

1 **The structure and context of male and female song in dippers**

2

3 Lucy Magoolagan^{1*}, Peter J. Mawby², Flora A. Whitehead³ and Stuart P. Sharp¹

4

5 ¹Lancaster Environment Centre, Lancaster University, UK

6 ²Lowhill, Haverbreaks Road, Lancaster, LA1 5BJ, UK

7 ³Hole House, Garsdale, Sedbergh, Cumbria, LA10 5NX, UK

8 *Correspondence:

9 L. Magoolagan, Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ

10 Email: lucy.magoolagan@hotmail.co.uk

11 ORCID: 0000-0002-1961-1114

12 Tel: +447825578275

13 Word count: 4,347

14

15

16 **ACKNOWLEDGEMENTS**

17

18 We would like to thank the many local landowners and Paul Wilkinson at Yorkshire Dales National Park for
19 providing access and supporting our work; all of the students and volunteers who provided assistance in the
20 field, especially Tess Moore; Robert Lachlan for advising on acoustic analyses; and Mark Mainwaring, Rupert
21 Marshall and Jos Barlow for comments on an earlier draft. LM was supported by a NERC studentship.

22

23 **Abstract**

24 Female song in birds is more widespread than previously thought but remains poorly studied.
25 Relatively few researchers have compared the structure and function of female song with that of conspecific
26 males, especially in non-duetting species. Here, we investigate male and female song in the Dipper (*Cinclus*
27 *cinclus*), a highly territorial and largely monogamous passerine with a complex song in both sexes. The songs of
28 individually marked birds were recorded over a three-year period in order to compare the acoustic structure and
29 production of song in males and females at different stages of the breeding cycle. No differences were found in
30 the complexity, frequency or temporal characteristics of male and female songs. However, unpaired males
31 recorded early in the breeding season sang more complex songs than males that were paired up and nest-
32 building or whose breeding attempts were underway, suggesting that male song is used for mate attraction. By
33 contrast, females sang most often during aggressive encounters with birds from outside their territory.
34 Furthermore, males sang throughout the breeding season when they are highly territorial, whereas females rarely
35 sang after laying had begun. Together, these results support findings from other species that song structure
36 varies with context and suggest that female song in Dippers may be used primarily in mate or territory defence.

37

38 Keywords: acoustic structure, birdsong, *Cinclus cinclus*, Dipper, female song, vocal communication

39 **Introduction**

40

41 The two main functions of song in male birds are mate attraction and territorial defence (Catchpole and
42 Slater, 2008). Song is thought to be an honest signal of male quality because it is costly to produce (Searcy and
43 Yasukawa, 1996; Nowicki, Peters and Podos, 1998; Gil and Gahr, 2002; Catchpole and Slater, 2008). While
44 several studies have shown that song production may not be demanding in terms of metabolic energy
45 consumption (Franz and Goller, 2003; Ward, Lampe and Slater, 2004), singing at a high amplitude or from
46 obvious song posts can increase predation risk (Gil and Gahr, 2002) and time spent singing is time taken away
47 from other activities such as foraging (Oberweger and Goller, 2001). The complexity of male song is widely
48 considered to be a sexually selected trait in many species (Searcy and Andersson, 1986; Catchpole, 1987;
49 Macdougall-Shackleton, 1997; but see Byers and Kroodsma, 2009) and, in some cases, the size of regions of the
50 brain such as the HVC is positively correlated with song complexity and the ability to learn a larger quantity of
51 songs or song components (Nowicki, Searcy and Peters, 2002; Pfaff *et al.*, 2007; but see Gahr, 2007; Hall *et al.*,
52 2011).

53 Repertoire size is a measure of the number of either unique songs or syllable types used by an
54 individual (Hiebert, Stoddard and Arcese, 1989; Potvin and Clegg, 2015). In many species, males and females
55 are sensitive to the diversity of syllables within a song, and repertoire size is thought to play an important role in
56 intrasexual selection, mate choice and reproductive stimulation (Searcy and Yasukawa, 1996; Nowicki, Peters
57 and Podos, 1998; Gil and Gahr, 2002). Correlations have been found between repertoire size and a number of
58 individual and life history traits including condition (Kipper *et al.*, 2006), territory size (Buchanan and
59 Catchpole, 1997) and tenure (Hiebert, Stoddard and Arcese, 1989; but see Beecher *et al.*, 2000), parental effort
60 (Buchanan and Catchpole, 2000) and reproductive success (Potvin, Crawford, Macdougall-Shackleton, and
61 MacDougall-Shackleton, 2013). Furthermore, several studies have shown that song complexity (Järvi, 1983;
62 Nelson and Croner, 1991; Ammer and Capp, 1999) and specific acoustic characteristics (Catchpole, 1983; Nagle
63 and Couroux, 2000) can change with motivation, season or age. For instance, it has been shown that migratory
64 and sedentary Blackcap (*Sylvia atricapilla*) populations have different intra- and inter-sexual song
65 characteristics (Collins *et al.*, 2009).

