak was around 46 min +/- 14

412 min, and in 100% pairs groups the peak was around 61min +/- 15min. The time lag tended to be

413 significant between 0% and 100% pairs groups (Figure 3b, Table 4), suggesting that 0% pairs

414 groups had shorter cycles of collective vocalizations than 50% and 100% pairs groups.

415

416 In 4-bird groups, the vocalization rate autocorrelation in 0% pairs groups presented a peak at

417 around 47min +/- 15min (mean +/- sd). In 50% pairs groups, the peak was around 58 min +/- 13

418 min, and in 100% pairs groups the peak was around 60min +/- 11min. We found no significant

419 difference between groups (Figure 3b, Table 4).

420

421 **Effect of Pair-Bonds and spatial proximity on Short-Term Vocal Dynamics**

422

423 *Vocal synchrony is higher within pairs and decreases with the distance between*

424 *individuals*

425 We compared cross-correlation between paired/unpaired and neighbour/non-neighbour birds. Two

426 birds showed a high cross-correlation value if they usually vocalized (or stayed silent) closely in

427 time (within 500ms) (i.e "vocal synchrony"). The full model showed no effect of group size or

428 percentage of pairs on dyads' cross-correlation (Table 5). We then split the dataset by group size

429 (see Methods). First, in 2-bird groups, paired and unpaired birds did not differ in cross-correlation

430 (Table 5, Figure 4a). In 4-bird groups, the cross-correlation of a dyad was significantly higher if the

431 birds were paired, and decreased with the distance (Figure 4b, Table 5). There was no effect of

432 the percentage of pairs in 4-bird groups. Finally, in 8-bird groups, the cross-correlation also

433 decreased with the distance (Figure 4c). At distance = 1, the cross-correlation between two paired

434 birds was higher than between two unpaired birds (unpaired female/male dyads or same sex

435 unpaired dyads, Supplementary Figure 3, Table 5). The cross-correlation between two paired birds

436 was lower in groups composed of 50% of pairs than in groups composed of 100% of pairs (Table

437 5, Figure 4d). The detailed results on the cross-correlation for each group of 8 birds with 100% of

438 pairs are presented in Supplementary Figure 4.

439

440 *Turn-taking transitions probability is higher within pairs, and is higher between*

441 *neighbours.*

442 We compared the mean transition probabilities between two birds when paired/unpaired and

443 neighbour/non-neighbour. Two birds showed a high mean transition probability if they usually

444 vocalized one after the other. Figure 5 shows the distributions of mean transition probabilities

445 between two birds (paired/unpaired and neighbour/non-neighbour). For both group sizes (4 birds

446 and 8 birds), the mean transition probabilities were higher for UnPaired – Neighbour birds than for

447 UnPaired – NonNeighbour, and even higher for Paired – Neighbour birds. In other words, two

448 paired birds were more likely to vocalize one after the other than two unpaired birds. Within the

449 unpaired birds, two neighbour birds were more likely to vocalize one after the other than two non-

450 neighbour birds. The statistical results are presented in Table 6.

Discussion

In this article, we showed that the organization of group vocal activity reveals some aspects of group structure (such as group size and composition) and group acoustic network. On a long-term scale (several minutes to an hour), zebra finches groups synchronize their general vocal activity with waves of collective vocalizations that increase with group size and whose cycles' duration increases with the percentage of pairs in the group. We also showed that the group influences individual vocal activity, with individual vocalization rates increasing with group size and decreasing with the percentage of pairs in the group. On a short-term scale (a few seconds), acoustic interactions are shaped by pair-bonds and distance, as birds preferentially vocalize at the same time (synchrony) or directly after (turn-taking) their partner when it is present, and the nearest neighbour when the partner is not available.

Our setup allowed automatically detecting and extracting vocalizations from hours of passive recording depicting a 'basal' social situation. Our system is able to extract a lot of individual vocalizations (a bit less than 2M for all experiments combined) with individual tagging. We retrieved a bimodal distribution of duration (well predicted by a sum of two Gaussian) that may relate to the two main types of calls uttered in that context: tets/stacks and distance calls (as well as song syllables).

First, on a long-term scale (several minutes to an hour), we saw that large groups have a higher burst rate, and a higher vocal activity within these bursts. This bursting activity can be compared to other waves of collective behaviour (G. Fernandez, Capurro, & Reboreda, 2003; Pays et al., 2007). For example, in Defassa waterbuck, (*Kobus ellipsiprymnus defassa*), waves of collective vigilance against predators emerge from group members synchronizing scanning and non-scanning bouts and are triggered by allelomimetic effects, i.e. each individual copying its

477 neighbour's behaviour (Pays et al., 2007). Focusing on a short-term scale (a few seconds), we

478 saw that neighbouring birds are more likely to vocalize together within a short time window and

479 one after the other. Some individuals could initiate bursts and then neighbours would vocalize as

480 well, triggering waves by an allelomimetic effect. With this hypothesis, the higher bursting activity

481 observed in large groups would be the consequence of the observed increase of the individual

482 vocalization rate. This could be due to a driving effect, because in larger groups there are more

483 individuals to interact with. In killer whales (*Orcinus orca*), an increase of the production of some

484 vocalization types has been described during socializing and beach-rubbing activities, also

485 corresponding to periods when the group size increases (Ford, 1989). In savanna elephants

486 (*Loxodonta africana*), it has been shown that the group vocal activity increases when the group

487 size increases (Payne, Thompson, & Kramer, 2003).

488 One alternative hypothesis to the allelomimetic effect would be that group members exchange

489 information during group vocal interactions. In black-capped chickadees (*Poecile atricapillus*),

490 dawn choruses can be seen as an interactive communication network. In a recent study, males'

491 dawn chorus singing behaviour was examined by determining the level of song frequency

492 matching between neighbours: male black-capped chickadees were observed having a high level

493 of matching with their neighbours and they also match other individuals simultaneously and

494 sequentially (Foote, Fitzsimmons, Mennill, & Ratcliffe, 2010).

495 If allelomimetic effects structure group vocal activity, the bursting activity of the group would

496 correlate with the mean individual vocalization rate in the group. To test this prediction, recordings

497 on more groups are needed. On the other hand, if group vocal activity is an information exchange,

498 the group would display strategies to maintain communication efficacy in response to noise. To

499 test this prediction, recordings of groups subjected to background noise playbacks and measures

500 of the response of the group vocal dynamics are needed.

501 As highlighted above, in our study two birds at short distance are more likely to vocalize together

502 (or stay silent together) within a short time window, but this is even more likely if they are paired. In

503 4-bird groups, neighbour birds were always one male and one female, thus we cannot conclude if

504 the difference of cross-correlation observed is due to the distance or to the intersexual nature of

505 the dyad. Also, we chose to put pairs in neighbour cages to avoid the stress of separation. This is

506 why we could not test whether pairs would show the same behaviour when at longer distance.

507 However the results show that unpaired birds being located at short distance are less likely to

508 vocalize together within a short time window than paired birds at this same distance. In many

509 taxonomic groups, a likely candidate for directing signals to a specific individual is relative signal

510 timing, that is, close temporal association (McGregor, Otter, & Peake, 2000; Naguib, 1999). In

511 African elephant (*Loxodonta africana)*, it has been shown that females are more likely to produce

512 rumbles shortly after rumbles from other group members. Also, an affiliative relationship with a

513 caller has a strong influence on the probability of a rumble response, whereas the relative

514 dominance rank and reproductive state has no effect (Soltis, Leong, & Savage, 2005). Another

515 study showed that in Squirrel Monkeys (*Saimiri Sciureus*), mutually preferred partners exchange

516 chucks more often and with shorter latencies of response than other individuals (Biben, Symmes,

517 & Masataka, 1986). This result is also consistent with recent studies on zebra finches groups: Ter

518 Maat et al. (2014) show that paired males and females recorded in groups communicate using

519 bilateral stack calling, Gill et al. (2015) show that zebra finches calls occur non-randomly in vocal

520 interactions. Also, Stowell et al. (2016) developed a model that reflects fine details of zebra finches

521 vocal interactions networks, and that especially models the timing and influence strengths between

522 individuals in a group. They showed that within-pair vocal interactions were dominant in the group

523 calling network.

524 The analysis of the transition probabilities between callers also shows that two birds at short

525 distance were more likely to vocalize one after the other. This result on the preferred turn-taking is

526 even stronger if birds are paired. Studies on mammal and bird species with different levels of

527 social coordination show that the social structure of the species relate to different dynamics in their

vocal interactions. A recent study shows that in the European starling, the direct and general social context, as well as the individual history, and the internal state of the caller can influence the dynamics of vocalizations in time and structure (Henry, Craig, Lemasson, & Hausberger, 2015). In our study, we set up the cages in a way that each bird was able to see the whole group, but it was perhaps less easy for a bird to get the visual signals from a bird located far away. If neighbour birds could exchange more visual signals, they might be more likely to answer each other's vocalizations. In human conversation, changes in gazing is one of the signs used to guide conversational turn-taking (Gérard, 1987; Hauser, 1992).

The vocalization rate was lower for the 8-bird groups containing only paired birds than for 8-bird groups containing only unpaired birds. This is consistent with a previous study (Elie et al., 2011) that described zebra finch groups' communal vocalizations (without identification of the callers). Birds involved in a pair-bond could answer preferentially to their partner and less to other members of the group. On the contrary, unpaired birds would have no initial preference and would interact with more birds in the group ("driving effect" suggested above).

Additionally, the autocorrelation analysis showed that the vocal cycling pattern differed with group composition. Groups of eight unpaired birds have shorter cycles that peak around 36min, with a more consistently cycling activity. This is consistent with the previous study from Elie et al. (2011) showing that groups of zebra finches comprising less pairs had shorter vocal cycles.

In larger groups, pairs were more likely to be vocally synchronized in groups containing only pairs than in groups also containing unpaired birds. This could be explained by the fact that, in groups containing unpaired birds, more birds are available for interaction, whereas in groups containing only pairs, each bird may be busy interacting with its own partner as suggested above (Biben et al., 1986; Soltis et al., 2005).

553 This last result is not observed in intermediate group sizes. One reason could be that 4-bird groups

554 with 50% of pairs are actually composed of one unique pair, one unpaired male and one unpaired

555 female. The number of unpaired birds potentially available is thus smaller than in 8-bird groups of

556 50% of pairs (composed by two pairs, two unpaired females and two unpaired males).

557 For this same metric, groups of two birds showed no difference between paired or unpaired birds.

558 In these dyads, birds had only one other individual to interact with. Because zebra finches are

559 gregarious birds that use vocal interactions to find and keep social contact (Perez, Fernandez,

560 Griffith, Vignal, & Soula, 2015; Zann, 1996), they might interact with whoever is available when

561 placed in dyads.

562 In this study we decided to keep all vocalizations types together because among all vocalizations

563 types that zebra finches can produce, in the conditions of our experiment (non-breeding birds and

564 cages at short distances) only three of them were produced: tets, distance calls and songs with a

565 clear bimodal distribution of durations. Separating vocalizations according to duration did not

566 change our results. However it would probably be interesting to study the vocal dynamics by

567 separating the different vocalization types, because the dynamic of vocal exchange could change

568 according to call type, as suggested by (Gill et al., 2015).

