1 **Title: A superb solo, or a deviant duet? Overlapping songs in superb fairy-wrens**

2 **Short title: Overlapping songs in superb fairy-wrens**

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32　Analyses reported in this article can be reproduced using the data provided by Taylor et

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47

48   ABSTRACT

49   Avian duets are formed when two birds coordinate their songs. Most research on the

50   evolution and function of duetting has focused on species with highly coordinated duets,

51   and less is known about the context and function of overlapping songs that are more

52   loosely coordinated, in part due to the challenge of determining whether such

53   vocalisations coincide by chance or through coordination between the partners. Here, we

54   use field recordings and playback experiments to test whether breeding pairs of superb

55   fairy-wrens *Malurus cyaneus*, coordinate their territorial songs to form duets. We test

56   three key characteristics of duetting; whether partners' songs 1) overlap more than

57   expected by chance; 2) have a stereotyped structure that occurs repeatedly and

58   predictably in time, and 3) show evidence of a constant time lag between the

59   contributions of the two participants, indicating that individuals are coordinating their

60   songs. This is the first study to quantify the temporal precision of song between partners

61   to investigate coordination in the *Malurus* genus, an important model taxon for song,

62   sexual selection, and speciation. We found variation in the extent to which partners'

63   songs overlapped, with some individuals overlapping their partners' songs more than

64   expected by chance, no difference in structure of solo and overlapping songs, and no

65   evidence of a consistent response interval. Thus song overlap in superb fairy-wrens meets

66   only some criteria for duetting. We suggest that overlapping songs in this species may be

67   due to individuals responding independently to the same stimulus and/or 'call and

68   answer' between pair members.

69

70   KEY WORDS: avian duetting, temporal coordination, superb fairy-wren, female song

71

72   Duetting is a widespread phenomenon across taxa, yet a unifying framework for

73   understanding the evolution of duetting that considers the level of coordination between

74   partners (Farabaugh 1982), relative to coordination in other species, remains obscure. In

75   part, this may reflect difficulty in determining whether some species should be

76   considered to duet or not. There are two broad types of duet; antiphonal duets, which are

77   precisely coordinated songs that alternate between pair members (Watson 1969; Thorpe

78   et al. 1972), and synchronous duets, in which both partners sing at the same time,

79   sometimes producing identical song elements at exactly the same time (Wickler and Seibt

80   1980). However, difficulties in classification arise when two birds produce songs at the

81   same time, but the elements differ or are not precisely coordinated. Alternative

82   explanations for these overlapping songs are that males and females might produce songs

83   at the same time: (i) simply by chance; (ii) because they are responding to the same

84   stimulus (e.g. territorial counter-singing), or (iii) because they are calling to or

85   responding to one another. Song overlap that occurs by chance is unlikely to serve any

86   particular function, and overlapping songs without coordination performed in the other

87   two contexts are likely to serve a broader range of functions than coordinated duets. A

88   clear definition of duetting is needed to identify which species are producing coordinated

89   duets versus just overlapping songs, thus facilitating investigations of the functional

90   significance of duetting and developing a better understanding of how duetting evolves,

91   with different levels of compliance with the definition possibly forming a continuum of

92   song coordination behaviour between species.

93

94 The cornerstone of definitions of duetting is the coordination between the contributions

95 of the two individuals (Farabaugh 1982, Langmore 2002, Hall 2004). This is

96 characterised as 'precise timing' (Farabaugh 1982), 'constant time lag' (Langmore 2002),

97 or 'low coefficient of variation' (Hall 2004) in the intervals between the contributions of

98 the two individuals. Beyond this characteristic, authors differ in the features they use to

99 define duets. Farabaugh (1982) defines duets as occurring between members of a mated

100 pair, whereas Langmore (2002) and Hall (2004) propose that this definition may be too

101 narrow, given the highly coordinated vocalisations used in male-male displays (Snow

102 1977) and between unpaired males and females of some bird species (Rogers et al. 2007).

103 Farabaugh (1982) and Langmore (2002) define songs used in duets as having a

104 stereotyped structure ('elements of the duet must be in a sequence which has a low

105 coefficient of variation between elements or element alternation percentage is high, or

106 both' Farabaugh 1982; Duets have 'a stereotyped structure that occurs repeatedly and

107 predictably in time' Langmore 2002). In addition, Farabaugh (1982) states that temporal

108 precision should be achieved 'due to coordination rather than simply coinciding by

109 chance'. Here we focus on synchronous duets, and distil these definitions into three key

110 features of these duets: (i) song overlap should occur more than expected by chance,

111 given natural rates of solo song of the participants; (ii) there is a constant time lag

112 between the contributions of the two individuals, and (iii) the contributions of the two

113 individuals have a stereotyped structure that occurs repeatedly and predictably in time.

114

To date, most research on duetting has focused on species that duet with high levels of precision and coordination (Watson 1969; Farabaugh 1982). These species also typically exhibit several key social, morphological and habitat characteristics; a monogamous mating system, sexual plumage monomorphism, a tropical distribution and year round territoriality (Thorpe et al. 1972; Kunkel 1974; Benedict 2008; Logue and Hall 2014). However, in some species male and female song contributions are less tightly coordinated and it is unclear whether or not these species are duetters. These species may also lack some, or all, of the key characteristics of duetters. Such species have attracted attention amongst researchers in recent times because they may represent the early stages of duet evolution or the loss of the trait and therefore provide valuable insights into factors that favour the evolution of duetting or factors required to maintain the trait. Different levels of song coordination may also reflect different functions of duetting. If song overlap occurs due to cooperation (e.g. to defend a territory) or conflict (e.g. jamming each other's signals, reviewed by Hall 2004) between the pair, this could be another source of variation in the level of song coordination, including within species and individuals.

One such species is the superb fairy-wren *Malurus cyaneus*. In this species, both sexes are prolific singers and the songs of members of a pair sometimes overlap (Cooney and Cockburn 1995; Rowley and Russell 1997), suggesting the possibility that they duet. There is a lack of consensus amongst researchers as to whether or not superb fairy-wrens duet, possibly reflecting different definitions of duetting. Rowley and Russell (1997)

137   suggest that playbacks may sometimes elicit a duetting response from partners, but other

138   researchers state that they do not duet (Cooney and Cockburn 1995; Kleindorfer et al.

139   2013). In addition, this species does not share many of the social, morphological or

140   habitat characteristics typical of duetters. Instead, superb fairy-wrens have one of the

141   highest rates of extra-pair paternity in birds (Griffith et al. 2002), are strikingly sexually

142   dichromatic during the breeding season (Mulder and Magrath 1994), occur in temperate

143   south-eastern Australia (Rowley and Russell 1997) and do not defend territories during

144   the non-breeding season, though they are resident year-round (Rowley 1964). Here, we

145   aim to quantify attributes of the overlapping songs of male and female superb fairy-wrens

146   to provide a rigorous test of whether they constitute duets. Specifically, we use focal

147   watches and playback experiments to test whether; (i) the songs of mated partners

148   overlap more frequently than expected by chance, (ii) there is a stereotyped structure of

149   songs involved in overlap, and (iii) members of a pair respond to a simulated territorial

150   intruder independently, or whether the second respondent coordinates its response with

151   that of the first.