66 Female song was once thought to be rare but recent work has shown that it is widespread, especially in
67 the tropics and Australasia (Odom *et al.*, 2014; Hall and Langmore, 2017). Most research has focussed on
68 duetting species (Langmore, 1998; Slater and Mann, 2004; Logue and Krupp, 2016) but far less is known about

69 the function of solo female song in other birds. In some cases there is evidence for a role in territory or resource
70 defence, including monogamous species with year-round territoriality (Brunton and Li, 2006; Price *et al.*, 2008;
71 Tobias *et al.*, 2016) and polygynous species such as the Red-winged Blackbird (*Agelaius phoeniceus*), in which
72 females defend their own sub-territories within a male's territory (Beletsky, 1982). In other cases it may reduce
73 the incidence of polygyny (Langmore, 1998), coordinate breeding activities (Ritchison, 1983) or maintain pair
74 bonds (Hovekamp, 1996). Mate attraction has rarely been reported as the function of female song, although this
75 has been suggested for the polygynandrous Alpine Accentor (*Prunella collaris*; Langmore *et al.* 1996).
76 However, female song can be easily overlooked in species where individuals only sing for a small window of
77 the breeding season or in monomorphic species where it is difficult to distinguish between the sexes (Langmore,
78 1998; Hahn, Krysler and Sturdy, 2013; Odom and Benedict, 2018). Moreover, few studies have directly
79 compared the acoustic structure of male and female song, or the behavioural and seasonal contexts in which the
80 two sexes sing. In House Wrens (*Troglodytes aedon*), it has been shown that males use song for mate attraction
81 but both sexes can sing to defend resources or to communicate with their partner (Krieg and Getty, 2016). Such
82 comparisons may offer important insights into the function and evolution of female song in other non-duetting
83 species.

84 Here, we investigate the structure and potential functions of song in male and female White-Throated
85 Dippers (*Cinclus cinclus*, hereafter 'Dippers'). The Dipper is a sexually monochromatic, riverine songbird that
86 defends linear territories year-round and is one of relatively few passerines of the Northern temperate zone in
87 which both sexes are known to sing regularly (Tyler and Ormerod, 1994; Odom *et al.*, 2014; Odom and
88 Benedict, 2018). Song in Dippers has been reported year-round with the exception of the late summer months
89 when birds undergo a post-breeding moult (Tyler and Ormerod, 1994). High rates of song have been noted
90 particularly during territory settlement and defence, early in the breeding season (Tyler and Ormerod, 1994).
91 The song has been described as "a very sweet rippling warble" with female song "a less sweet series of whistles
92 and disconnected units", but no formal analysis of song has been carried out to date (Cramp and Simmons,
93 1988; Villain *et al.*, 2017). We recorded and analysed the songs of individually marked birds in a wild
94 population in order to compare: (1) the acoustic structure of male and female song; (2) the acoustic structure of
95 song produced at different stages of the reproductive cycle; and (3) the seasonal patterns in song production for
96 males and females.

97

98

99 **Methods**

100

101 **Song recording and spectrogram production**

102

103 Song was recorded from January to July (2014-2016) in a marked population of 40-50 pairs of Dippers
104 in the River Lune catchment near Sedbergh, Cumbria, UK (54°323'N, 2°528'W). Each year, all unmarked
105 adults are trapped and ringed using mist nets or hand nets placed over the nest; nestlings are ringed when they
106 are nine days old. Every individual is given a unique combination of three plastic colour rings and a standard
107 British Trust for Ornithology metal ring. All individuals were identifiable from their unique combination of
108 colour rings and had been sexed at capture according to their wing length (Andersson and Wester, 1971;
109 Svensson, 1992); for most individuals, sexing could be confirmed from observations of reproductive behaviour
110 (e.g. incubation is carried out by the female only; Tyler & Ormerod 1994) and in no cases was there a
111 discrepancy between the two methods. Each year, all nests within the study population were found and closely
112 monitored to record parental identity, the timing and outcome of reproduction, and a number of behavioural and
113 life history traits. Within this population, some pairs remain together throughout the winter but other individuals
114 start to pair up in January or early February. Nest-building typically begins in late February or March and most
115 clutches are laid in March and April; the female alone incubates the eggs (for 16-17 days) but both parents then
116 provision the offspring throughout the nestling period (21-22 days), with the last nests fledging in June or early
117 July. Dippers are socially monogamous with a low frequency of extrapair paternity (Øigarden, Borge and
118 Lifjeld, 2010), and adults in the study population typically breed for 2-3 years but exceptionally up to 8 years
119 (SPS, unpublished data).