569 Also, constraining the birds in one location can be seen as a limitation. Using this protocol we are

570 able to study the acoustic network by constraining the position (in addition to be able to tag

571 individual vocalization more easily). Of course, these position constraints will affect calling

572 dynamics and cannot describe neither situations like group gathering in a social tree, nor

573 interaction contexts like agonistic or physical affiliative behaviours, foraging, etc. So, constraining

574 the spatial position of individuals may have direct and indirect effects on vocal dynamics (Elie et

575 al., 2011). A recent study used devices mounted on the birds to assign vocalizations in bird groups

576 (Gill et al., 2015). This method allows for the study of free-ranging networks of birds in different

577 contexts (agonistic and affiliative behaviours, foraging, and different breeding conditions), and has

578   the advantage of investigating the calling behaviour of birds behaving freely in a social group.

579   However, it does not give the spatial position of each bird, which can also have an impact on the

580   vocal dynamics. New technologies need to be explored to be able to control for these different

581   aspects at the same time.

582   Here we show that zebra finches groups synchronize their general vocal activity with waves of

583   collective vocalizations, which depend on group size and group composition. Furthermore, at a

584   finer level we show that the group vocal activity is structured by the presence of pairs in the group.

585   Thus we demonstrate that from the acoustic network measured at the individual level we can

586   extract information about the social network.

587

588

Figures legends

590

Figure 1: Schematic of the protocol.

Groups of 2, 4, and 8 birds were built, with one bird per cage and one microphone on the top of each cage. Pair mates were put in neighbour cages to reduce stress (distance=1).

594

Figure 2: Impact of group size on long-term vocal dynamics (a) Effect of group size on individual vocalization rates. (b) Effect of group size on burst rate (number of bursts per hour). (c) Effect of group size on vocalization rate in bursts. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end. *: $P<0.05$, **:$P<0.001$, ***:$P<0.0001$

603

Figure 3: Impact of the percentage of pairs on the long-term vocal dynamics

(a) Effect of group composition (0%, 50%, and 100% of pairs in the group) on individual vocalization rates in 8-bird groups. (b) Autocorrelation of the number of vocalizations (time step=3min, overlap=1.5min). Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end.. *: $P<0.05$

612

Figure 4: Vocal cross-correlation between two birds

(a) Effect of pair-bonds on cross-correlation in 2-bird groups, (b) Effect of pair-bonds and distance (1, 2) on cross-correlation in 4-bird groups, (c) Effect of pair-bonds and distance (1, 2, 3, 4) on cross-correlation in 8-bird groups, (d) Effect of pair-bonds and group composition (% of pairs) on cross-correlation in 8-bird groups. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end. *: $P<0.05$, **:$P<0.001$, ***:$P<0.0001$.

Figure 5: Vocal transition probabilities between two birds

Distribution of the average vocal transition probability in (a) 4-bird groups, (b) 8-bird groups. *: $P<0.05$, **:$P<0.001$, ***:$P<0.0001$.

Supplementary Figure 1: **Detection and attribution of calls to individuals.** We tested the detection and attribution of vocalizations to individuals in the three possible positions of a bird in the room (i.e. one angle and two edges, the remaining cages being symmetrical). We put one bird in a cage and recorded it, and repeated the recording in the three possible positions. We had a success rate of 100% over 240 calls produced (containing tets/stacks and distance calls). The figure provides the sonograms (in green/yellow) and oscillograms (in red) from the 8 microphones for two examples of vocalizations.

Supplementary Figure 2: **Histograms of all female and male vocalizations' durations of this study.** (a) Female vocalizations' durations, (b) Male vocalizations' duration. Tets/stacks and distance calls were detected (resp. first and second peaks) for each sex. Songs were also automatically detected but split so each syllable was considered as a vocalization.

640

Supplementary Figure 3: **Vocal cross-correlation between two birds at distance 1 in 8-bird groups.**

Effect of sex and pair-bond on cross-correlation at distance 1 in 8-bird groups. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end. NS: non-significant, ***: P<0.0001.

Supplementary Figure 4: **Acoustic networks for each group in 8-bird groups with 100% of pairs.** Nodes are individuals (P_i states for individual in pair i). Edges thickness is an affine function of the average vocal cross-correlation on the four recording days for each dyad.

Tables legends

Table 1: Number of groups for each social composition

For each group size and composition, we give the number of groups recorded (i.e. groups with different birds, X= impossible group social composition). In brackets is the number of recording days for each group. The third element is the total number of hours recorded for each combination.

Table 2: Statistical results of the impact of group composition on individual vocal activity.

The full model is presented. Then each group size is analyzed separately and each model is provided. NVocN stands for the number of vocalizations in groups of N birds.

R^2_c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

666   from the summary of the model.

667

668   **Table 3**: Statistical results of the impact of group composition on bursts activity

669   R^2c value, which represents the conditional coefficient of determination of the model, is indicated

670   for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

671   from the summary of the model.

672

673   **Table 4**: Statistical results of the impact of group composition on the autocorrelation of the number

674   of vocalizations over time

675   R^2c value, which represents the conditional coefficient of determination of the model, is indicated

676   for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

677   from the summary of the model.

678

679   **Table 5**: Statistical results of the impact of group composition on vocal cross-correlation

680   The full model is presented. Then each group size is analyzed separately and each model is

681   provided. CrossCorrN stands for the cross-correlation values in groups of N birds.

682   R^2c value, which represents the conditional coefficient of determination of the model, is indicated

683   for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

684   from the summary of the model.

685

686   **Table 6**: Statistical results of the impact of group composition on vocal mean transitions

687   probabilities.

688   Groups with four and eight birds are analyzed separately, and each model is provided.

689   MeanTransitionProbaN stands for the mean transition probability values in groups of N birds.

690   R^2c value, which represents the conditional coefficient of determination of the model, is indicated

691   for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

692   from the summary of the model.

693

694

695   **Supplementary Table 1:** Results on the estimation of vocalization duration parameters.

696   We used a sum of two Gaussians and the fit was made on the duration histogram (time

697   step=10ms on 0-1s interval) with the least square method.

698

References

Adret-Hausberger, M. (1982). Social influences on the whistled songs of starlings. *Behavioral Ecology and Sociobiology*, *11*(4), 241–246. https://doi.org/10.1007/BF00299300

Agetsuma, N. (1995). Foraging synchrony in a group of Yakushima macaques (Macaca fuscata yakui). *Folia Primatol*, *64*, 167–179.

Aubin, T., & Jouventin, P. (1998). Cocktail-party effect in king penguin colonies. *Proc. R. Soc. Lond. B*, *265*, 1665–1673.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7*. Retrieved from URL: http://CRAN.R-project.org/package=lme4

Bates, M. E., Cropp, B. F., Gonchar, M., & Knowles, J. (2010). Spatial location influences vocal interactions in bullfrog choruses. *J. Acoust. Soc. Am.*, *127*, 2664–2677.

Beauchamp, G. (1992). Diving behavior in surf scoters and Barrow's goldeneyes. *Auk*, *109*, 819–827.

Bebbington, K., & Hatchwell, B. J. (2015). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arv198

Biben, M., Symmes, D., & Masataka, N. (1986). Temporal and Structural Analysis of Affiliative Vocal Exchanges in Squirrel Monkeys (Saimiri Sciureus). *Behaviour*, *98*(1), 259–273. https://doi.org/10.1163/156853986X00991

Black, J. M., & Hulme, M. (1996). *Partnerships in Birds: The Study of Monogamy*. Oxford University Press, 432 pages.

Blanc, F., & Thériez, M. (1998). Effects of stocking density on the behaviour and growth of farmed red deer hinds. *Appl Anim Behav Sci*, *56*, 297–307.

Blanc, F., Thériez, M., & Brelurut, A. (1999). Effects of mixed-species stocking and space allowance on the behaviour and growth of red deer hinds and ewes at pasture. *Appl Anim Behav Sci*, *63*, 41–53.

724   Boucaud, I. C. A., Mariette, M. M., Villain, A. S., & Vignal, C. (2015). Vocal negotiation over parental care?

725   Partners adjust their time spent incubating based on their acoustic communication at the nest.

726   *Biological Journal of the Linnean Society*, *117*(2), 322–336. https://doi.org/10.1111/bij.12705

727   Boyd, L., & Bandi, N. (2002). Reintroduction of takhi, Equus ferus przewal- skii, to Hustai National

728   Park, Mongolia: time budget and synchrony of activity pre- and post-release. *Appl Anim Behav*

729   *Sci*, *78*, 87–102.

730   Breiman, L. (2001). Random Forests. *Machine Learning*, *45*(1), 5–32.

731   Brumm, H., & Zollinger, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic

732   research. *Behaviour*, *148*, 1173–1198.

733   Burt, J. M., & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication network. In

734   *Animal communication networks* (P. K. McGregor, pp. 320–343). Cambridge University Press.

735   Chivers, D. J. (1974). *The siamang in Malaya: a field study of a primate in tropical rain forest*. Basel:

736   Karger.

737   Conradt, L. (1998). Could asynchrony in activity between the sexes cause intersexual social

738   segregation in ruminants? *Proc R Soc Lond B*, *265*, 1359–1363.

739   Côte, S. D., Schaefer, J. A., & Messier, F. (1997). Time budgets and synchrony of activities in muskoxen:

740   the influence of sex, age and season. *Can J Zool*, *75*, 1628–1635.

741   Coulson, J. C. (1966). The influence of the pair-bond and age on the breeding biology of the kittiwake

742   gull Rissa tridactyla. *The Journal of Animal Ecology*, *35(2)*, 269–279.

743   Daan, S., & Slopsema, S. (1978). Short-term rhythms in foraging behavior of the common vole,

744   Microtus arvalis. *J Comp Physiol A*, *127*, 215–227.

745   Davis, L. S. (1988). Coordination of incubation routines and mate choice in Adelie penguins (Pygoscelis

746   adeliae). *The Auk*, *35(3)*, 428–432.

747   Doutrelant, C., McGregor, P. K., & Oliveira, R. F. (2001). The effect of an audience on intrasexual

748   communication in male Siamese fighting fish, Betta splendens. *Behavioral Ecology*, *12*(3), 283–

749   286. https://doi.org/10.1093/beheco/12.3.283

750   D'spain, G. L., & Berger, L. P. (2004). Unusual spatiotemporal patterns in fish chorusing. *J. Acoust. Soc.*
751   *Am.*, *115*, 2559–2559.

752   Elie, J. E., Mariette, M. M., Soula, H. A., Griffith, S. C., Mathevon, N., & Vignal, C. (2010). Vocal
753   communication at the nest between mates in wild zebra finches: a private vocal duet? *Animal*
754   *Behaviour*, *80*(4), 597–605.

755   Elie, J. E., Soula, H. A., Mathevon, N., & Vignal, C. (2011). Dynamics of communal vocalizations in a
756   social songbird, the zebra finch (Taeniopygia guttata). *The Journal of the Acoustical Society of*
757   *America*, *129*(6), 4037–4046.

758   Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, Gallus gallus: Their
759   relationships to food availability, courtship and social facilitation. *Animal Behaviour*, *47*(5),
760   1159–1170.