152

153   METHODS

154   **Study species**

155   Superb fairy-wrens are cooperatively-breeding, insectivorous passerines endemic to

156   south-eastern Australia (Rowley and Russell 1997). Breeding groups comprise a breeding

157   pair that may be assisted by one or more helpers, which are usually sons from a previous

158 brood. Both male and female superb fairy-wrens sing the typical 'Maluridae reel'

159 (Rowley and Russell 1997) or Type I song (Figure 1; Langmore and Mulder 1992). Each

160 individual has a repertoire of different song types within this broad category. A 'Type II'

161 song (Figure 1), comprising a long trill followed by the typical reel, is commonly

162 produced by males in response to a loud sound (Langmore and Mulder 1992) and during

163 the dawn chorus (Dalziell and Cockburn 2008). There have been no prior studies of how

164 these song types are used in song overlap. The songs of members of a pair and members

165 of the same social group often overlap, with 60% of female songs occurring in

166 conjunction with those of other group members in a previous study (Cooney and

167 Cockburn 1995).

168

169 **Field site and field methods**

170 Fieldwork was conducted between September 2015 and January 2016 in Campbell Park

171 (149°10'E, 35°16'S), a eucalypt woodland located in Canberra, south-eastern Australia

172 and the long-term study site for a population of colour-banded superb fairy-wrens

173 (Langmore et al. 2016).

174

175 The territories and composition of all fairy-wren groups were monitored throughout the

176 breeding season. Female breeding activities were monitored and all nests were found so

177 that we could identify the breeding stage of individuals used for focal watches and

178 playback experiments. Fieldwork occurred predominantly during the morning, after the

179 dawn chorus, which is when superb fairy-wrens have the most constant song rate

180   (Cooney and Cockburn 1995). Pairs with no helper or a single helper were selected to

181   make identification of singing individuals easier.

182

183   **Focal watches**

184   Females and males of 20 socially mated pairs were used as 40 separate, focal individuals.

185   Before commencing focal watches, the date, time, colour band code/s of individual/s

186   involved and stage of the breeding cycle of the pair was recorded. Each individual was

187   followed for a 15-minute period and recorded using Sennheiser ME66 directional

188   microphone with a Sennheiser MZW 66 windshield mounted on a Sennheiser MZ 20-1

189   pistol grip linked to a Tascam DR40 recorder. The observer verbally annotated which

190   individual of the pair sang and when a neighbour's song was heard. Pairs were readily

191   located because superb fairy-wrens establish and defend territories during the breeding

192   season, so they can be found reliably in the same general location (Rowley and Russell

193   1997). In 13 fairy-wren groups, one member of the pair was not colour-banded and in one

194   pair, both individuals were unbanded. We were confident of the identity of unbanded

195   females for the duration of a single nesting attempt, because a replacement female does

196   not use nests of other females. This allows within-female comparisons across breeding

197   stages in both banded and unbanded females. There was a small chance that unbanded

198   males may have died and been replaced by another unbanded male during the study, but

199   male mortality rates are low during the breeding season (Cockburn et al. 2008) so this

200   would be unlikely to influence the results.

201

202 Song rates of many species vary in relation to breeding stage (Schwabl and Sonnenschein

203 1992; Hanski and Laurila 1993). To control for this, we attempted to conduct focal

204 watches on each individual at three stages of the breeding cycle: pre-fertile (PF) - the nest

205 building stage before the fertile period; fertile period (F) - 2-4 days before the first egg

206 was laid (Double and Cockburn 2000), and with an active nest (AN) - eggs or nestlings

207 were present. The stage of the breeding cycle was determined by checking the nest (at a

208 different time to focal watches, to minimise nest disturbance) every 3 days until the

209 commencement of incubation (to determine lay date), and only after focal watches once

210 incubation had commenced. We succeeded in recording both members of the pair during

211 the pre-fertile stage in 17 pairs, the fertile stage in 13 pairs and with an active nest in 16

212 pairs.

213

214 **Playback experiments**

215 To assess whether the songs of members of a pair responding to a stimulus were more

216 synchronised with one another than with the stimulus, we elicited songs using playback

217 experiments. Fourteen pairs received two playback treatments: a solo song of a male

218 superb fairy-wren and a solo song of a female superb fairy-wren. The order of the two

219 treatments was alternated between pairs. Playbacks occurred when pairs had an active

220 nest.

221

222 The solo superb fairy-wren songs used as playback stimuli were recorded from the study

223 site (N = 22) during the focal watches and from the Australian National Botanic Gardens

224   in Canberra (referred to as the Botanic Gardens throughout this paper; 149°06'E, 35°16'S,

225   N = 17), 6 km from the study site, during a previous experiment (see Cain and Langmore,

226   2015). Song recordings of high quality with a high signal to noise ratio were chosen using

227   spectrograms produced using Raven Pro software (version 1.4, Cornell Laboratory of

228   Ornithology, Ithaca, NY, USA). Recordings from both locations were edited using a High

229   Pass Filter to remove background noise below 1000 Hz and the maximum amplitude was

230   normalised to –1.0 dB using Audacity (version 2.1.1, audacity.sourceforge.net). The

231   amplitude of the recording was then standardised using Raven Pro to be within 1 kU (U is

232   the Raven Pro measure of amplitude, kU is 1000 U's) of a maximum amplitude of 20 kU

233   (Charif et al. 2010). The format for all playbacks was 5 seconds of silence followed by 3

234   repeats of the same solo song, each separated by 20 seconds of silence (Cooney and

235   Cockburn 1995). Files containing each stimulus were saved in the format of 16-bit WAV

236   files with a sampling rate of 44100 Hz. Both the male and the female playback stimuli

237   that each pair received were recorded from the same location, making the treatments as

238   similar as possible. Eight pairs received stimuli from individuals residing in the Botanic

239   Gardens and six pairs received stimuli from individuals residing in Campbell Park. The

240   pairs were randomly allocated to either group, while ensuring that all birds received

241   playbacks of an unfamiliar individual. Playback songs recorded in Campbell Park were

242   played to pairs residing at the opposite side of the park (> 727m), so they received non-

243   neighbour songs. Playbacks of songs recorded in the Botanic Gardens were randomly

244   allocated to pairs. Due to a finite number of playback stimuli, stimuli were swapped

245   between pairs whilst ensuring that songs were from the same location and from an

246 unfamiliar individual. If a playback elicited song from both pair members it was not used

247 as a stimulus again, to prevent pseudo-replication. The presentation of the two treatments

248 occurred on separate days to reduce habituation and carry-over effects (Hall et al. 2006;

249 Kovach et al. 2014).

250

251 The playback and response were recorded with the same recording equipment as above.

252 Before commencing playback experiments the date, time, colour band code/s of

253 individual/s involved was recorded. A Pignose Legendary 7100 speaker was used to

254 broadcast the playbacks from a portable digital audio player (Apple iPod) linked by a 2

255 meter cable. The volume of the speaker was adjusted to a playback amplitude of

256 approximately 60 dB from 5 metres, which is within the natural range of superb fairy-

257 wren songs (based on measurements with a sound level meter). The speaker was placed

258 in an area of the territory that the pair frequented ~ 15-20 meters from the nest,

259 simulating a realistic territorial intrusion (Rowley and Russell 1997; Cain et al. 2015).