120 Songs were recorded from distances of 10-15m using a Sennheiser ME66-K6 shotgun microphone with
121 a Rycote Softie windshield and a standard pistol grip connected to a Marantz PMD661 MKII solid state recorder
122 with a sampling frequency of 44.1 kHz; files were stored in WAV format. The site was visited daily throughout
123 the breeding season in 2014 and from January to May in other years, with only a few exceptions due to extreme
124 weather conditions; sampling effort was spread evenly across the field site throughout these periods, with each
125 territory visited at least once per week. Recordings were made opportunistically after May in 2015 and 2016.
126 Upon sighting a given individual, the observer waited 30 minutes; if it did not produce song in that time the
127 observer moved onto the next individual. If a focal individual (male or female) began to sing this was recorded
128 until the bird: (1) disappeared and could not be relocated; (2) changed behaviour, e.g. to foraging; (3) remained

129 silent for 30 minutes; or (4) had been recorded for more than an hour and a large amount of song had been
130 collected. Complete songs were defined as having a minimum of a 0.5 s pause between them. The mean (\pm SD)
131 pause between syllables was 0.23 ± 0.05 s (range = 0.11-0.33; n = 10 songs from each of 45 individuals). The
132 mean pause between songs was 6.50 ± 3.70 s (range = 0.6-64.0; n = 10 pairs of successive songs from 26
133 individuals).

134

135 **Acoustic structure**

136

137 A minimum of 10 songs was recorded for each of 34 males and 11 females. In order to standardise the
138 number of songs analysed (see below) but maximise the number of individuals included, analyses were
139 restricted to 10 songs per bird. If more songs than this had been recorded for a particular individual, 10 were
140 selected after those with the lowest signal to noise ratio had been excluded. For each individual, all 10 songs
141 were recorded in the same 2-3 week period and birds were categorised according to their breeding stage during
142 this time (see below). A number of complexity, frequency and temporal song characteristics were then measured
143 for each individual and compared between males at different breeding stages, and between males and females
144 recorded at the same stage. These measures were as follows: syllable diversity and versatility (complexity);
145 maximum, minimum and average peak frequency (frequency); and average song length, average syllables per
146 second and song rate (temporal).

147 Syllable repertoire size in Dippers appears to be large. We carried out preliminary analyses of this trait
148 using simple enumeration (Botero *et al.*, 2008), but when plotting the cumulative number of unique syllables
149 against the total number of syllables analysed, the curve for only 1 out of 45 individuals reached an asymptote.
150 One individual, for which 22 songs had been recorded and analysed, was found to produce in excess of 157
151 unique syllables with no asymptote reached. Rather than estimating syllable repertoire size, we therefore
152 calculated the number of unique syllables produced in a standardised sample of 10 songs (hereafter, 'syllable
153 diversity'), the minimum number of songs recorded with sufficient quality for analysis. This was considered a
154 biologically meaningful sample as individuals rarely produce more than 10 songs in a single bout, hence most
155 receivers would typically hear fewer songs before responding (LM, unpublished data).

156 Syllable diversity was measured using visual and auditory inspections of spectrograms (Fig. 1),
157 produced using Avisoft SASLab Pro, version 5.2.08 (Specht, 1993), with a 512-point fast Fourier transform
158 length and Hamming window function, 75% frame size, a 87.5% window overlap 86 Hz frequency resolution

159 and 1.45 ms time resolution. All songs were also high pass filtered at 1 kHz to remove low frequency
160 background noise (e.g. the sound of the river); this threshold was chosen because preliminary analyses revealed
161 that a small number of Dipper songs contained elements as low as 1.03 kHz. First, elements were identified (the
162 smallest continuous tracing on a spectrogram) which were then grouped into syllables where appropriate.
163 Syllables comprised multiple elements, each of which was never produced in isolation; the pause between
164 elements within a syllable was less than 0.1 s and therefore smaller than the minimum pause between syllables.
165 Measurements were first carried out in full by one observer (LM), with each unique syllable being given an
166 identifier. This process was then validated by a second observer (SPS) using a sub-sample of songs and applying
167 the same procedures but without knowing the previous results. Using one full song from each of 10 individuals,
168 93.9% of all syllables (= 279/297) were catalogued in the same way by both observers and there was no
169 significant difference in the total number of unique syllables per song measured by the two (paired t-test: $t =$
170 1.309 , $df = 9$, $P = 0.223$; 9 measures differed by 1 and the other differed by 2). Versatility was calculated by
171 dividing the number of unique syllables found within one song by the total number of syllables found in that
172 song (Järvi, 1983). This measure was then averaged across each of an individual's 10 songs.

173 A range of frequency and temporal characteristics were also measured using Luscinia version
174 2.02.10.15; spectrograms were produced using a fast Fourier transformation with a Gaussian analysis window,
175 80% spectrogram overlap, 10 kHz max frequency, 5 ms frame duration, 1 ms time step and 2 dB noise removal
176 (Lachlan, 2007). All measurements were based on peak frequency, which is the frequency of maximum
177 intensity (i.e. highest amplitude) for each syllable; this was calculated from 50 measurements taken across every
178 syllable in each song (using the standard settings in Luscinia). The maximum, minimum and average (per
179 syllable) peak frequency (in kHz) were taken for each individual from the total sample of songs. Average song
180 length (in seconds) was calculated across the 10 songs to the nearest 0.05 s; average syllables per second was
181 calculated by dividing the number of syllables found in each song by song length and then averaging over the 10
182 songs analysed for each individual. Song rate was calculated using the number of complete songs produced
183 within a single 30-minute period of observation for each individual during which the bird sang at least once,
184 starting at the time when the bird was first observed singing.