761   Farabaugh, S. M. (1982). The ecological and social significance of duetting. *Acoustic Communication in*
762   *Birds*, *2*, 85–124.

763   Fernandez, G., Capurro, A. F., & Reboreda, J. C. (2003). Effect of group size on individual and collective
764   vigilance in greater rheas. *Ethology*, *109*, 413–425. https://doi.org/10.1046/ j.1439-
765   0310.2003.00887.x

766   Fernandez, M. S. A., Mariette, M. M., Vignal, C., & Soula, H. A. (2016). A New Semi-automated Method
767   for Assessing Avian Acoustic Networks Reveals that Juvenile and Adult Zebra Finches Have
768   Separate Calling Networks. *Frontiers in Psychology*, *7*(1816).
769   https://doi.org/10.3389/fpsyg.2016.01816

770   Foote, J. R., Fitzsimmons, L. P., Mennill, D. J., & Ratcliffe, L. M. (2010). Black-capped chickadee dawn
771   choruses are interactive communication networks. *Behaviour*, *147*(10), 1219–1248.

772   Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (Orcinus orca) off Vancouver Island,
773   British Columbia. *Canadian Journal of Zoology*, *67*(3), 727–745. https://doi.org/10.1139/z89-
774   105

775   Forslund, P., & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends Ecol Evol*,

776   *10*, 374–378.

777   Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models:

778   overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1),

779   47–55. https://doi.org/10.1007/s00265-010-1038-5

780   Frommolt, K.-H. (1999). Acoustic structure of chorus howling in wolves and consequences for sound

781   propagation. *J. Acoust. Soc. Am*, *105*, 1203–1203.

782   Gérard, J. (1987). La conversation et les tours de parole. In *Savoir Parler, Savoir Dire, Savoir*

783   *Communiquer* (J. Gérard, pp. 33–37). Neuchâtel-Paris: Delacheaux and Niestlé.

784   Gerhardt, H. C., & Klump, G. M. (1988). Masking of acoustic signals by the chorus background noise in

785   the green tree frog: a limitation on mate choice. *Animal Behaviour*, *36*(4), 1247–1249.

786   Gerkema, M. P., & Verhulst, S. (1990). Warning against an unseen predator: a functional aspect of

787   synchronous feeding in the common vole, Microtus arvalis. *Animal Behaviour*, *40*, 1169–1178.

788   Gillingham, M. P., & Klein, D. R. (1992). Late-winter activity patterns of moose (Alces alces gigas) in

789   Western Alaska. *Can J Zool*, *70*, 293–299.

790   Gill, L. F., Goymann, W., Ter Maat, A., & Gahr, M. (2015). Patterns of call communication between

791   group-housed zebra finches change during the breeding cycle. *eLife*, *4*, e07770.

792   https://doi.org/10.7554/eLife.07770

793   Greenfield, M. D. (1994). Synchronous and alternating choruses in insects and anurans: common

794   mechanisms and diverse functions. *Amer. Zool.*, *34*, 605–615.

795   Hall, M. L. (2004). A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and*

796   *Sociobiology*, *55(5)*, 415–430.

797   Harrington, F. H., & Mech, L. D. (1979). Wolf howling and its role in territory maintenance. *Behaviour*,

798   *68*(3), 207–249.

799 Hauser, M. D. (1992). A mechanism guiding conversational turn-taking in vervet monkeys and rhesus

800   macaques. In *Topics of Primatology, Vol. 1. Human Origins* (T. Nishida, F. B. M. de Waal, W.

801   McGrew, P. Marler, and M. Pickford, pp. 235–248). Tokyo: Tokyo University Press.

802 Hector, A. C. K., Seyfarth, R. M., & Raleigh, M. J. (1989). Male parental care, female choice and the effect

803   of an audience in vervet monkeys. *Animal Behaviour*, *38*(2), 262–271.

804   https://doi.org/10.1016/S0003-3472(89)80088-0

805 Henry, L., Craig, A. J., Lemasson, A., & Hausberger, M. (2015). Social coordination in animal vocal

806   interactions. Is there any evidence of turn-taking? The starling as an animal model. *Frontiers in*

807   *Psychology*, *6*, 1416. https://doi.org/10.3389/fpsyg.2015.01416

808 Jones, D. L., Jones, R. L., & Ratman, R. (2009). Dynamical interactions in a green treefrog chorus. *J.*

809   *Acoust. Soc. Am.*, *126*, 2270–2270.

810 Kavanagh, M. (1978). The diet and feeding behaviour of Cercopithecus aethiops tantalus. *Folia*

811   *Primatol*, *30*, 30–63.

812 Langemann, U., Tavares, J. P., Peake, T. M., & McGregor, P. K. (2000). Response of Great Tits to

813   Escalating Patterns of Playback. *Behaviour*, *137*(4), 451–471.

814 Lee, J. W., Kim, H. Y., & Hatchwell, B. J. (2010). Parental provisioning behaviour in a flock-living

815   passerine, the Vinous-throated Parrotbill Paradoxornis webbianus. *Journal of Ornithology*, *151*,

816   483–490.

817 Linnane, M. I., Brereton, A. J., & Giller, P. S. (2001). Seasonal changes in circadian grazing patterns of

818   Kerry cows (Bos taurus) in semi-feral conditions in Killarney National Park, Co. Kerry, Ireland.

819   *Appl Anim Behav Sci*, *71*, 277–292.

820 Locascio, J. V. (2004). Diel periodicity of fish sound production in Charlotte Harbor, Florida. *J. Acoust.*

821   *Soc. Am.*, *116*, 2640–2640.

822 Locascio, J. V., & Mann, D. A. (2005). Effects of Hurricane Charley on fish chorusing. *Biology Letters*, *1*,

823   362–365.

824 Mann, D. A. (2003). Patterns of fish sound production. *J. Acoust. Soc. Am.*, *113*, 2275–2275.

825 Mariette, M. M., & Griffith, S. C. (2012). Nest visit synchrony is high and correlates with reproductive

826   success in the wild Zebra finch Taeniopygia guttata. *Journal of Avian Biology*, *43(2)*, 131–140.

827 Mariette, M. M., & Griffith, S. C. (2015). The adaptive significance of provisioning and foraging

828   coordination between breeding partners. *The American Naturalist*, *185*(2), 270–280.

829 Marshall, V. (2003). The chorus environment and the shape of communication systems in frogs. *J.*

830   *Acoust. Soc. Am.*, *113*, 2275–2275.

831 Mathevon, N. (1997). Individuality of contact calls in the Greater Flamingo Phoenicopterus ruber and

832   the problem of background noise in a colony. *Ibis*, *139*(3), 513–517.

833   https://doi.org/10.1111/j.1474-919X.1997.tb04667.x

834 Matos, R. J., & McGregor, P. K. (2002). The effect of the sex of an audience on maleemale displays of

835   Siamese fighting fish (Betta splendens). *Behaviour*, *139*, 1211e1222.

836 McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between

837   groups of female lions, Panthera leo. *Animal Behaviour*, *47*(2), 379–387.

838 McGowan, L. S. C., Mariette, M. M., & Griffith, S. C. (2015). The size and composition of social groups in

839   the wild zebra finch. *Emu*. https://doi.org/http://dx.doi.org/10.1071/MU14059

840 McGregor, P. K., & Dabelsteen, T. (1996). Communication networks. In *Ecology and evolution of*

841   *acoustic communication in birds.* (Kroodsma D. E., Miller E. H., pp. 409–425). Cornell University

842   Press, Ithaca, N.Y.

843 McGregor, P. K., & Horn, A. G. (2014). Communication and social networks. In *Animal social networks*

844   (Jens Krause, Richard James, Daniel W. Franks, Darren P. Croft). Oxford University Press.

845 McGregor, P. K., Otter, K. A., & Peake, T. M. (2000). Communication networks: receiver and signaller

846   perspectives. In *Animal signals. Adaptive significance of signalling and signal design in animal*

847   *communication.* (Espmark Y, Amundsen T, Rosenqvist G, pp. 405–416). Trondheim: Tapir.

848 McMahon, B. F., & Evans, R. M. (1992). Foraging strategies of American white pelicans. *Behaviour*,

849   *120*(69-89).

850   Mennill, D. J., Ratcliffe, L. M., & Boag, P. T. (2002). Female eavesdropping on male song contests in

851   songbirds. *Science*, *296*(5569), 873.

852   Mitani, J. C. (1984). Gibbon song duets and intergroup spacing. *Behaviour*, *92*(1-2), 59–96.

853   Naguib, M. (1999). Effects of song overlapping and alternating on nocturnally singing nightingales.

854   *Animal Behaviour*, *58*, 1061–1067.

855   Payne, K. B., Thompson, M., & Kramer, L. (2003). Elephant calling patterns as indicators of group size

856   and composition: the basis for an acoustic monitoring system. *African Journal of Ecology*, *41*(1),

857   99–107. https://doi.org/10.1046/j.1365-2028.2003.00421.x

858   Pays, O., Renaud, P.-C., Loisel, P., Petit, M., Gerard, J.-F., & Jarman, P. (2007). Prey synchronize their

859   vigilant behaviour with other group members. *Proc. R. Soc. B*, *274*, 1287–1291.

860   https://doi.org/doi:10.1098/rspb.2006.0204

861   Perez, E. C., Fernandez, M. S. A., Griffith, S. C., Vignal, C., & Soula, H. A. (2015). Impact of visual contact

862   on vocal interaction dynamics of pair-bonded birds. *Animal Behaviour*, *107*, 125–137.

863   https://doi.org/http://dx.doi.org/10.1016/j.anbehav.2015.05.019

864   Plath, M., Blum, D., Schlupp, I., & Tiedemann, R. (2008). Audience effect alters mating preferences in a

865   livebearing fish, the Atlantic molly, Poecilia mexicana. *Animal Behaviour*, *75*(1), 21–29.

866   https://doi.org/10.1016/j.anbehav.2007.05.013

867   Prior, N. H., Heimovics, S. A., & Soma, K. K. (2013). Effects of water restriction on reproductive

868   physiology and affiliative behavior in an opportunistically breeding and monogamous

869   songbird, the zebra finch. *Hormones and Behavior*, *63*(3), 462–74.

870   Rasmussen, K. L. R. (1985). Changes in the activity budgets of yellow baboons (Papio cynocephalus)

871   during sexual consortships. *Behav Ecol Sociobiol*, *17*, 161–170.

872   R Core Team. (2014). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R

873   Foundation for Statistical Computing. Retrieved from http://www.R-project.org

874   Rook, A. J., & Huckle, C. A. (1995). Synchronization of ingestive behaviour by grazing dairy cows. *Anim*

875   *Sci*, *60*, 25–30.

876   Rook, A. J., & Penning, R. D. (1991). Synchronisation of eating, ruminating and idling activity by grazing

877   sheep. *Appl Anim Behav Sci*, *32*, 157–166.

878   Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal*

879   *Behaviour*, *56*, 99–106.

880   Ruckstuhl, K. E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males?

881   *Behaviour*, *136*, 805–818.

882   Ruckstuhl, K. E., & Neuhaus, P. (2001). Behavioral synchrony in ibex groups: effects of age, sex and

883   habitat. *Behaviour*, *138*, 1033–1046.