260 The playback began when both pair members were visible, within 10 meters of each

261 other, within 25 meters of the speaker and not singing. The entire playback file,

262 comprising three repetitions of the solo song, was played. The playback was considered

263 successful if both pair members sang in response to the stimulus i.e. there was potential

264 for song overlap.

265

266 Since some playbacks elicited no song response, or song from only one pair member, we

267 repeated playbacks, with at least one day between them, as necessary to elicit response

268   songs from both pair members. Overall, 17 pairs received 58 playbacks and pairs heard

269   from 1 to 8 playbacks throughout the breeding season. From these we obtained responses

270   from both pair members in 14 playback experiments: 6 playbacks of male song and 8

271   playbacks of female song. When pairs responded to both the female and male playback

272   (n = 4 pairs) for the variance analysis, one playback was chosen randomly to be included

273   in the analysis to prevent repeated measures (resulting in N = 10), this did not affect the

274   significance of the result.

275

276   **Acoustic Analysis**

277   Each focal watch recording was visualised as a spectrogram using the Hann algorithm in

278   Raven Pro with the default settings (16-bit sample format; discrete Fourier transform

279   (DFT) = 256 samples; frequency resolution = 172 Hz; time resolution = 2.90 ms; frame

280   overlap = 50%). The commentary of field observations combined with the spectrogram

281   visual and time cursor in the Raven Pro program, were used to extract which pair member

282   sang the song, the duration of the song, the start and end times of the song and the

283   presence of neighbour's song within the recording. Songs were categorised into 3 classes;

284   solo song (defined as a song by a single individual which did not occur at the same time

285   as, and therefore does not overlap with, its partner's song), overlapped songs (a song that

286   started before but occurs at the same time as a song by the partner) and overlapping songs

287   (a song that begins when the partner is already singing). Occasionally it was not possible

288   to identify which bird sang (4%, 49 of 1171 songs); these songs were excluded from the

289   analysis. We calculated the percentage of an individual's song that began while their

290   partner was singing and the percentage of an individual's song that were overlapped by

291   their mate, for both sexes. The average number of songs sung by males (n = 19) and

292   females (n = 20) per 15-minute focal watch was calculated, as well as the sum of songs

293   that were sung solo and involved in overlap.

294

295   We measured structural differences between overlapped, overlapping and solo songs

296   (Figure 1), for songs of 37 individuals. For each individual, from all of the recordings of

297   that individual, we selected a single exemplar solo song, an overlapped song and an

298   overlapping song, each with a high signal to noise ratio for measurement (resulting in:

299   solo n = 37, overlapped n = 18 and overlapping n = 13). Measurements of acoustic

300   variables of overlapped and overlapping songs were constrained, due to not being able to

301   completely distinguish the elements of the overlapped songs from the overlapping songs

302   on the spectrogram (Catchpole and Slater 1995). This meant the entire solo song could

303   not be compared to the entire overlapped and overlapping song. To overcome this

304   limitation, three non-overlapping syllables of each song were measured (Catchpole and

305   Slater 1995). Spectrograms created using Raven Pro were used to quantify the structural

306   properties of the three syllables and the duration of the whole song (Charif, Waack and

307   L.M, 2010; Table 1).

308

309   When two individuals respond to a stimulus, both individuals may be responding

310   independently. Alternatively, if the response comprises a duet, the second responder will

311   coordinate its response with that of the first responder, creating a more constant response

312   interval between the songs of the first and second responders than between the song of

313   the second responder and the 'intruder'. To test this possibility we compared (1) the

314   variance in the time period between the start of the first responder's song and the start of

315   the second responder's song, with (2) the variance in the time period between the start of

316   the playback and the start of the first responder's song and (3) the variance in the time

317   period between the start of the playback and the start of the second responder's song.

318   Using Raven Pro we measured the duration of these time periods for comparison.

319

320   **Statistical Analysis**

321   To determine whether individuals overlapped their partner's songs more than expected by

322   chance, we used a statistical package in R called the 'Song Overlap Null Model

323   Generator' (SONG; Masco et al. 2016). This software package has two methods by

324   which overlap is calculated: the 'duty cycle' method and a randomisation method. The

325   duty cycle method has been traditionally used to assess if song overlap occurs more than

326   expected by chance (Ficken et al. 1974), but does not take into account variation in song

327   length and inter-song intervals, which may influence the probability of song overlap. The

328   randomisation method incorporates song duration and timing using randomisation

329   methods (Masco et al. 2016) and therefore appears to provide a more robust null

330   hypothesis for assessing song overlap. However, it is relatively untested, and performs

331   less well for recordings without song overlap and very short sequences of song so we

332   report results from both methods.

333

334   We analysed 38 focal watches during which both individuals produced at least three

335   songs. We recorded the start and end times of all songs produced by both sexes, which

336   reveals song overlap between two individuals. Focal watches with less than 3 songs per

337   individual (N = 54) were excluded because randomisation of the order of an individual's

338   songs is limited or non-existent with less song than this. Specifically the, SampleGaps

339   randomisation method was used, producing 1000 randomisations for each analysis

340   (Masco et al. 2016). This method maintains the duration of the songs and randomises the

341   gaps between them and the song order for each sex to create a null distribution of song

342   overlap. The observed song overlap is compared to the null distribution, generated by the

343   randomisations, to determine if overlap occurs more than expected by chance.

344

345   To assess if the stage of the breeding cycle, sex or neighbour songs affected the number

346   of an individuals' songs that overlapped their partner (began while their partner was

347   already singing), a generalised linear mixed model (GLMM) with a binomial distribution

348   and a logit link function was used (Bolker et al. 2009). For this model, the numerator was

349   the number of songs that the individual began whilst its partner was singing in each focal

350   watch (number of overlapping songs) and the denominator was the number of

351   opportunities the individual had to overlap their partner's song (the sum of their partner's

352   solo and overlapped songs; N = 43 birds in 92 focal watches, excluding cases where the

353   partner did not sing so there was no opportunity for overlap i.e. denominator = 0). In this

354   model three factors were included: breeding stage (three levels: pre-fertile (PF), fertile

355   (F) and with an active nest (AN)), sex (two levels: male and female) and number of times

356   a neighbour's song occurred before song overlap. We also tested for two-way interactions

357   between these factors (sex*stage, sex*neighbour song, stage*neighbour song). Pair

358   identity was included as a random effect because pairs were sampled multiple times

359   across breeding stages, and to account for the non-independence of individuals from the

360   same pair.

361

362   We analysed structural differences between overlapped, overlapping and solo songs using

363   a multivariate discriminant function model. A stepwise procedure was used to identify

364   the most significant variables, however all variables were included in the final model.

365

366   **Types I and II songs**

367   To assess if the number of Type I and Type II songs differed between the song classes

368   (solo, overlapped and overlapping songs), we used a GLMM with a Poisson distribution

369   for count data and a log link function (Bolker et al. 2009). Two factors were included:

370   class (three levels: solo, overlapped and overlapping) and type (two levels: Type I and

371   Type II). The interaction between these factors (class*type) was also included and

372   individual identity (N = 26 individuals) was included as a random effect.