185

186 **Breeding stage**

187

188 For every individual, the breeding stage was classified according to the paired status and reproductive
189 stage of the bird at the time of recording. Three mutually exclusive categories were defined: (1) 'solo' songs
190 were those of individuals recorded in January or February that had yet to be seen with a partner; (2) 'pre-
191 breeding' songs were given by individuals that had been seen with the same partner on at least two occasions
192 foraging, prospecting or nest-building together; and (3) 'breeding' songs were those of individuals which had
193 paired up and had nests at the laying, incubation or nestling stage. The identity of any conspecifics which could
194 be seen by the observer, other than the breeding partner of the singer, was recorded whenever possible. Each
195 individual's 10 songs were recorded during the same breeding stage (the first in which the complete sample size
196 of 10 songs was obtained), so comparisons of songs produced at different stages were not pseudoreplicated
197 (males: n = 10 solo, 14 pre-breeding and 10 breeding; females: n = 2 solo, 8 pre-breeding and 1 breeding).
198 Insufficient recordings were obtained to allow comparisons of the songs produced by the same individual (male
199 or female) at different breeding stages. Statistical comparisons between the sexes were restricted to pre-breeding
200 individuals due to the small sample of females recorded singing at other stages; similarly, statistical
201 comparisons between stages were restricted to males. Solo females are rarely encountered as they are highly
202 mobile (SPS, unpublished data) and only a single breeding female was ever recorded singing.

203

204 **Female song context and seasonal trends**

205

206 To further investigate the possible function of female song, all observations over the data collection
207 period were classified according to the behavioural context in which the song was produced: (1) 'aggression'
208 described situations in which a singing female was observed in the presence of at least one conspecific other
209 than her partner and during which antagonistic behaviour (e.g. chasing or fighting) was observed; (2) 'nest-
210 building' was used for songs recorded during the prospecting or nest-building phase of the breeding season
211 which were almost always given in the presence of her mate; and (3) 'other' was used for the small number of
212 songs recorded which could not be classified into either of the other contexts. The use of song in these contexts
213 was then compared over the season by using the context in which each female was first recorded singing in each
214 month; only one female produced song in more than one context per month, and only on a single occasion.

215 To investigate seasonal variation in song production, the proportion of individuals of each sex which
216 sang at least once during a sampling session was calculated for every day of the 2014 season (mean number of
217 individuals sampled per day = 4.59 ± 2.44). Data from 2015 and 2016 were excluded due to insufficient

218 coverage during the latter part of the season in those years. All dates were converted to a Julian date (1 = 1st
219 January).

220

221 **Statistical analysis**

222

223 To compare the acoustic structure of male and female song, t-tests and Mann-Whitney U tests were
224 carried out for normally and non-normally distributed song characteristics, respectively. The songs of males in
225 different contexts were compared using one-way ANOVAs for parametric data and Kruskal-Wallis tests for
226 non-parametric data, with post-hoc Tukey tests or Dunn tests, respectively. All analyses were carried out in R,
227 version 3.2.2 (R Core Team, 2015). We used the Benjamini–Hochberg false discovery rate procedure to control
228 for multiple testing and provide adjusted P values accordingly (Benjamini and Hochberg, 1995).

229

230

231 **Results**

232

233 **Acoustic structure, sex and breeding stage**

234

235 There was no significant difference between the songs of pre-breeding males and pre-breeding females
236 in any of the complexity, frequency or temporal characteristics measured (Table 1, Fig. 2). However, males
237 singing at different breeding stages used significantly different numbers of unique syllables (Table 2); post-hoc
238 tests showed that solo males had a significantly higher syllable diversity than pre-breeding males ($q = 3.48$, $P =$
239 0.02) or breeding males ($q = 3.48$, $P = 0.02$; Table 2, Fig. 2a). Furthermore, versatility was significantly lower in
240 songs from breeding males than in those from males at other breeding stages (versus solo males: $q = 3.48$, $P <$
241 0.001 ; versus pre-breeding males: $q = 3.48$, $P = 0.01$; Table 2, Fig. 2b).

242 There was no difference in any of the frequency characteristics or in the average length of male songs
243 produced at different breeding stages (Table 2). The number of syllables per second was higher in the songs of
244 breeding males than in those of males from the other stages (Fig. 2c), and song rate was higher in solo males
245 than pre-breeding or breeding males (Fig. 2d); however, these differences were marginally non-significant after
246 correcting for multiple testing (Table 2).

247

248 **Female song context and seasonal trends**

249

250 Female song was frequently recorded during aggressive encounters in the early part of the season (Fig.
251 3). In the encounters during which all individuals present were identified, the female was singing during an
252 interaction with a lone female on five occasions, a lone male on two occasions and a pair on three occasions.
253 The remaining two observations involved unringed individuals and so their sex was unknown. Some females
254 also sang during the nest-building period and occasionally in other contexts, but song was less frequently
255 recorded later in the season (Fig. 3). This seasonal decline was also apparent from the decrease in the proportion
256 of observed females which were recorded singing as the season progressed (Fig. 4b). The proportion of
257 observed males which were recorded singing also peaked early in the season but remained at a relatively high
258 level throughout (Fig. 4a).