884   Saino, N., Fasola, M., & Waiyaki, E. (1995). Do white pelicans Pelecanus onocrotalus benefit from

885   foraging in flocks using synchronous feeding? *Ibis*, *137*, 227–230.

886   Schenkeveld, L. E., & Ydenberg, R. C. (1985). Synchronous diving by surf scoter flocks. *Can J Zool*, *63*,

887   2516–2519.

888   Schusterman, R. J. (1978). Vocal communication in pinnipeds. In *Behavior of Captive Wild Animals* (H.

889   Markowitz and V. J. Stevens (Nelson-Hall, Chicago, IL), pp. 247–307).

890   Simmons, A. M., Bates, M. E., & Knowles, J. (2009). Non-random patterns of acoustic interactions in

891   chorusing bullfrogs. *J. Acoust. Soc. Am.*, *126*, 2270–2270.

892   Soltis, J., Leong, K., & Savage, A. (2005). African elephant vocal communication I: antiphonal calling

893   behaviour among affiliated females. *Animal Behaviour*, *70*(3), 579–587.

894   https://doi.org/doi:10.1016/j.anbehav.2004.11.015

895   Southall, B. L., Schusterman, R. J., & Kastak, D. (2003). Acoustic communication ranges for northern

896   elephant seals (Mirounga angustirostris). *Aquat. Mamm.*, *29*, 202–213.

897   Spoon, T. R., Millam, J. R., & Owings, D. H. (2006). The importance of mate behavioural compatibility in

898   parenting and reproductive success by cockatiels, Nymphicus hollandicus. *Animal Behaviour*,

899   *71(2)*, 315–326.

900   Stowell, D., Gill, L., & Clayton, D. (2016). Detailed temporal structure of communication networks in

901   groups of songbirds. *Journal of The Royal Society Interface*, *13*(119).

902   https://doi.org/10.1098/rsif.2016.0296

903   Tayler, J. C. (1953). The grazing behaviour of bullocks under two methods of management. *Brit J Anim*

904   *Behav*, *1*, 72–77.

905   Ter Maat, A., Trost, L., Sagunsky, H., Seltmann, S., & Gahr, M. (2014). Zebra Finch Mates Use Their

906   Forebrain Song System in Unlearned Call Communication. *PLoS ONE*, *9*(10), e109334.

907   https://doi.org/10.1371/journal.pone.0109334

908   Tremblay, Y., & Cherel, Y. (1999). Synchronous underwater foraging behavior in penguins. *Condor*,

909   *101*(179-185).

910   Van Rooij, E., & Griffith, S. C. (2013). Synchronised provisioning at the nest: parental coordination over

911   care in a socially monogamous species. *PeerJ*, *1*, e232.

912   Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's

913   voice. *Nature*, *430*(6998), 448–451.

914   Villain, A. S., Fernandez, M. S. A., Bouchut, C., Soula, H. A., & Vignal, C. (2016). Songbird mates change

915   their call structure and intrapair communication at the nest in response to environmental

916   noise. *Animal Behaviour*, *116*, 113–129. https://doi.org/10.1016/j.anbehav.2016.03.009

917   Wilson, R. P., Wilson, M.-P. T., & McQuaid, L. (1986). Group size in foraging African penguins

918   (Spheniscus demersus). *Ethology*, *72*, 338–341.

919   Zann, R. A. (1996). *The Zebra Finch : A Synthesis of Field and Laboratory Studies*. OUP Oxford, 335

920   pages.

921
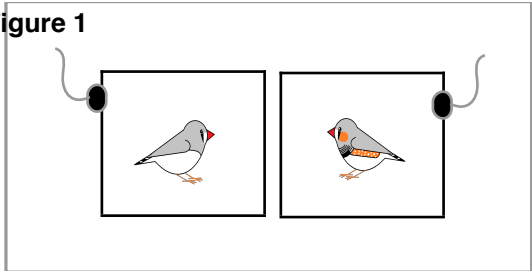
Figure 1
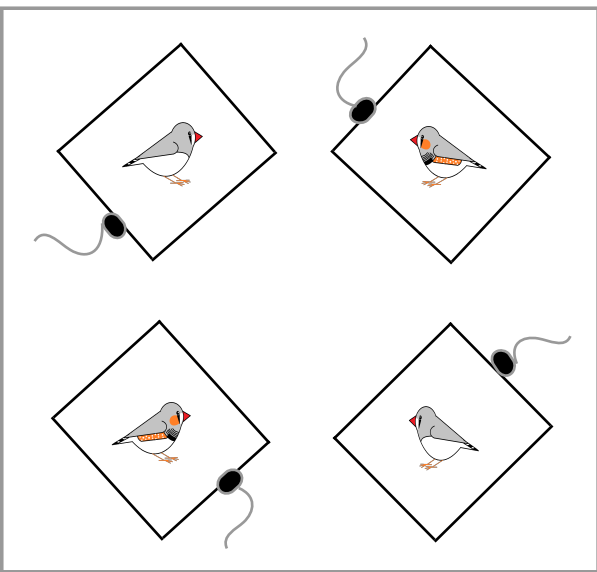
Group size = 2