373

374   The statistical software GenStat 16th edition (VSNi Australia Pty Ltd., Hemel Hempstead,

375   Hertfordshire, U.K.) was used for these analyses.

376

377   We used the Brown-Forsythe test to compare the homogeneity of variance in the time

378   intervals (between the; (I) playback and the start of the first responders song, (II)

379   playback and the start of the second responders song and (III) the start of the first

380   responders song and the start of the second responders song) in response to playback

381   using JMP v. 13 (SAS Institute, Inc., Cary, NC). The mean reaction time and the

382   coefficient of variation (CV = 100 x standard deviation / mean) were also calculated for

383   the three response periods. In addition, to test whether the sex of the first responder was

384   influenced by the sex of the unfamiliar individual's song that was used as a playback

385   stimulus, a two-tailed Fisher's exact test was used. The result was considered significant

386   if P was less than 0.05.

387

388   **Ethical note**

389   This research was conducted with approval from the Australian National University

390   Animal Experimentation Ethics committee (protocol number A2015/50), and with

391   permission to study superb fairy-wrens in Campbell Park from the ACT Territory and

392   Municipal Services (protocol number LT2014776). This study was mainly observational

393   and the minor interference to individuals through response to playbacks and nest checks

394   did not have any perceivable lasting effects.

395

396   RESULTS

397   **Do individuals overlap their partner's songs more than expected by chance?**

398   Overlap was relatively uncommon in superb fairy-wrens: males began 13% of all their

399   own songs while their partner was singing, and overlapped 11% of all the female's songs.

400   Females began 7% of all their own songs while their partner was singing, and overlapped

401   9% of all the male's songs. On average, males sang 6 songs per 15-minute focal watch (n

402   = 19 individuals) while females sang 7 songs (n = 20 individuals). Of all recorded songs,

403   907 songs were sung solo while 215 were involved in overlap (103 potential 'duets' of

404   which 64 were initiated by females (female song overlapped by male song), and 39 by

405   males, including 9 'sandwich duets' where the initiator sang again to overlap its

406   overlapper).

407

408   Based on the randomisation method, overlap in songs occurred more often than expected

409   by chance in less than half of the focal watches (42% of 38 watches; all P < 0.025, Table

410   2). Eleven percent of females and 34% of males overlapped their mate's song more than

411   expected by chance (all $P < 0.025$). In one pair, both individuals overlapped each other's

412   songs more than expected by chance, in 15 pairs only one individual did, and in 22 pairs

413   neither individual overlapped their partner's songs more often than expected by chance.

414

415   Similarly, based on the duty cycle method, overlap in songs occurred more than expected

416   by chance in over half of the focal watches (55% of 38 focal watches; Table 2). Twenty-

417   six percent of females and 45% males overlapped their mate's song more than expected

418   by chance (all $P < 0.05$). In six pairs, both individuals overlapped each other's song more

419   than expected by chance, in 15 pairs only one individual did, and in 17 pairs neither

420   individual overlapped their partner's songs more often than expected by chance.

421

422   The results of the randomisation method and the duty cycle method were consistent for

423   females in 32 of 38 focal watches, and for males in 30 of 38 focal watches (Table 2).

424   Where they differed, the duty cycle method was usually, but not always, more likely to

425   identify significant overlap than the randomisation method (Table 2).

426

427   The proportion of its partner's songs that an individual overlapped (began singing while

428   its partner was singing) was higher when more overlapped songs were preceded by

429   neighbour songs in the 10 seconds prior to song overlap (Table 3 and Figure 2).

430   Excluding the one data point with 100% overlap had no qualitative effect on the results.

431   The proportion of its partner's songs that an individual overlapped did not differ between

432   the sexes or between breeding stages or with the interaction between sex and breeding

433   stage (Table 3). Furthermore, song overlap did not differ with the interaction between sex

434   and neighbour response or between stage and neighbour response (Table 3).

435

436   **Do solo songs differ in structure from overlapped or overlapping songs?**

437   Solo, overlapped and overlapping songs did not differ significantly in a discriminant

438   function analysis. This analysis classified solo, overlapped and overlapping songs with

439   46, 50 and 46% accuracy, respectively (Wilk's $\lambda = 0.825$, Approximate $F_{10} = 1.2301$, $P =$

440   0.2786, Figure 3). None of the factors were significantly different between the song

441   classes. Although non-significant, duration accounted for the most variability between

442   song classes (p= 0.077) with overlapped songs generally having a longer duration than

443   non-overlapped songs (Table 4). However, as sample sizes were small, these results

444   should be treated with caution.

445

446   Type I songs were more common than Type II songs and solo songs were more common

447   than overlapped and overlapping songs (Table 5). However, there was no difference in

448   the frequency at which the two different song types were involved in overlap (no

449   significant interaction between these factors, Table 5).

450

451   **Is there a consistent response interval between the start times of songs in response to**

452   **a stimulus?**

453   To test the constant time lag hypothesis, 17 socially mated pairs received 58 playbacks in

454   total, of which 24% (n = 14) elicited a response from both pair members. When both

455   individuals in the pair responded, 43% of the responses (n = 6) overlapped. Individuals

456   were first responders more often when they were the same sex as the playback, but this

457   relationship between playback sex and first responder sex was not statistically significant

458   (male responded first to 67% of male playbacks, and 38% of female playbacks, female

459 responded first to 63% of female playbacks, and 33% of male playbacks; two-tailed

460 Fisher's Exact Test: $N = 14$, $P = 0.5921$).

461

462 There was no significant difference in the variance of the time intervals between (1) the

463 start of the stimulus and start of song 1 (first responder), (2) the start of the stimulus and

464 the start of song 2 (second responder), and (3) the start of song 1 and start of song 2,

465 when both the male and the female sang in response to playback (Brown-Forsythe test: N

466 $= 10$, $F_2 = 1.0408$, $P = 0.3669$; Figure 4). This indicates that an individual's songs are no

467 more coordinated to their partner's songs than they are to the playback stimulus.

468

469 The first responder initiated its song 4.07 ± 2.49 seconds (mean $\pm$ SD, CV = 61.21) after

470 the start of the playback song, while the second responder initiated its song 8.20 ± 4.50

471 seconds (mean $\pm$ SD, CV = 54.89) after the start of the playback song, which was $4.12 \pm$

472 2.80 seconds (mean $\pm$ SD, CV = 68.01) after the start of the first responder's song (N =

473 10).

474

475 When overlapping songs occurred naturally (during focal watches) the second song was

476 initiated 1.5 ± 0.8 seconds (mean $\pm$ SD, CV = 54.4, N = 112) after the start of the first

477 song.

478

479   DISCUSSION

480   Overlapping songs of superb fairy-wrens satisfy few of the criteria for duetting. Some

481   individuals overlapped their partner's song more than expected by chance. However, the

482   structure of songs involved in overlap did not differ significantly from solo songs,

483   overlapping songs were relatively uncommon (fewer than 15% of spontaneous songs, and

484   43% of responses to playback) and there was no evidence of fine-scale temporal

485   coordination. This suggests that song overlap is likely to be due to individuals responding

486   independently to the same stimulus (e.g. a territorial neighbour), rather than deliberately

487   coordinating songs to produce duets.