259

260

261 **Discussion**

262

263 No differences were detected in the acoustic structure of songs produced by male and female Dippers.
264 This may be because analyses were restricted to pre-breeding individuals and songs produced during this stage
265 might play a similar role in the two sexes. For example, pre-breeding song may function primarily in territorial
266 defence, which is carried out by both males and females (Tyler and Ormerod, 1994; Logue and Krupp, 2016), or
267 the coordination of breeding activities. Alternatively, there may be sexual differences in song characteristics
268 which were not measured here. Studies of other species have reported a difference between males and females
269 in several acoustic parameters which may facilitate sex discrimination, though such differences are sometimes
270 subtle (Yamaguchi, 1998; Pavlova, Pinxten and Eens, 2005; Geberzahn and Gahr, 2011); our sample sizes were
271 relatively small and further analyses are required, especially of songs at other breeding stages and, ideally,
272 including comparisons of the songs produced by the same individual at different stages.

273 Solo males were found to use significantly more unique syllables within their songs than males at other
274 breeding stages; they also sang at a higher rate, although this trend was no longer significant after correcting for
275 multiple testing. Breeding males produced songs with significantly lower versatility than those of other males
276 and there was a non-significant tendency for these songs to contain fewer syllables per second, suggesting
277 greater repetition. Variation in song characteristics according to an individual's breeding status has been

278 reported in several species (Ballentine, Badyaev and Hill, 2003; Hall and Langmore, 2017) and presumably
279 relates to the motivational state of the singer. In Dippers, the differences in complexity and song rate between
280 solo males and breeding males suggest that the former may use song for mate attraction. Singing is thought to be
281 an expensive behaviour, in terms of increased predation risk and reduced foraging time if not metabolic costs
282 (Mougeot and Bretagnolle, 2000; Gil and Gahr, 2002; Franz and Goller, 2003; Ward, Lampe and Slater, 2004),
283 and solo males may compensate for this through the increased probability of securing a mate. Measures of song
284 complexity such as syllable diversity or repertoire size are widely reported as sexually selected traits in other
285 species (Catchpole and Slater, 2008), and a similar role has been suggested for versatility (e.g. Järvi, 1983).
286 Further work on sexual selection in Dipper song should investigate the fitness consequences of variation in
287 complexity but might also focus on performance-based song traits, such as consistency, which are thought to be
288 important in some species (Podos, 1997; Botero *et al.*, 2010; but see Kroodsma, 2017).

289 Observations of females singing were most frequent during the start of the breeding season when
290 territory boundaries are being established between neighbours. Most female song was recorded during
291 aggressive encounters, usually involving another female, during which song presumably functions in defence,
292 either of a territory or a mate. Members of a pair may only defend against same-sex intruders, which would
293 increase the efficiency of defence (Langmore, 1998). This behaviour has been observed in Northern Cardinals
294 (*Cardinalis cardinalis*), in which female song was shown not to deter intrusions by new males but was thought
295 to deter other females (McElroy and Ritchison, 1996). In our study, female song was also recorded during nest-
296 building when the male was present and may play a role in pair-bonding or the coordination of breeding
297 activities, as has been shown in Black-headed Grosbeaks (*Pheucticus melanocephalus*; Ritchison, 1983).
298 Finally, on three occasions females were recorded singing when neither aggressive interactions nor nest-
299 building were taking place. In two cases, the same female was observed singing in the presence of a male who
300 was not her partner; this was at a time when egg-laying was imminent and it is possible that she may have
301 attempted to advertise her fertility to increase chances of extra-pair copulation (Baptista *et al.*, 1993). Another
302 female was observed singing in May whilst accompanied by her partner and when their chicks were a few days
303 from fledging; this female may have been using song to advertise her fertility in preparation for a second clutch
304 (Baptista *et al.*, 1993). Only twelve solo females were observed throughout the entire study, eight of which were
305 recorded singing (two with sufficient regularity to be included in our sample). While our results suggest that
306 mate attraction may not be the primary function of female song, it may be that solo females do sing to attract
307 males but are rarely encountered.

308 The seasonal decline in the production of song by females is likely due to the energetic constraints
309 imposed by parental care, particularly during incubation and brooding (Brunton, Evans, Cope, and Ji, 2008).
310 Singing on or near the nest may also compromise offspring survival by making nests more conspicuous to
311 predators (Kleindorfer, Evans and Mahr, 2016). In contrast, male song was recorded regularly throughout the
312 breeding season which is in keeping with a role in territorial defence and mate guarding. Our fieldwork ended
313 shortly after each breeding season, and future research on singing behaviour in the second half of the year may
314 shed further light on the different contexts in which both males and females sing.

315 Finally, it is worth noting that the average peak frequency used by both sexes is similar to that reported
316 for calls in this species, which are concentrated within a narrow frequency range of 4-6.5 kHz (Tyler and
317 Ormerod, 1994). This is likely to enable communication over long distances given the low frequency
318 background noise of their riverine environment (Tyler and Ormerod, 1994), and it has also been reported that
319 individuals sing more frequently in the quieter parts of their territory (Magoolagan, 2012). Even so, the
320 complexity of song has the potential to be masked by the noise of running water and it may be that the frequent
321 visual signals given by dippers, such as dipping, wing flashing and blinking, play a role in increasing perception
322 of song characteristics (Tyler and Ormerod, 1994; Johnstone, 1996).