Group size = 4
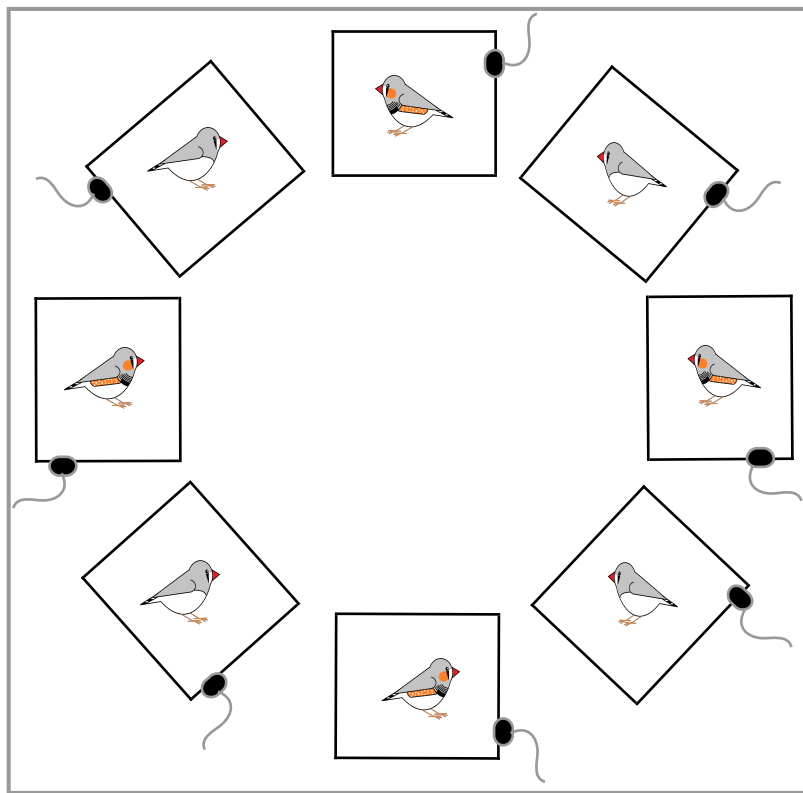
Group size = 8

Figure 2
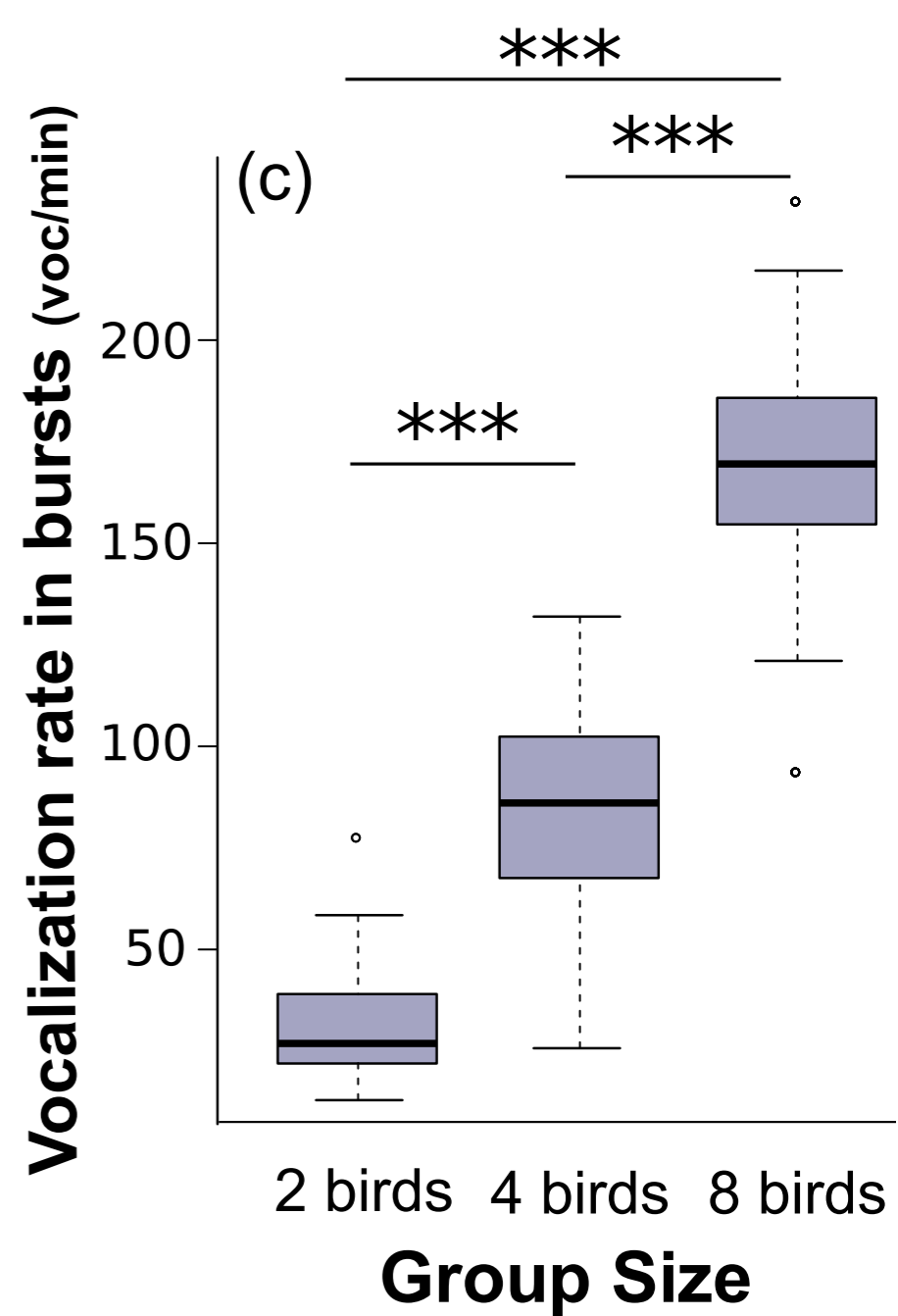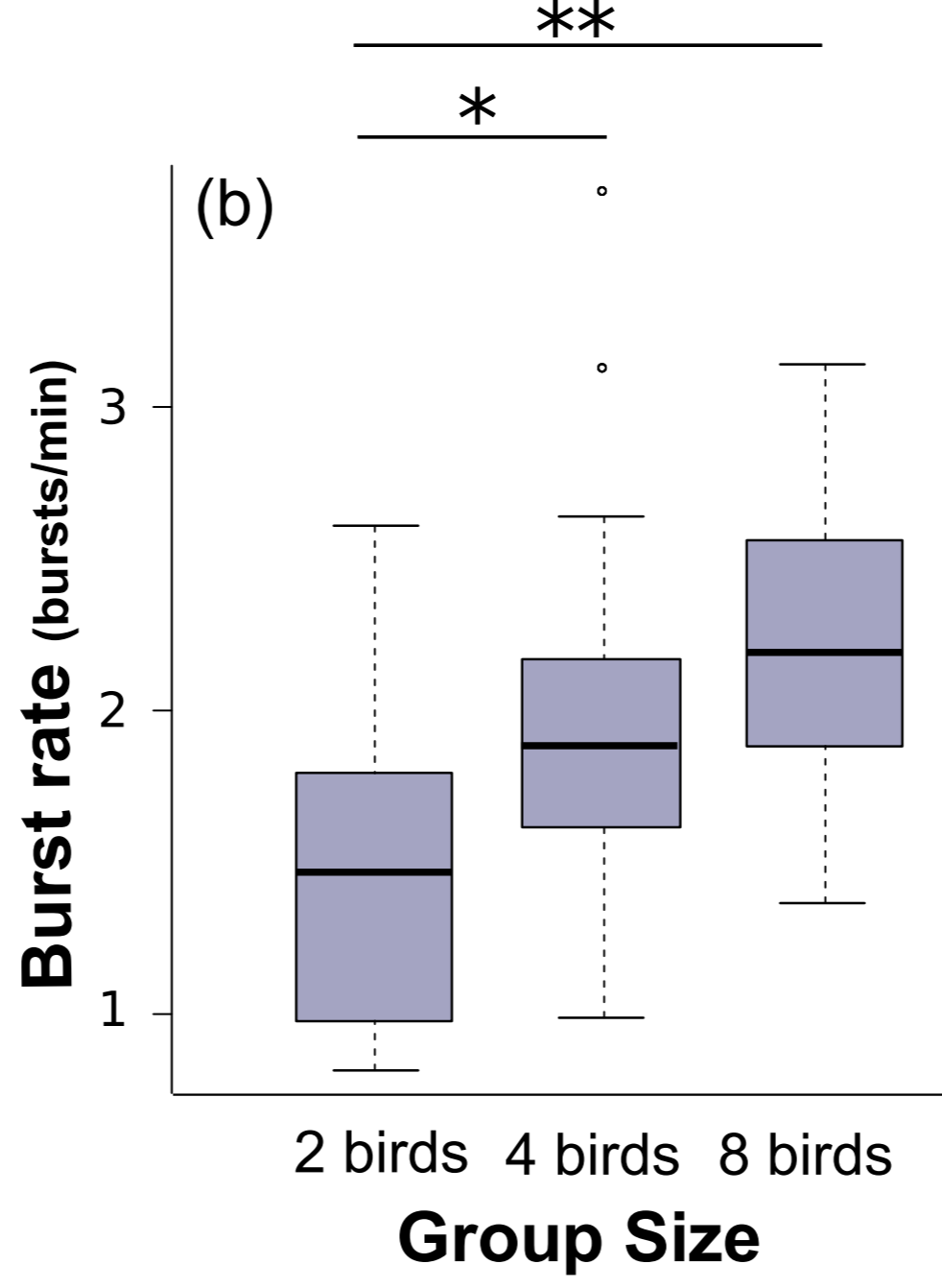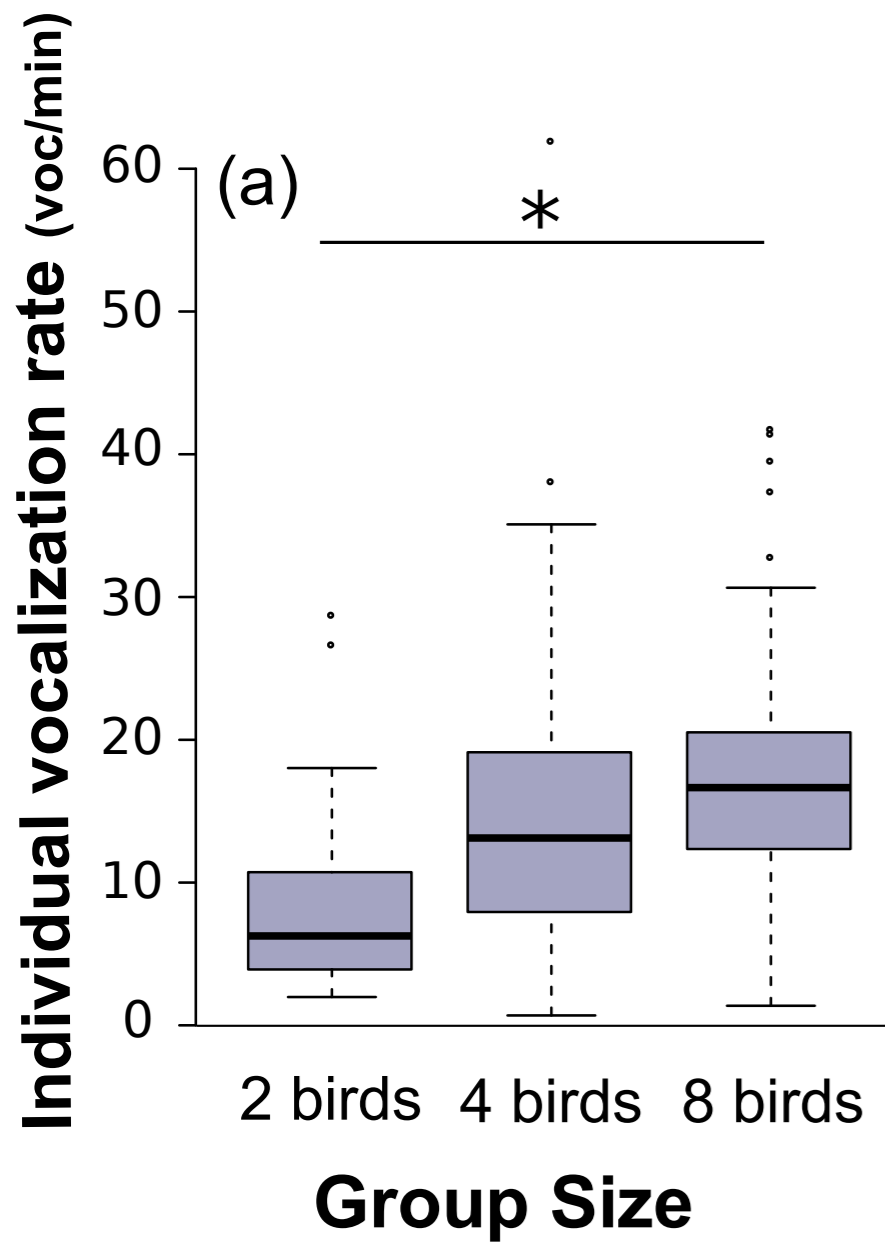
Figure 3
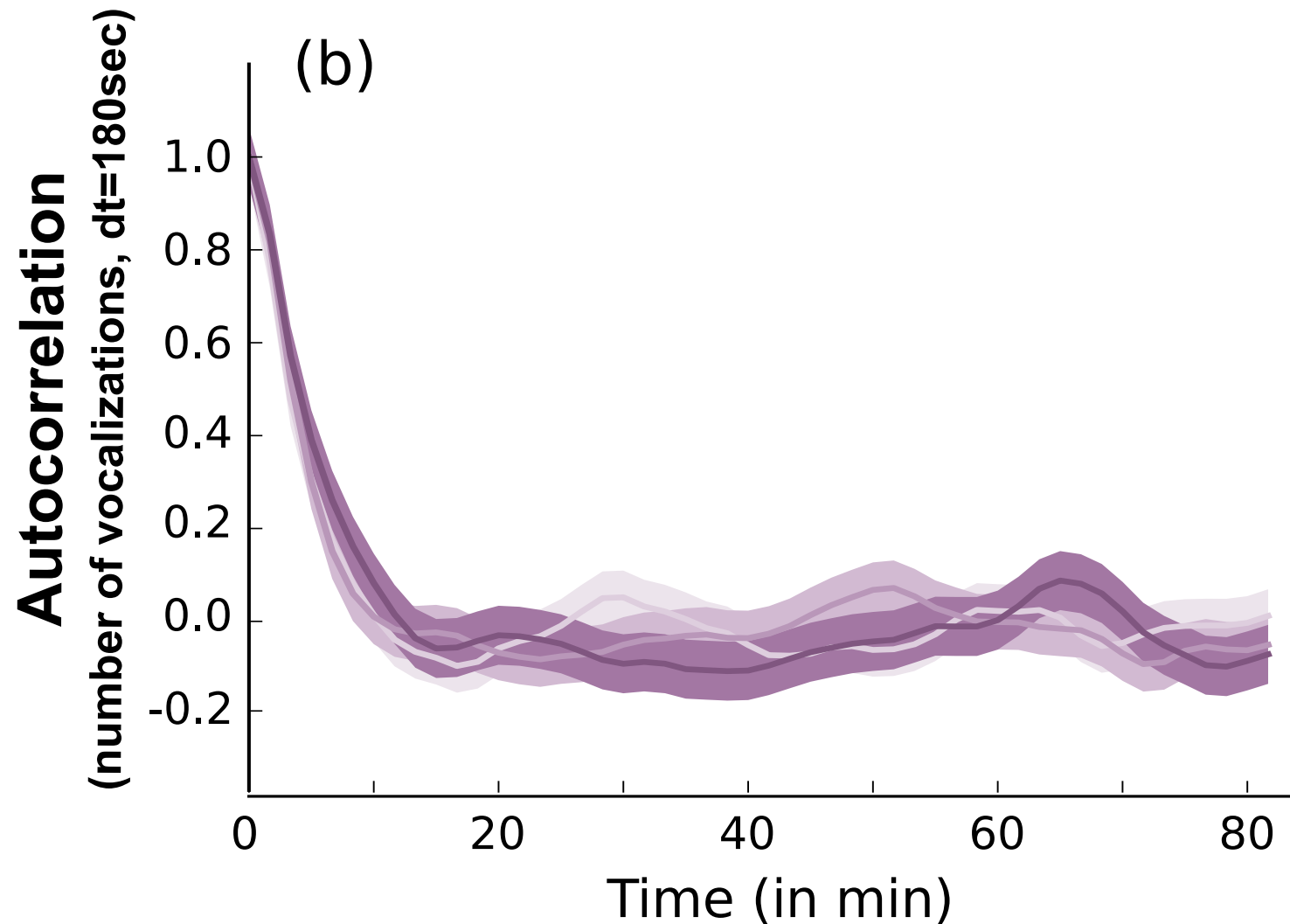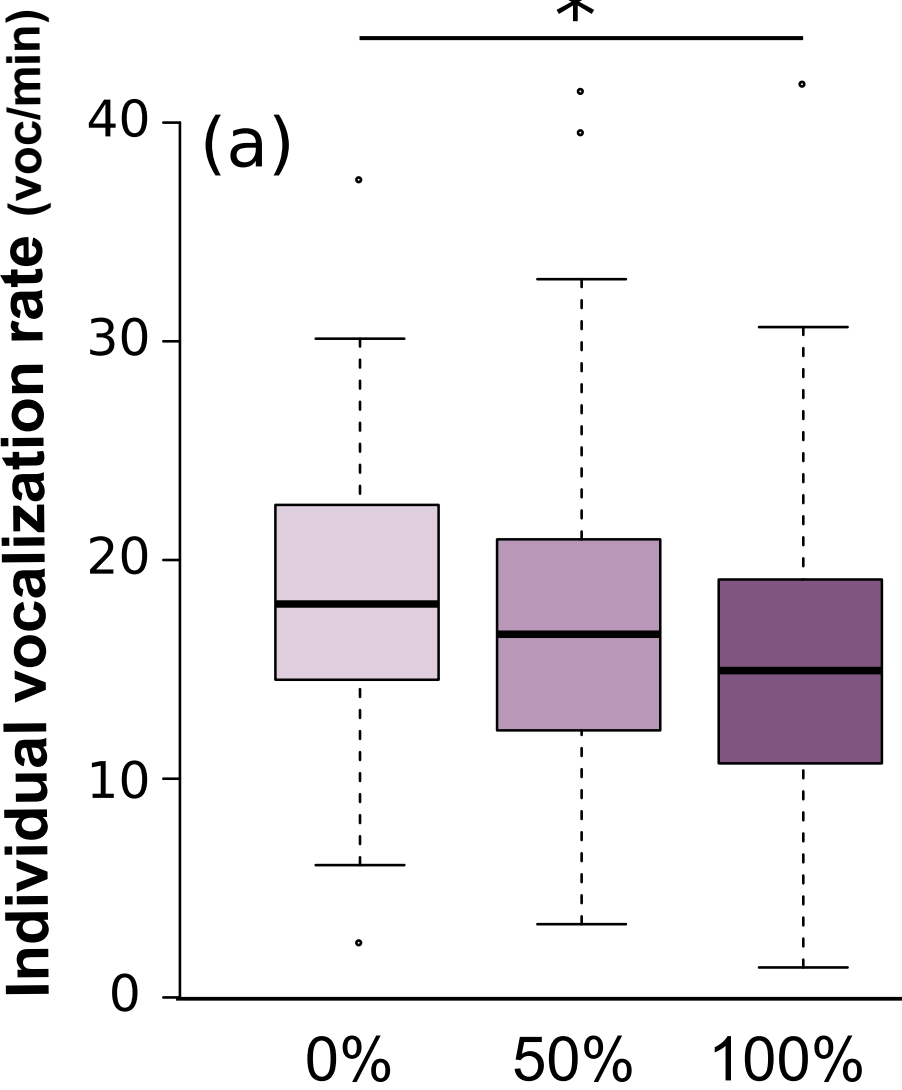
Figure 4
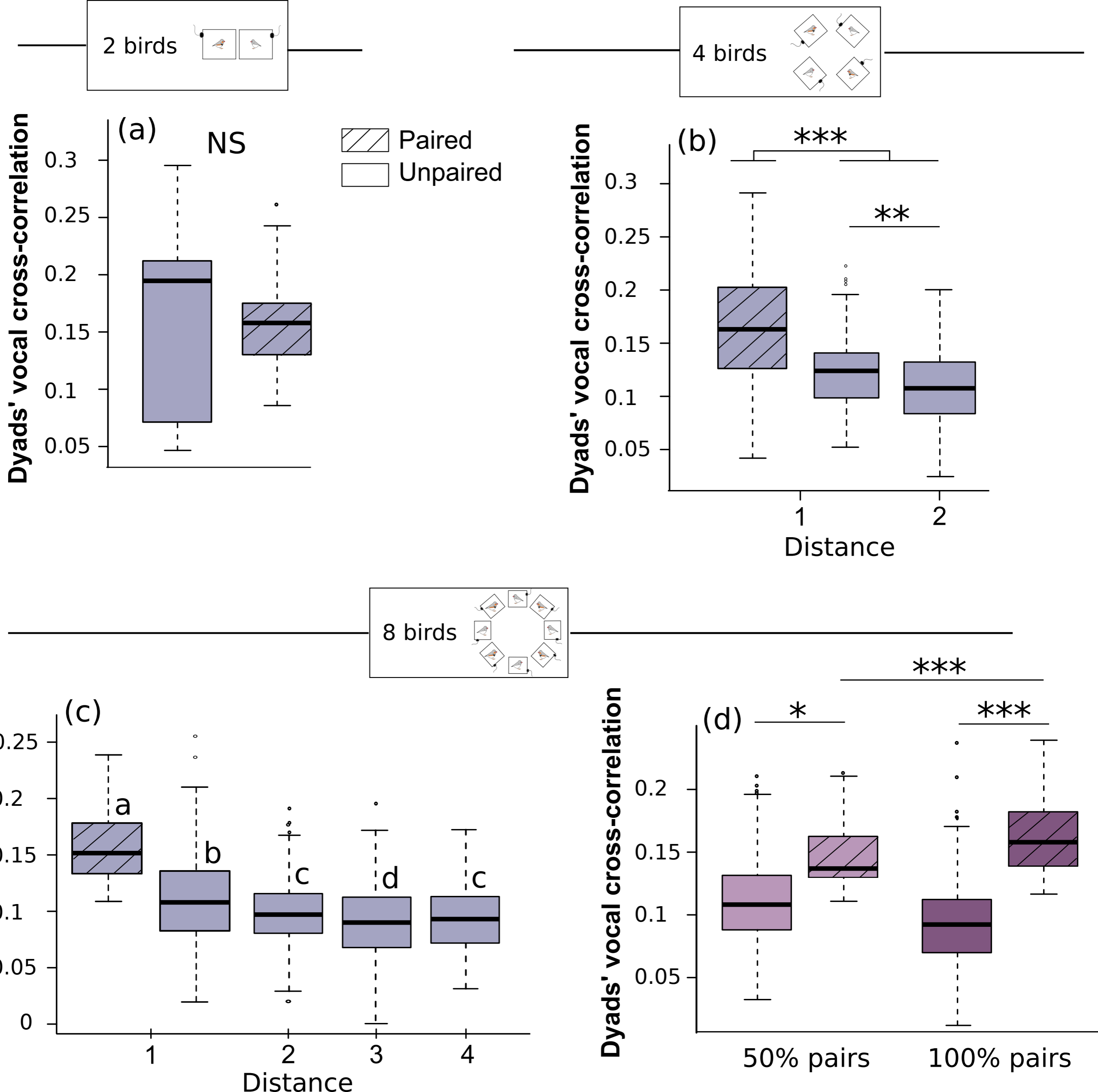