488

489   **Individuals overlap their partner's songs more than expected by chance**

490   There is some limited evidence the superb fairy-wrens may duet; 13% of male song and

491   7% of female song began whilst their partner was singing, resulting in 11% of female

492   song and 8% of male song being overlapped. However, in species where both sexes sing,

493   especially a species with relatively high daytime song rates such as superb fairy-wrens

494   (Cooney and Cockburn 1995; Cain and Langmore 2015), overlapping song is likely to

495   occur by chance to some extent. In this study, some individuals showed higher levels of

496   song overlap than would be expected to occur by chance. One explanation for this result

497   is coordinated duetting between pair members in a subset of pairs (Farabaugh 1982; Hall

498   and Peters 2008; Dowling and Webster 2013). Alternatively, pair songs may overlap

499   more than expected by chance because some of the time individuals are both responding

500   independently to the same stimulus (e.g. a territorial neighbour; Helfer and Osiejuk 2015;

501   Masco et al. 2016). Consistent with this, we found that individuals overlapped more of

502   their partner's songs in focal watches when there were more cases of neighbour song

503   preceding overlaps (Figure 2). The response of both pair members could occur for many

504   reasons, as duetting can have many cooperative functions (Hall 2004). However both

505   individuals could also have conflicting interests, and as a result may sing to signal jam

506   the other's song, which may overlap but is not necessarily coordinated into a duet (Tobias

507   and Seddon 2009).

508

509   In most duetting species (84%), males initiate more than 50% of duets (Hall, 2009). By

510   contrast, in superb fairy-wrens males initiated only 38% of song overlap (39 of 103).

511   Higher female duet initiation rates are often attributed to a form of mate-guarding where

512   males create duets by responding to their partner's song to indicate her mated status (see

513   Levin 1996). However, if this were the case in superb fairy-wrens we would expect that

514   males should overlap significantly more of their partner's songs when the female is

515   fertile, which was not the case (no interaction between sex and breeding stage).

516

517   **Solo songs do not differ in structure from overlapped or overlapping songs**

518   The temporal and structural properties of superb fairy-wren solo songs and songs that

519   overlap were essentially indistinguishable, indicating that there is not a stereotyped song

520   structure exclusively used for song overlap, although there was a non-significant trend for

521   overlapped songs to be longer than non-overlapped songs. This could be a cooperative

522   behaviour where individuals extend their song when their partner overlaps their song

523 (Farabaugh 1983; Hall 2006), and possibly the early stages of duet evolution. However, it

524 is also possible longer overlapped song simply reflects the fact that longer songs are more

525 likely to be overlapped by chance (Searcy and Beecher 2009).

526

527 In addition to a stereotyped song structure, in some bird species the song type sung by the

528 first individual predicts the song type sung by the second (Logue 2006). Answering a

529 partners song with a particular song type occurs in many species (Todt and Naguib 2000).

530 Pairs in these species have been found to follow a duet 'code' when responding to their

531 partners song to form a duet (e.g. Logue, 2007; Seibt & Wickler 2000; Mennill &

532 Vehrencamp 2005; Rogers 2005). On a broad scale there is no evidence of this in superb

533 fairy-wrens as Type I and Type II songs were not overlapped or used to overlap other

534 songs more than expected by chance. Future studies that specifically characterise the

535 syllables of Type I songs and those involved in overlap would be beneficial to evaluate

536 further if particular song types are associated with song overlap (Rivera-Cáceres 2015).

537

538 **No consistent response interval between the start times of songs in response to a**

539 **stimulus**

540 Superb fairy-wrens have lower precision in response time compared to reports for other

541 duetting species. A large range of precision of response times have been reported, from

542 the very precise duets of bay wrens *Cantorchilus nigricapillus* (CV ~ 6%, Levin 1996) to

543 the less tightly coordinated rufous-and-white wrens *Thryophilus rufalbus* (CV = 45%,

544 Mennill and Vehrencamp 2005) and a range in between, such as in whipbirds *Psophodes*

545 *olivaceus* (CV = 25%, Rogers, 2005). The response times of superb fairy-wrens were less

546 variable in natural song (CV = 54%) than song in response to a playback (CV = 68%),

547 however this was probably due to different sampling, since the natural song calculation

548 included only songs that overlap, whereas the playback calculation included both

549 overlapping and non-overlapping songs. When put in context with other species the

550 comparatively large variance in the response time of superb fairy-wrens suggests that

551 responses are likely to be independent rather than coordinated. This suggests the

552 possibility that a CV for response times of 50% could be a cut-off for distinguishing

553 duetting from non-duetting species, but further research on species with occasional

554 overlap is required to determine whether there is a biologically meaningful cut-off. If the

555 variation in precision spans a continuum (with no natural break-point), this may indicate

556 that independent responses to intruders that result in overlapping songs could be a first

557 step in the evolution of duetting.

558

559 We did not find less variable response times to a partner than to playback. This suggests

560 that individuals were not coordinating songs with their partner. Moreover, playbacks that

561 were designed to simulate a territorial intruder rarely elicited a song from both members

562 of a pair. These results suggest that overlapping songs in superb fairy-wrens are not

563 duets; they lack the temporal coordination that defines duets and they are not used

564 routinely in one of the most common contexts for duetting, territorial defence. It is

565 possible that individuals may be signal jamming each other's song as a form of mate

566 guarding as this does not require temporal coordination (Grafe and Bitz 2004). Further

27

567   investigation is required to explore the function of song overlap of superb fairy-wrens.

568   Due to this lack of temporal coordination, we hypothesise that song overlap in superb

569   fairy-wrens is most likely to occur through a combination of chance, due to the high song

570   rates of both sexes, and as a by-product of both individuals responding independently to

571   the same stimulus (Logue 2006), and/or pair members calling to and answering one

572   another.

573

574   **Conclusions and future directions**

575   This is the first study to assess quantitatively the temporal coordination between male and

576   female *Malurus* songs. Close relatives of superb fairy-wrens, red-backed fairy-wrens

577   *Malurus melanocephalus* (Dowling and Webster 2013; Dowling and Webster 2016) and

578   purple-crowned fairy-wrens *Malurus coronatus* (Hall and Peters 2008) have been

579   classified as duetters, based on evidence that their songs overlap more than expected by

580   chance. However, consideration of this criterion for duetting alone neglects the other

581   aspects of the definition of duetting, particularly disentangling whether birds are

582   responding to each other or responding to the same external stimuli (e.g. neighbour or

583   intruder song), which is an important feature to help distinguish between songs

584   overlapping by chance and a coordinated signal. The evidence presented in this paper

585   gives a more definitive conclusion and highlights the need for rigorous testing of

586   temporal coordination in proposed duetters.