323 In conclusion, our study provides one of relatively few direct comparisons of the acoustic structure and
324 seasonality of male and female song in a non-duetting species, together with evidence of context-specific song
325 characteristics in males. The results support previous findings that song structure can vary within a species
326 according to the breeding status of the singer. The observed differences in seasonality between the sexes may
327 simply reflect the energetic constraints of breeding in females, but may also arise from differences in song
328 function between males and females. While no structural differences were detected, sample sizes were relatively
329 small and comparisons were restricted to the pre-breeding stage; further analyses including playback
330 experiments are required to better understand functionality. Furthermore, it is still unknown whether song is a
331 sexually selected trait in female birds (Pavlova, Pinxten and Eens, 2005), and recent findings that female song
332 was likely present in the early ancestors of songbirds raise the question of why this trait has since been lost in
333 some species (Odom *et al.*, 2014; Hall and Langmore, 2017; Odom and Benedict, 2018). Analyses of the
334 relationship between song complexity and fitness would shed further light on the function and evolution of
335 female song in Dippers.

336

337

338 **Data availability**

339

340 The datasets analysed during the current study available from the corresponding author on reasonable
341 request.

342

343

344 **Compliance with ethical standards**

345

346 All procedures performed were in accordance with the ethical standards of Lancaster University. The
347 trapping and ringing of birds was licensed by the British Trust for Ornithology.

348

349

350 **References**

351 Ammer, F. K. and Capp, M. S. (1999) Song Versatility and Social Context in the Bobolink. *The Condor*, 101(3):
352 686–688.

353 Andersson, J. S. and Wester, S. A. L. (1971) Length of wing, bill, and tarsus as a character of sex in the Dipper
354 *Cinclus cinclus*. *Ornis Scandinavica*, 2(1): 75–79.

355 Ballentine, B., Badyaev, A. and Hill, G. E. (2003) Changes in song complexity correspond to periods of female
356 fertility in blue grosbeaks (*Guiraca caerulea*). *Ethology*, 109(1): 55–66.

357 Baptista, L. F., Trail, P. W., DeWolfe, B. B. and Morton, M. L. (1993) Singing and its functions in female
358 white-crowned sparrows. *Animal behaviour*, 46: 511–524.

359 Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. and Nordby, J. C. (2000) Song type matching between
360 neighbouring song sparrows. *Animal Behaviour*, 59: 21–27.

361 Beletsky, L. (1982) Aggressive response to “self” songs by female Red-winged Blackbirds, *Agelaius*
362 *phoeniceus*. *Canadian Journal of Zoology*, 61: 462–465.

363 Benjamini, Y. and Hochberg, Y. (1995) Controlling the False Discovery Rate : A Practical and Powerful
364 Approach to Multiple Testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1): 289–
365 300.

366 Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., Kort, S. R. De and Vehrencamp, S. L.
367 (2010) Syllable Type Consistency is Related to Age, Social Status, and Reproductive Success in the Tropical
368 Mockingbird. *Animal Behaviour*, 77(3): 701–706.

369 Brunton, D. H., Evans, B., Cope, T. and Ji, W. (2008) A test of the dear enemy hypothesis in female New
370 Zealand bellbirds (*Anthornis melanura*): Female neighbors as threats. *Behavioral Ecology*, 19(4): 791–798.

371 Brunton, D. H. and Li, X. (2006) The song structure and seasonal patterns of vocal behavior of male and female
372 bellbirds (*Anthornis melanura*). *Journal of Ethology*, 24(1): 17–25.