Figure 5
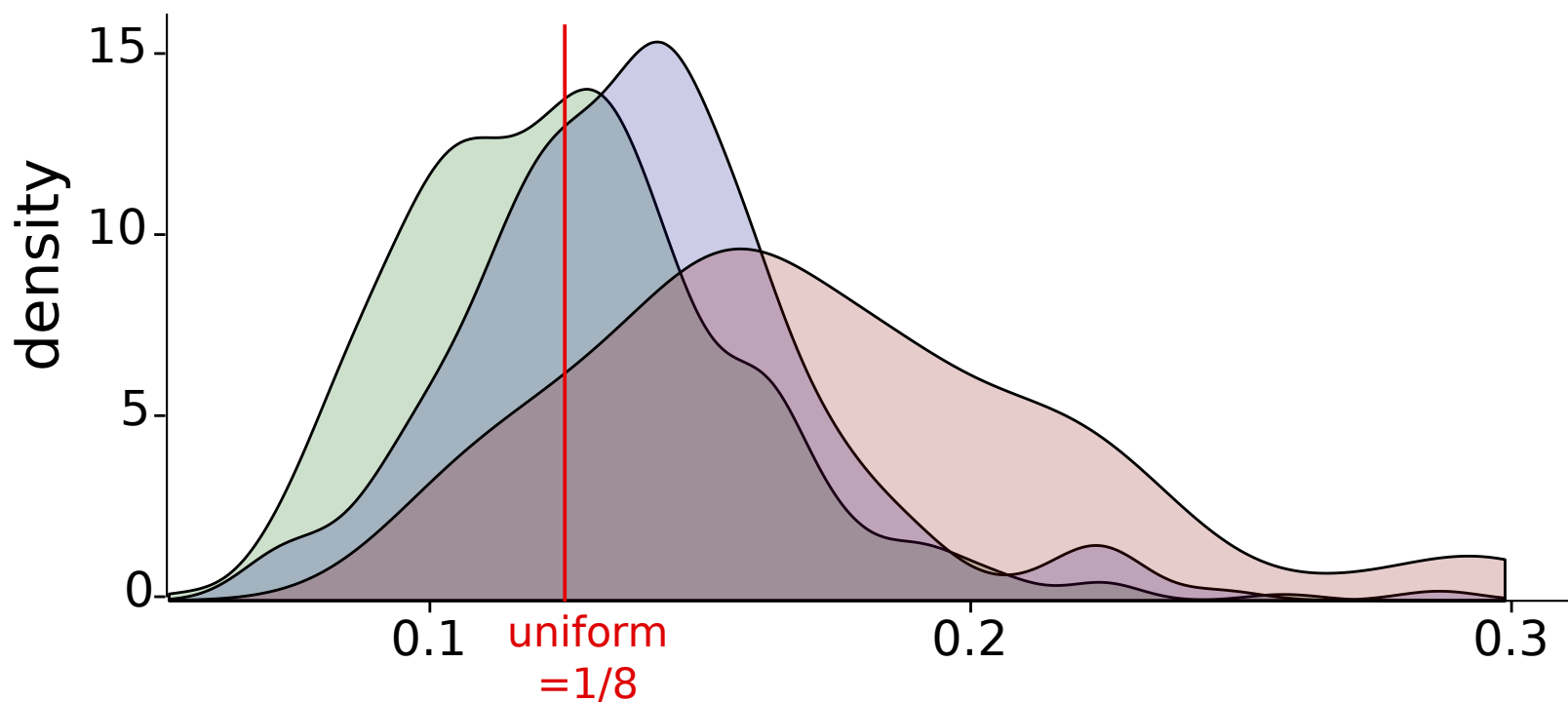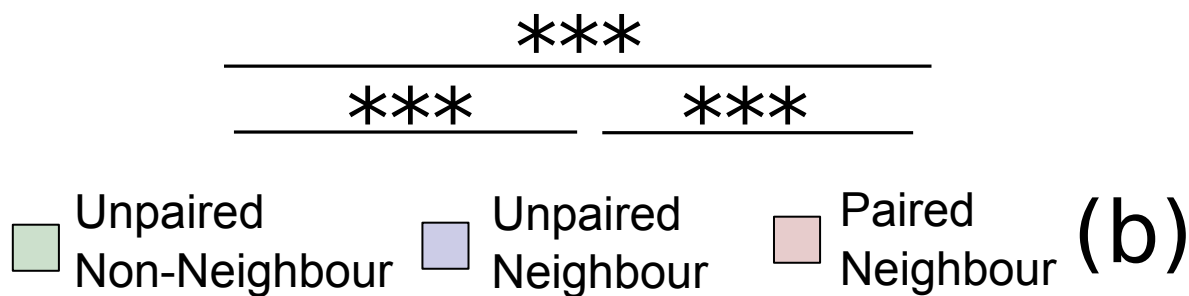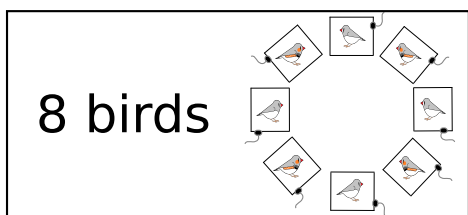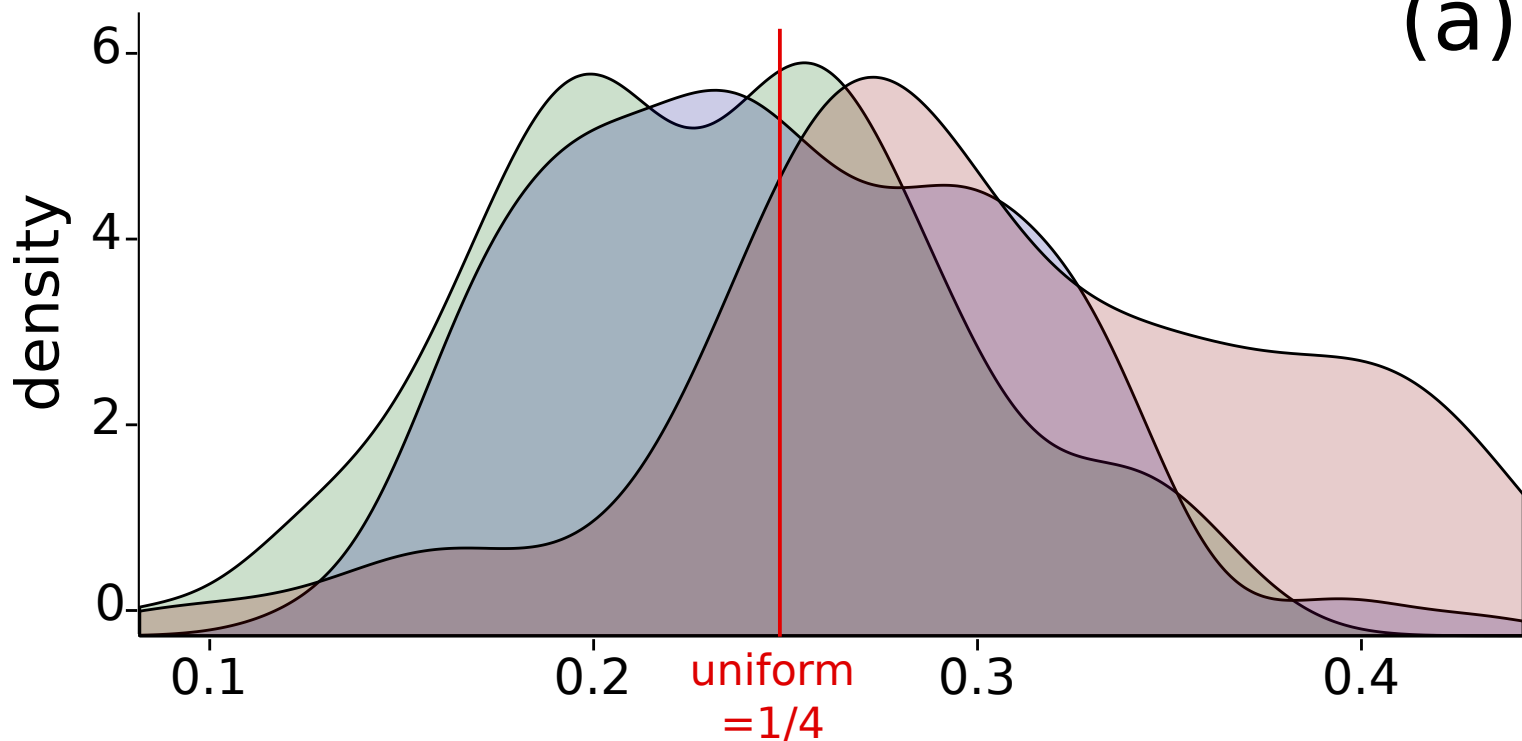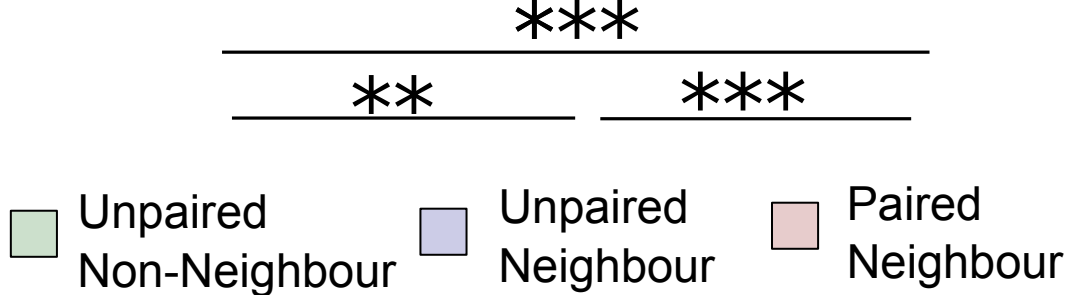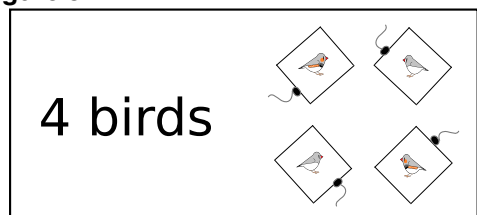
Average of transition probabilities between 2 birds