587

588   The conclusion that superb fairy-wrens are not duetters is also consistent with the strong

589   phylogenetic signal associated with duetting (Logue and Hall 2014) as their sister

590   species, the splendid fairy-wren *Malurus splendens*, is also considered a non-duetting

591   species based on the current evidence, although research into temporal coordination in

592   this species is needed (Greig and Pruett-Jones 2008). As superb fairy-wrens possess

593   some, but not other, characteristics of duetting species, this suggests the characteristics of

594   duetters that are lacking in superb fairy-wrens (such as sexual monomorphism, no or low

595   extra pair paternity and occurrence in the tropics, Thorpe et al. 1972; Farabaugh 1982;

596   Kingma et al. 2009), may be more important in favouring the evolution of duetting.

597   Further comparative research on species within the genus *Malurus*, which displays a

598   spectrum of the key characteristics and duetting behaviour (Rowley and Russell 1997),

599   would be valuable for elucidating the importance of shared characteristics of duetting

600   species. By extension, more quantitative studies on species that are suspected to sing less

601   coordinated duets, particularly polyphonic duets, to classify displays according to the

602   level of temporal precision, would help to further refine the definition of duetting. This

603   insight may also give a better understanding of early stages of duet evolution and the

604   ecological and social contexts which favour its evolution.

605

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730   TABLES AND TABLE LEGENDS

731   Table 1 Structural variables measured to quantify the structural properties of solo, overlapped

732   and overlapping songs and a description of each variable.

Variable	Description
Peak frequency (kHz)	the frequency at the highest amplitude
5% frequency (kHz)	the frequency which splits the total range of the frequency into a section containing 5% of the total energy and 95% of the total energy
95% frequency (kHz)	the frequency which splits the total range of the frequency into a section containing 95% of the total energy and 5% of the total energy
90% bandwidth (kHz)	the difference in frequency between the 5% frequency and the 95% frequency
Duration (seconds)	Length of the whole song

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746   Table 2 Tests for song overlap above chance levels by males and females.

Pair	Number of songs	**Female overlap of social mate song**		**Male overlap of social mate song**	
		Randomisation	Duty cycle	Randomisation	Duty cycle
		P-value	P-value	P-value	P-value
1	19	0.163	0.255	0.350	0.348
2	46	0.002*	0.001*	0.010*	0.105
3	14	0.023*	0.004*	0.048	0.004*
4	24	0.079	0.079	>0.990	0.604
5	9	0.025*	0.005*	>0.990	0.812
6	12	0.062	0.007*	0.004*	0.000*
7	21	0.179	0.112	0.196	0.082
8	12	0.062	0.038*	0.039	0.000*
9	16	>0.990	0.726	0.006*	0.000*
10	13	>0.990	0.816	<0.010*	0.000*
11	17	0.182	0.688	0.333	0.000*
12	10	0.113	0.000*	>0.990	0.809

13	21	0.073	0.000*	0.033	0.076
14	20	0.071	0.028*	0.008*	0.000*
15	35	>0.990	0.548	0.007*	0.291
16	16	>0.990	0.687	0.015*	0.000*
17	9	>0.990	0.730	0.069	0.001*
18	7	>0.99	0.872	0.005*	0.000*
19	28	0.121	0.342	0.430	0.960
20	27	0.029	0.003*	0.009*	0.005*
21	29	0.200	0.116	0.008*	0.000*
22	26	>0.990	0.697	<0.010*	0.000*
23	15	>0.990	0.723	0.002*	0.000*
24	29	0.122	0.448	0.115	0.148
25	32	0.001*	0.000*	0.160	0.004*
26	14	0.111	0.066	0.085	0.011*
27	57	0.182	0.258	0.001*	0.000*
28	86	0.823	0.737	0.448	0.119
29	33	0.237	0.257	0.286	0.251
30	13	1	0.715	1	0.736
31	15	1	0.771	1	0.714
32	12	1	0.806	1	0.737

33	8	1	0.809	1	0.814
34	9	1	0.801	1	0.826
35	9	1	0.784	1	0.781
36	30	1	0.441	1	0.487
37	22	1	0.632	1	0.560
38	14	1	0.692	1	0.598

The singing behaviour of the male and female in each pair was assessed by two analysis methods: randomisation and duty cycle. Disagreement in the results between the two methods is highlighted. Individuals that overlap their partner's songs more often than expected by chance are indicated with asterisks and the number of songs in each focal watch assessed is listed.

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770   Table 3 Mixed model analysis of the effect of breeding stage, sex and neighbour song on the
771   number of an individual's songs that were overlapped by their partner per focal watch.
772   Significant p-values have been italicized, and effect size and standard error have been included
773   for the significant term, (n = 92 focal watches of 43 individuals).

fixed term	$β±s.e$	F	n.d.f.	d.d.f.	p-values
neighbour song	0.997 ± 0.343	20.21	1	133.9	*<0.001*
sex		0.13	1	125	0.718
breeding stage		0.11	2	131.1	0.893
sex x breeding stage		0.14	2	123.6	0.871
sex x neighbour song		0.01	1	122.5	0.909
breeding stage x neighbour song		0.96	2	141.9	0.387
random effects		variance component			
pair ID		0.646			

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788   Table 4 The average values and standard deviation for song variables measured for each song
789   class (solo n = 37, overlapped n = 18 and overlapping n = 13).
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song class	duration (s)	90% bandwidth (kHz)	peak frequency (kHz)	5% frequency (kHz)	95% frequency (kHz)
overlapped	3.05 ± 0.81	2593.56 ± 750.81	6440.83 ± 679.21	4976.56 ± 831.20	7570.12 ± 485.35
overlapping	2.53 ± 0.91	2716.50 ± 536.31	6042.55 ± 939.51	4889.69 ± 698.12	7606.18 ± 869.46
solo	2.45 ± 0.96	2481.56 ± 578.58	6303.99 ± 606.45	4967.76 ± 652.19	7449.33 ± 606.91

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804 Table 5 Mixed model analysis of the type of songs (type I [n = 366] or II [n = 38]) in each song
805 class (solo [n = 310], overlapped [n = 49] and overlapping [n = 45]), with an overall sample size of
806 404 songs. Significant p-values have been italicised, and effect size and standard error have
807 been included for each level of the significant terms.

fixed term		β±s.e	F	n.d.f.	d.d.f.	p-values
song type	overlapped	0.000 ± 0.393	11.65	1	46.7	*0.001*
	overlapping	0.095 ± 0.825				
	solo	1.791 ± 0.242				
song class	type I	0.000 ± 0.219	40.79	2	44.2	*<0.001*
	type II	-0.479 ± 0.617				
song type x song class			0.36	2	43.9	0.703
random effects		**variance component**				
individual ID		0.753				