- 373 Buchanan, K. L. and Catchpole, C. K. (1997) Female choice in the sedge warbler *Acrocephalus schoenobaenus*:
374 multiple cues from song and territory quality. *Proceedings of the Royal Society B: Biological Sciences*,
375 264:521–526.
- 376 Buchanan, K. L. and Catchpole, C. K. (2000) Song as an indicator of male parental effort in the sedge warbler.
377 *Proceedings. Biological sciences / The Royal Society*, 267(1441): 321–326.
- 378 Byers, B. E. and Kroodsma, D. E. (2009) Female mate choice and songbird song repertoires. *Animal Behaviour*,
379 77(1): 13–22.
- 380 Catchpole, C. K. (1983) Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to
381 mate attraction and territorial defence. *Animal Behaviour*, 31(4): 1217–1225.
- 382 Catchpole, C. K. (1987) Bird song, sexual selection and female choice. *Trends in Ecology & Evolution*, 2(4):
383 94–97.
- 384 Catchpole, C. K. and Slater, P. J. B. (2008) *Bird song-biological themes and variations*. Cambridge University
385 Press.
- 386 Collins, S. A., de Kort, S. R., Pérez-Tris, J. and Tellería, J. L. (2009) Migration strategy and divergent sexual
387 selection on bird song. *Proceedings of the Royal Society B: Biological Sciences*, 276(1656): 585–590.
- 388 Cramp, S. and Simmons, K. E. L. (1988) *Handbook of the Birds of Europe, the Middle East and North Africa:*
389 *Tyrant Flycatchers to Thrushes v.5: The Birds of the Western Palearctic: Tyrant Flycatchers to Thrushes Vol 5.*
390 Oxford University Press.
- 391 Franz, M. and Goller, F. (2003) Respiratory patterns and oxygen consumption in singing zebra finches. *The*
392 *Journal of experimental biology*, 206: 967–978.
- 393 Gahr, M. (2007) Sexual Differentiation of the Vocal Control System of Birds. *Advances in Genetics*, 59: 67–
394 105.
- 395 Geberzahn, N. and Gahr, M. (2011) Undirected (solitary) birdsong in female and male blue-capped cordon-
396 bleus (*Uraeginthus cyanocephalus*) and its endocrine correlates. *PLoS one*, 6(10): 1-11.
- 397 Gil, D. and Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology*
398 *& Evolution*, 17(3): 133–141.
- 399 Hahn, A. H., Kryslar, A. and Sturdy, C. B. (2013) Female song in black-capped chickadees (*Parus atricapillus*):
400 acoustic song features that contain individual identity information and sex differences. *Behavioural*
401 *processes* 98: 98–105.
- 402 Hall, M. L. and Langmore, N. E. (2017) *Fitness Costs and Benefits of Female Song*. Lausanne: Frontiers Media.
403 DOI 10.3389/978-2-88945-258-3.
- 404 Hall, Z. J., MacDougall-Shackleton, S. A., Osorio-Beristain, M. and Murphy, T. G. (2011) Male bias in the song
405 control system despite female bias in song rate in streak-backed orioles (*Icterus pustulatus*). *Brain, Behavior and*
406 *Evolution*, 76(3–4):168–175.
- 407 Hiebert, S. M., Stoddard, P. K. and Arcese, P. (1989) Repertoire size, territory acquisition and reproductive
408 success in the song sparrow. *Animal Behaviour*, 37: 266–273. doi: 10.1016/0003-3472(89)90115-2.
- 409 Hovekamp, N. (1996) Intersexual Vocal Communication in the Red-Winged Blackbird (*Comunicación Vocal*
410 *Intersexual en Agelaius phoeniceus*). *Journal of Field Ornithology*, 67(3): 376–383.
- 411 Järvi, T. (1983) The evolution of song versatility in the willow warbler *Phylloscopus trochilus*: A case of
412 evolution by intersexual selection explained by the “female’s choice of the best mate”. *Ornis Scandinavica*,
413 14(2): 123–128.
- 414 Johnstone, R. A. (1996) Multiple Displays in Animal Communication: ‘Backup Signals’ and ‘Multiple
415 Messages’. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351(1337): 329–338. doi:
416 10.1098/rstb.1996.0026.