Ethical Note

Experiments were performed under the authorization no. 42-218-0901-38 SV 09 (ENES Laboratory, Direction Départementale des Services Vétérinaires de la Loire) and were in agreement with French and European legislation regarding experiments on animals.

Table 1

group size	0% paired	50% paired	100% paired
2	6 (1) -36h	X	4 (2) + 7(1) - 89h
4	3 (4) - 46h	3 (4) - 42h	3 (4) - 86h
8	3 (4) - 45h	3 (4) - 36h	3 (4) - 46h

Table 2

NVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair), random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.10291	0.3208
BirdID : GroupID	0.06534	0.2556
RepetitionNB	0.0263	0.1622
Residual	0.9343	0.9666

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.3475	0.1887	12.436	<0.0001
BirdSexM	-0.2145	0.1671	-1.284	0.1991
GroupSize4	0.1904	0.1741	1.094	0.2742
GroupSize8	0.4565	0.1856	2.46	0.0139
PercentPair50	-0.0538	0.2071	-0.26	0.7951
PercentPair100	-0.2098	0.1556	-1.349	0.1774
BirdSexM : GroupSize4	0.4405	0.1715	2.568	0.0102
BirdSexM : GroupSize8	0.2524	0.1656	1.524	0.1275
BirdSexM : PercentPair50	-0.0016	0.1460	-0.011	0.991
BirdSexM : PercentPair100	0.0810	0.1243	0.652	0.5145

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.1904	0.1741	1.094	0.517
GroupSize8 - GroupSize2	0.4565	0.1856	2.46	0.0368
GroupSize8 - GroupSize4	0.2662	0.1604	1.66	0.22

NVoc2 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05774	0.2403
Residual	1.10656	1.0519

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	1.93702	0.25458	7.609	<0.0001
BirdSexM	-0.06731	0.35642	-0.189	0.85
PercentPair100	0.29708	0.31197	0.952	0.341
BirdSexM : PercentPair100	-0.22783	0.43006	-0.53	0.596

**NVoc4 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair,
random=GroupID/BirdID, RepetitionNb**

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05626	0.2372
GroupID	0.16096	0.4012
RepetitionNB	0.04658	0.2158
Residual	0.92949	0.9641

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.73556	0.29264	9.348	<0.0001
BirdSexM	0.07808	0.17659	0.442	0.658
PercentPair50	-0.30736	0.38237	-0.804	0.421
PercentPair100	-0.41704	0.31717	-1.315	0.189
BirdSexM : PercentPair50	0.29995	0.24969	1.201	0.23
BirdSexM : PercentPair100	0.22832	0.21404	1.067	0.286

**NVoc8 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random
BirdID, RepetitionNb**

Random effects:

Groups Name	Variance	Std.Dev.
BirdID	0.06748	0.2598
GroupID	0.01339	0.1157
RepetitionNB	0.01741	0.1319
Residual	0.91694	0.9576

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.8465	0.1334	21.329	<0.0001
BirdSexM	0.0618	0.1281	0.483	0.6293
PercentPair50	-0.0706	0.1624	-0.435	0.6635
PercentPair100	-0.2993	0.1526	-1.961	0.0499
BirdSexM : PercentPair50	-0.1042	0.1823	-0.571	0.5677
BirdSexM : PercentPair100	0.0981	0.1718	0.571	0.5678

n=GroupID,

Table 3

NumberOfBursts ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.00	0.00
RepetitionNB	0.001042	0.03228

Fixed effects:

	Estimate	Std. Error	zvalue	pvalue
(Intercept)	-3.6733	0.1169	-31.409	<0.0001
GroupSize4	0.2460	0.1096	2.243	0.0248
GroupSize8	0.3916	0.1232	3.177	0.0014
PercentPair50	0.0215	0.1023	0.21	0.8335
PercentPair100	-0.0437	0.0828	-0.528	0.5971

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.24605	0.10969	2.243	0.06196
GroupSize8 - GroupSize2	0.39161	0.12325	3.177	0.00411
GroupSize8 - GroupSize4	0.14556	0.08293	1.755	0.17993

VocalizationRateBurst ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

R2c = 0.89

Random effects:

Groups Name	Variance	Std.Dev.
GroupID (intercept)	230.1	15.17
RepetitionNB (intercept)	171.3	13.09
Residual	326.6	18.07

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	50.083	9.111	10.37	5.497	2.31 e-04
GroupSize4	41.308	6.538	47.1	6.318	<0.0001
GroupSize8	121.479	7.248	40.89	16.76	<0.0001
PercentPair50	-2.459	8.458	31	-0.291	0.7731
PercentPair100	-6.119	6.189	40.05	-0.989	0.3287

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	41.308	6.538	6.318	<0.0001
GroupSize8 - GroupSize2	121.479	7.248	16.76	<0.0001
GroupSize8 - GroupSize4	80.171	6.567	12.208	<0.0001

NbVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair), random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.10291	0.3208
BirdID : GroupID	0.06534	0.2556
RepetitionNB	0.0263	0.1622
Residual	0.9343	0.9666