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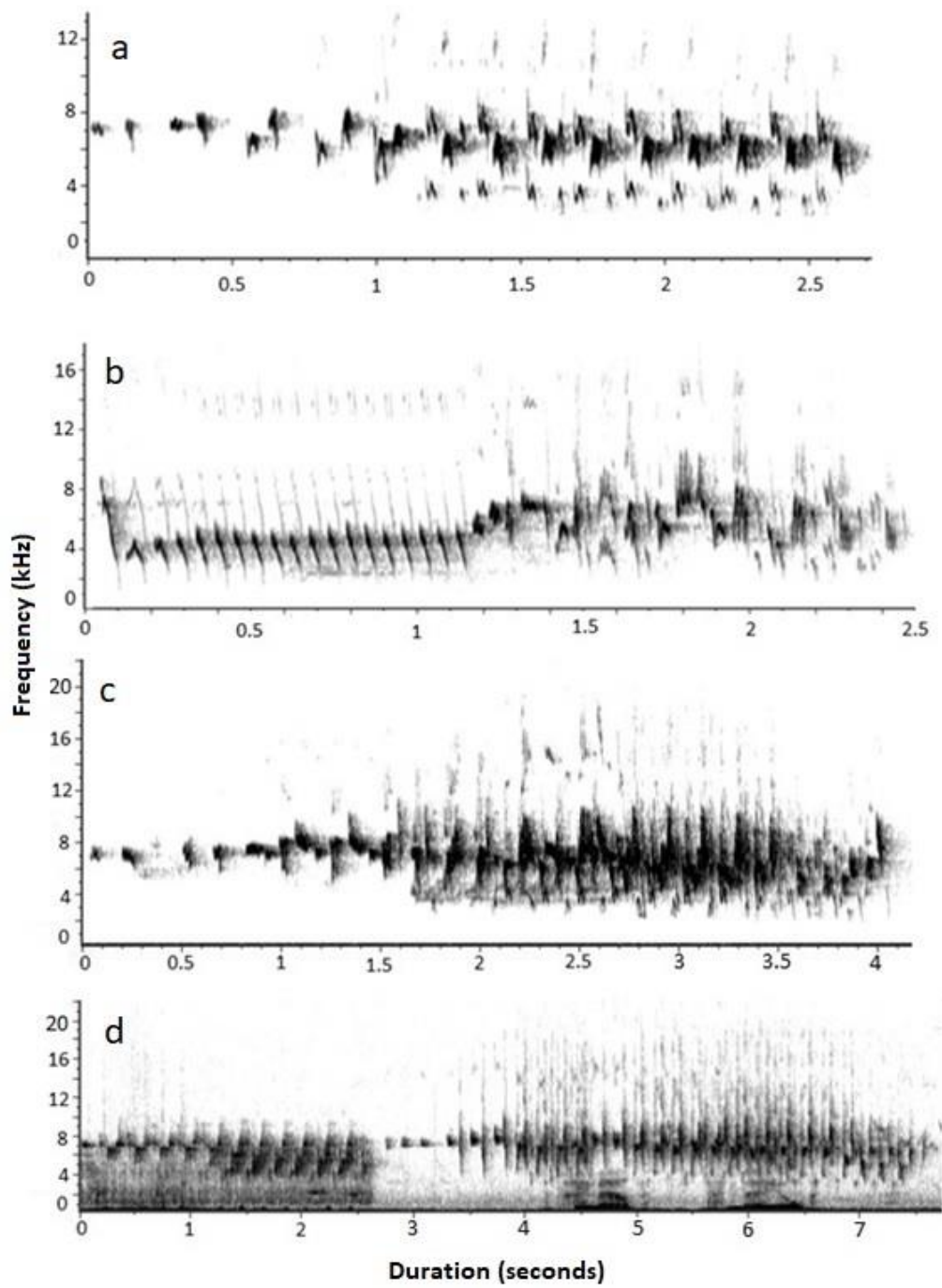
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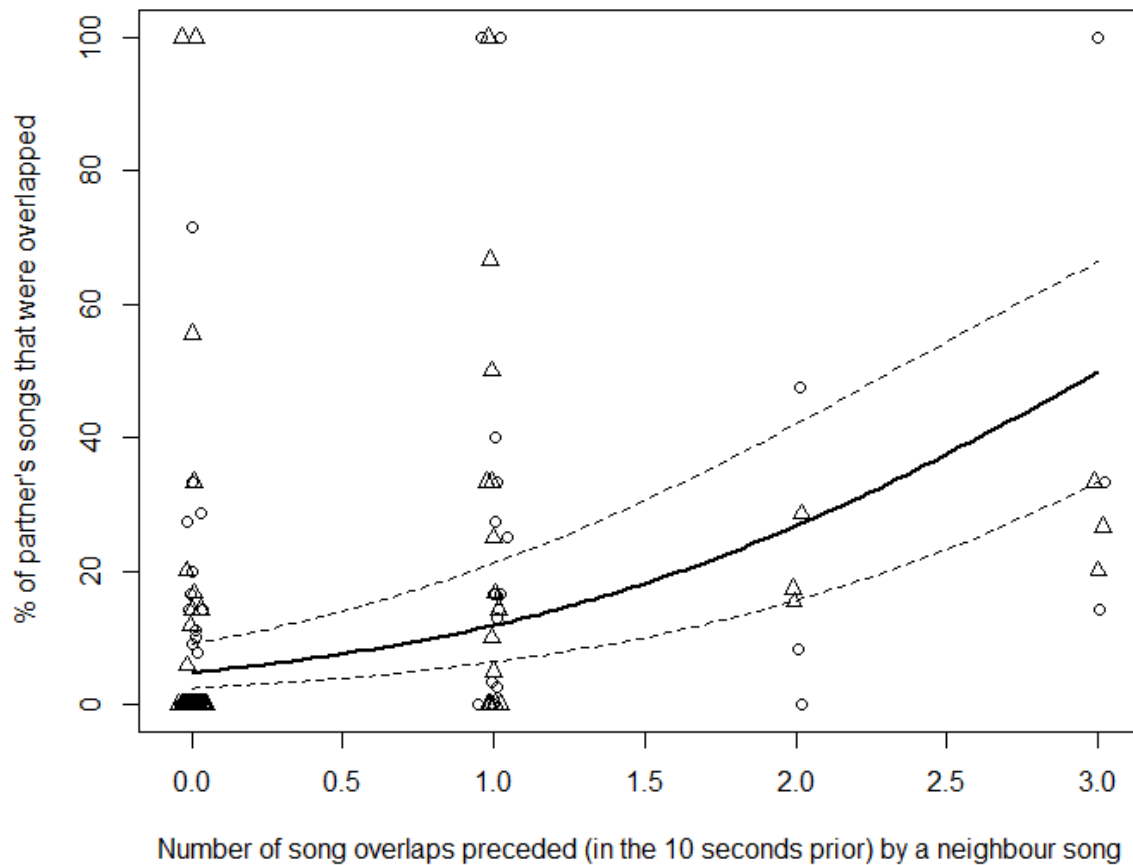
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Figure 1 Spectrogram of a solo (a) Type I and (b) Type II song, (c) a female and male song overlapping all recorded during focal watches and (d) a playback stimulus song and response.

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Figure 2 The percentage of the partner's songs that the individual overlaps increased
with the number of song overlaps that were preceded by a neighbour's song (in the
preceding 10 seconds). The solid trend line indicates that with more instances of
neighbour song in the preceding 10 seconds a higher percentage of the opportunities to
overlap the song of the individuals' partner were taken. The dotted lines show the 95%
confidence interval. For each focal watch (N =92), females are represented with a
triangle and males with a circle.

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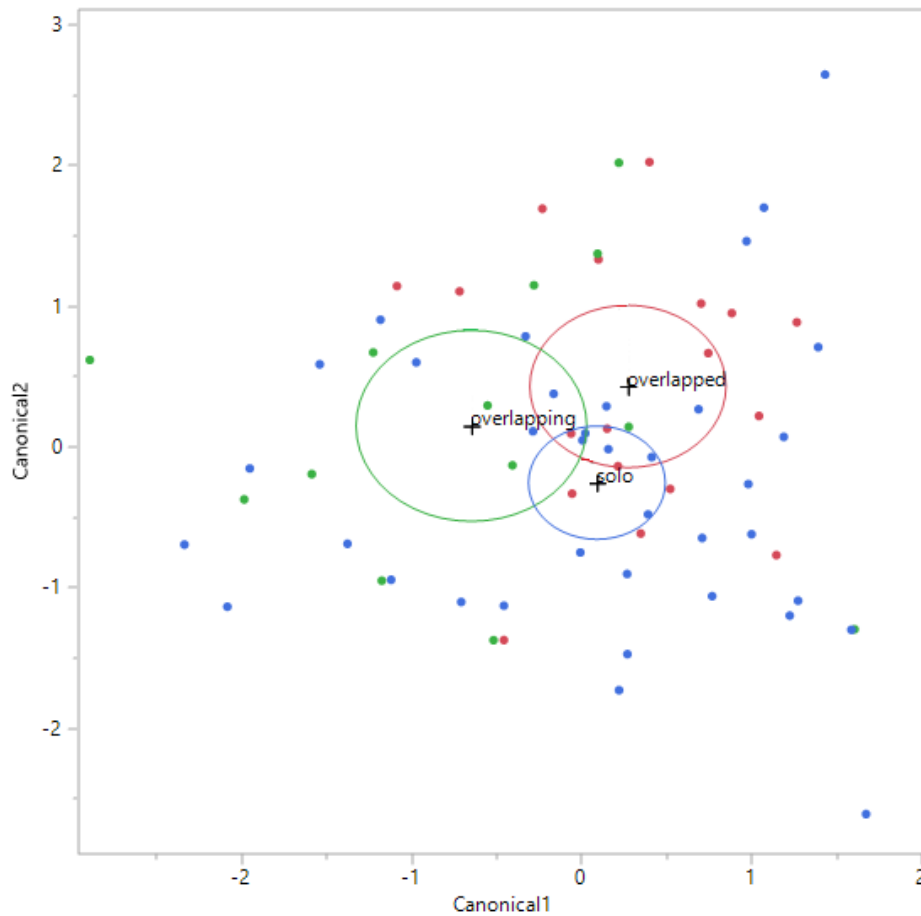
Figure 3 Canonical plots from discriminant function analysis showing no significant
structural difference between solo, overlapped and overlapping songs (N = 37 solo
songs, 18 overlapped songs and 13 overlapping songs). The colour of the points is
consistent with the colour of the circle surrounding the song class, indicating the data
spread for each song class. The multivariate means' in the discriminant function analysis
are individually depicted with a circle. The size of the circle is comparatively
representative of the sample size as it represents the mean with a 95% confidence limit.
Non-intersecting circles indicate groups that are significantly different.

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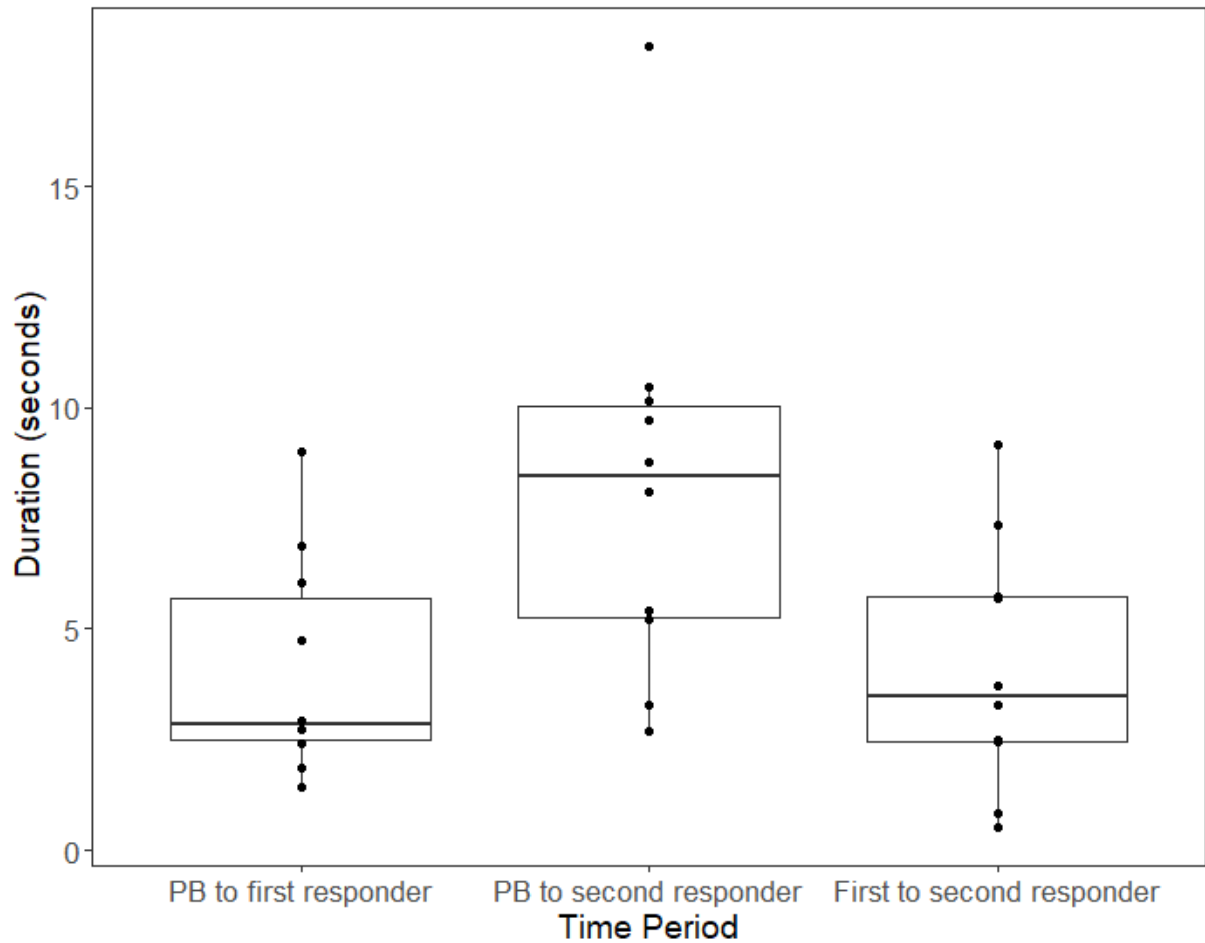
Figure 4 The duration of time periods between the start of the playback (PB) and the start of the first responders song, the start of the PB and the start of the second responders song, and the start of the first responders song and the start of the second responders song. Showing the minimum and maximum values (indicated by the whiskers), the first and third quantile (forming the upper and lower lines of each box) and the median value (the bold line in the box), as well as points showing the data spread and an outlier.

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