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.3475	0.1887	12.436	<0.0001
BirdSexM	-0.2145	0.1671	-1.284	0.1991
GroupSize4	0.1904	0.1741	1.094	0.2742
GroupSize8	0.4565	0.1856	2.46	0.0139
PercentPair50	-0.0538	0.2071	-0.26	0.7951
PercentPair100	-0.2098	0.1556	-1.349	0.1774
BirdSexM : GroupSize4	0.4405	0.1715	2.568	0.0102
BirdSexM : GroupSize8	0.2524	0.1656	1.524	0.1275
BirdSexM : PercentPair50	-0.0016	0.1460	-0.011	0.991
BirdSexM : PercentPair100	0.0810	0.1243	0.652	0.5145

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.1904	0.1741	1.094	0.517
GroupSize8 - GroupSize2	0.4565	0.1856	2.46	0.0368
GroupSize8 - GroupSize4	0.2662	0.1604	1.66	0.22

NbVoc2 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05774	0.2403
Residual	1.10656	1.0519

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	1.93702	0.25458	7.609	<0.0001
BirdSexM	-0.06731	0.35642	-0.189	0.85
PercentPair100	0.29708	0.31197	0.952	0.341
BirdSexM : PercentPair100	-0.22783	0.43006	-0.53	0.596

NbVoc4 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05626	0.2372
GroupID	0.16096	0.4012
RepetitionNB	0.04658	0.2158
Residual	0.92949	0.9641

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.73556	0.29264	9.348	<0.0001
BirdSexM	0.07808	0.17659	0.442	0.658
PercentPair50	-0.30736	0.38237	-0.804	0.421
PercentPair100	-0.41704	0.31717	-1.315	0.189
BirdSexM : PercentPair50	0.29995	0.24969	1.201	0.23
BirdSexM : PercentPair100	0.22832	0.21404	1.067	0.286

NbVoc8 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID, BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
BirdID	0.06748	0.2598
GroupID	0.01339	0.1157
RepetitionNB	0.01741	0.1319
Residual	0.91694	0.9576

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.8465	0.1334	21.329	<0.0001
BirdSexM	0.0618	0.1281	0.483	0.6293
PercentPair50	-0.0706	0.1624	-0.435	0.6635
PercentPair100	-0.2993	0.1526	-1.961	0.0499
BirdSexM : PercentPair50	-0.1042	0.1823	-0.571	0.5677
BirdSexM : PercentPair100	0.0981	0.1718	0.571	0.5678

Table 4

8 birds: Autocorrelation ~ PercentPair, random=GroupID

R2c = 0.25

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	24.97	4.997
Residual	184.78	13.594

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	42.1250	4.8704	5.9960	8.649	1.32.e-03
PercentPair50	0.9739	6.9954	6.3350	0.139	0.8936
PercentPair100	13.1045	6.6521	6.7760	1.970	0.0908

4 birds: Autocorrelation ~ PercentPair

R2c = 0.02

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	52.125	3.888	13.408	13.408	<0.0001
PercentPair50	3.500	5.498	0.637	0.637	0.528
PercentPair100	5.250	4.918	1.068	1.068	0.292

Table 5

CrossCorr ~ GroupSize + PercentPair + Paired, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.79

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.482e-02	0.121738
Bird1ID	3.734e-03	0.061110
Bird2ID	3.124e-03	0.055896
RepetitionNB	5.266e-05	0.007257
Residual	6.564e-03	0.081021

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3488	0.0511	35.3	-26.389	<0.0001
GroupSize4	0.0201	0.0539	27	0.374	0.708
GroupSize8	-0.0067	0.0596	24.8	-0.114	0.916
PercentPair50	-0.0621	0.0681	19.5	-0.913	0.381
PercentPair100	-0.0841	0.0500	24.4	-1.681	0.111
PairedYes	0.1892	0.0101	1109	18.564	<0.0001

CrossCorr2 ~ Paired, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.87

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.671e-04	0.0129
Bird1ID	0.0195	0.1398
Bird2ID	0.0113	0.1065
RepetitionNB	0.0000	0.0000
Residual	0.0047	0.0686

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.2680	0.0669	11.963	-18.934	<0.0001
Paired	0.0014	0.0403	1.781	0.035	0.976

CrossCorr4 ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.70

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0035	0.0593
Bird1ID	0.0051	0.0719
Bird2ID	0.0043	0.0660
RepetitionNB	0.0000	0.0000
Residual	0.0075	0.0871

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3184	0.0487	10.46	-27.075	<0.0001
PercentPair50	-0.0476	0.0696	10.91	-0.684	0.5081
PercentPair100	-0.0496	0.0589	12.38	-0.842	0.4156
PairedYes	0.1565	0.0244	139.36	6.398	<0.0001
Dist2	-0.0653	0.0240	210.69	-2.715	0.0071
PercentPair50:Dist2	0.0246	0.0341	209.11	0.723	0.4707
PercentPair100:Dist2	0.0512	0.0308	202.26	1.662	0.0980

*Pairwise comparisons Paired * Dist (Tukey adjustment):*

Contrast	Estimate	SE	df	tratio	pvalue
PairedNo Dist1 - PairedYes Dist1	-0.1565	0.0252	138.15	-6.208	<0.0001
PairedNo Dist1 - PairedNo Dist2	0.0400	0.0132	208.30	3.030	0.0145
PairedYes Dist1 - PairedNo Dist2	0.1965	0.0259	143.43	7.580	<0.0001

CrossCorr8 ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.74

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.344e-03	0.0366
Bird1ID	2.633e-03	0.0513
Bird2ID	2.182e-03	0.0467
RepetitionNB	4.229e-05	0.0065
Residual	2.774e-03	0.0526

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3003	0.0268	7.4	-48.503	<0.0001
PercentPair50	0.0469	0.0378	7.4	1.242	0.2524

PercentPair100	0.0327	0.0358	7.7	0.913	0.3885
PairedYes	0.1042	0.0120	839.1	8.687	<0.0001
Dist2	0.0236	0.0082	930.3	-2.868	0.0042
Dist3	-0.0679	0.0088	961.6	-7.706	<0.0001
Dist4	-0.0359	0.0106	949.8	-3.384	0.0007
PercentPair50:Dist2	-0.0202	0.0121	928.9	-1.671	0.0951
PercentPair100:Dist2	-0.0144	0.0121	922.4	-1.186	0.2360
PercentPair50:Dist3	0.0208	0.0129	960.8	1.602	0.1095
PercentPair100:Dist3	0.0074	0.0131	958.1	0.566	0.5713
PercentPair50:Dist4	-0.0143	0.0155	948.6	-0.927	0.3540
PercentPair100:Dist4	-0.0245	0.0152	942.3	-1.608	0.1081

Pairwise comparisons Dist (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
Dist2-Dist1	-0.0213	0.0077	-2.767	0.0285
Dist3-Dist1	-0.0615	0.0082	-7.453	<0.0001
Dist4-Dist1	-0.0324	0.0099	-3.262	0.0056
Dist3-Dist2	-0.0401	0.0074	-5.374	<0.0001
Dist4-Dist2	-0.0110	0.0092	-1.197	0.6252
Dist4-Dist3	0.0290	0.0089	3.262	0.0059

CrossCorr8_Dist1 ~ PercentPair + Paired + SameSexDyad, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.72

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.114e-03	0.0333
Bird1ID	2.426e-03	0.0492
Bird2ID	1.933e-03	0.0439
RepetitionNB	3.491e-05	0.0059
Residual	2.744e-03	0.0523

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.2708	0.0246	7.2	-51.575	<0.0001
PercentPair50	0.0339	0.0346	7	0.979	0.360
PercentPair100	0.0090	0.0325	7.1	0.279	0.788
PairedYes	0.1427	0.0097	793.2	14.628	<0.0001
SameSexDyadYes	0.0016	0.0035	882.7	0.477	0.634

Pairwise comparisons Paired*SameSexDyad(Tukey adjustment):

Contrast	Estimate	SE	df	t ratio	pvalue
Unpaired FM - Unpaired FF/MM	-0.0016	0.0035	888.17	-0.477	0.9642
Unpaired FM - Paired FM	-0.1427	0.0098	803.74	-14.529	<0.0001
Unpaired FF/MM - Paired FM	-0.1410	0.0098	804.26	-14.358	<0.0001

F: female, M: male

CrossCorr8_50&100%Pairs ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.75

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0011	0.0335
Bird1ID	0.0015	0.0396
Bird2ID	0.0015	0.0393
RepetitionNB	6.291e-05	0.0079
Residual	0.0020	0.0448

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.1553	0.0241	5.9	-47.799	<0.0001
PercentPair100	-0.0425	0.0320	5.9	-1.329	0.2328
PairedYes	0.0342	0.017	521.3	2.013	0.0446
Dist2	-0.0470	0.0079	610.9	-5.915	<0.0001
Dist3	-0.0510	0.0085	635.1	-5.941	<0.0001
Dist4	-0.0522	0.0098	623.7	-5.287	<0.0001
PercentPair:PairedYes	0.0850	0.0211	543.5	4.02	<0.0001
PercentPair100:Dist2	0.0260	0.0113	604.6	2.292	0.0223
PercentPair100:Dist3	0.0131	0.0123	632.1	1.068	0.2861
PercentPair100:Dist4	0.0121	0.0138	617.7	0.874	0.3825

*Pairwise comparisons Paired * Dist (Tukey adjustment):*

Contrast	Estimate	SE	df	tratio	pvalue
Unpaired Dist1 - Paired Dist1	-0.0935	0.0112	840.74	-8.313	<0.0001

Table 6

MeanTransitionProba4 ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.70

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0002	0.0164
Bird1ID	0.0059	0.0769
Bird2ID	0.0059	0.0769
RepetitionNB	0.0000	0.0000
Residual	0.0062	0.0791

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.0009	0.0320	34.9	-31.193	<0.0001
PercentPair50	0.0039	0.0460	34.6	0.085	0.9328
PercentPair100	-0.0116	0.0372	32.9	-0.313	0.7563
UnPairedNeighb	0.0243	0.0079	420.5	3.051	0.0024
PairedNeighb	0.1477	0.0106	429.8	13.914	<0.0001

Multiple comparisons PairedNeighb (Tukey adjustment):

Contrast	Estimate	StdError	z-value	pvalue
UnPairedNeighb - UnPairedNonNeighb	0.0243	0.0079	3.051	0.0062
PairedNeighb - UnPairedNonNeighb	0.1477	0.0106	13.914	<0.0001
PairedNeighb - UnPairedNeighb	0.1233	0.0109	11.286	<0.0001

MeanTransitionProba8 ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.68

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0000	0.0000
Bird1ID	0.0248153	0.15753
Bird2ID	0.0248153	0.15753
RepetitionNB	0.0001199	0.01095
Residual	0.0279268	0.16711

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-2.154	0.0463	139.6	-46.5	<0.0001
PercentPair50	-0.0260	0.065	138.1	-0.401	0.689
PercentPair100	-0.0631	0.0608	138.7	-1.037	0.301
UnPairedNeighb	0.1013	0.0093	1862	10.85	<0.0001

Supp Figure1

Click here to download Supplementary material for on-line publication only: SUPP_FIG1.pdf

Supp Figure2

Supp Figure3

Click here to download Supplementary material for on-line publication only: SUPP_FIG3.pdf

Supp Figure4

Click here to download Supplementary material for on-line publication only: SUPP_FIG4.pdf