- 417 Kipper, S., Mundry, R., Sommer, C., Hultsch, H. and Todt, D. (2006) Song repertoire size is correlated with
418 body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Animal Behaviour*, 71(1):
419 211–217. doi: 10.1016/j.anbehav.2005.04.011.
- 420 Kleindorfer, S., Evans, C. and Mahr, K. (2016) Female in-nest chatter song increases predation. *Biology letters*,
421 12(1): 18–21. doi: 10.1098/rsbl.2015.0513.
- 422 Krieg, C. A. and Getty, T. (2016) Not just for males: Females use song against male and female rivals in a
423 temperate zone songbird. *Animal Behaviour*. Elsevier Ltd, 113:39–47. doi: 10.1016/j.anbehav.2015.12.019.
- 424 Kroodsma, D. (2017) Birdsong “performance” studies: a sad commentary. *Animal Behaviour*. 133: 209–210.
- 425 Langmore, N., Davies, N., Hatchwell, B. J. and Hartley, I. R. (1996) Female song attracts males in the alpine
426 accentor *Prunella collaris*. *Proceedings: Biological Sciences*, 263(1367): 141–146.
- 427 Langmore, N. E. (1998) Functions of duet and solo songs of female birds.. *Trends in ecology & evolution*,
428 13(4): 136–40.
- 429 Logue, D. M. and Krupp, D. B. (2016) Duetting as a Collective Behavior. *Frontiers in Ecology and Evolution*,
430 4: 7. doi: 10.3389/fevo.2016.00007.
- 431 Macdougall-Shackleton, S. A. (1997) Sexual Selection and the Evolution of Song Repertoires. in Nolan, V.,
432 Ketterson, E. D., and Thompson, C. F. (eds) *Current Ornithology*. Boston, MA: Springer US: 81–124. doi:
433 10.1007/978-1-4757-9915-6_3.
- 434 Magoolagan, L. (2012) Song site choice and ambient noise in White- throated dippers and a comparative
435 analysis of vocalisations in the family Cinclidae. Dissertation, Manchester Metropolitan University.
- 436 McElroy, D. and Ritchison, G. (1996) Effect of mate removal on singing behavior and movement patterns of
437 female northern cardinals. *The Wilson Bulletin*, 108(3): 550–555.
- 438 Mougeot, F. and Bretagnolle, V. (2000) Predation as a cost of sexual communication in nocturnal seabirds: an
439 experimental approach using acoustic signals. *Animal behaviour*, 60(5): 647–656. doi: 10.1006/anbe.2000.1491.
- 440 Nagle, L. and Couroux, C. (2000) The influence of Song Mode on Responses of Male American Redstarts.
441 *Ethology*, 106: 1049–1055. doi: 10.1046/j.1439-0310.2002.00781.x.
- 442 Nelson, D. A. and Croner, L. J. (1991) Song Categories and Their Functions in the Field Sparrow (*Spizella-*
443 *Pusilla*). *The Auk*, 108(1): 42–52.
- 444 Nowicki, S., Peters, S. and Podos, J. (1998) Song Learning, Early Nutrition and Sexual Selection in Songbirds.
445 *Integrative and Comparative Biology*, 38(1): 179–190. doi: 10.1093/icb/38.1.179.
- 446 Nowicki, S., Searcy, W. A. and Peters, S. (2002) Brain development, song learning and mate choice in birds: a
447 review and experimental test of the “nutritional stress hypothesis”. *Journal of Comparative Physiology A*,
448 188(11–12): 1003–14. doi: 10.1007/s00359-002-0361-3.
- 449 Oberweger, K. and Goller, F. (2001) The metabolic cost of birdsong production. *The Journal of experimental*
450 *biology*, 204(19): 3379–88.
- 451 Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E. and Langmore, N. E. (2014) Female song is widespread and
452 ancestral in songbirds. *Nature Communications*. Nature Publishing Group, 5: 3379. doi: 10.1038/ncomms4379.
- 453 Odom, K. J. and Benedict, L. (2018) A call to document female bird songs: Applications for diverse fields. *The*
454 *Auk*, 135(2): 314–325.
- 455 Øigarden, T., Borge, T. and Lifjeld, J. T. (2010) Extrapair paternity and genetic diversity: the white-throated
456 dipper *Cinclus cinclus*. *Journal of Avian Biology*, 41(3): 248–257. doi: 10.1111/j.1600-048X.2009.04847.x.
- 457 Pavlova, D., Pinxten, R. and Eens, M. (2005) Female song in European starlings: sex differences, complexity,
458 and composition. *The Condor*, 107(3): 559–569.

459 Pfaff, J. A., Zanette, L., MacDougall-Shackleton, S. A. and MacDougall-Shackleton, E. A. (2007) Song
460 repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*).
461 Proceedings of the Royal Society of London B: Biological Sciences, 274(1621): 2035–2040. doi:
462 10.1098/rspb.2007.0170.

463 Podos, J. (1997) A Performance Constraint on the Evolution of Trilled Vocalizations in a Songbird Family
464 (Passeriformes: Emberizidae). *Evolution*, 51(2): 537–551.

465 Potvin, D. A. and Clegg, S. M. (2015) The relative roles of cultural drift and acoustic adaptation in shaping
466 syllable repertoires of island bird populations change with time since colonization. *Evolution*, 69(2): 368–380.
467 doi: 10.1111/evo.12573.

468 Potvin, D. A., Crawford, P. W., Macdougall-Shackleton, S. A. and MacDougall-Shackleton, E. A. (2013) Song
469 repertoire size, not territory location, predicts reproductive success and territory tenure in a migratory songbird.
470 *Canadian Journal of Zoology*, 93: 627–633. doi: dx.doi.org/10.1139/cjz-2015-0039.

471 Price, J., Yunes-Jiménez, L., Osorio-Beristain, M., Omland, K. E. and Murphy, T. G. (2008) Sex-Role Reversal
472 in Song? Females Sing More Frequently Than Males in the Streak-Backed Oriole. *The Condor*, 110(2): 387–
473 392. doi: 10.1525/cond.2008.8430.

474 R Core Team and R Development Core Team, R. (2015) R: A Language and Environment for Statistical
475 Computing. R Foundation for Statistical Computing. Edited by R. D. C. Team. Vienna, Austria: R Foundation
476 for Statistical Computing (R Foundation for Statistical Computing):409. doi: 10.1007/978-3-540-74686-7.

477 Ritchison, G. (1983) The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*):
478 family-group maintenance. *The Auk*, 100(1): 105–116.

479 Searcy, W. A. and Andersson, M. (1986) Sexual Selection and the Evolution of Song. *Annual Review of*
480 *Ecology and Systematics*, 17: 507–533.

481 Searcy, W. A. and Yasukawa, K. (1996) Song and Female Choice. In Kroodsma, D. and Miller, E. H. *Ecology*
482 *and Evolution of Acoustic Communication in Birds*, first edition, Cornell University Press.

483 Slater, P. and Mann, N. (2004) Why do the females of many bird species sing in the tropics?. *Journal of Avian*
484 *Biology*, 35(4): 289–294.

485 Specht, R. (1993) Avisoft-SASLab Pro. Available at: <http://www.avisoft.com/>.

486 Svensson, L. (1992) Identification Guide to European Passerines. Fourth. British Trust for Ornithology.

487 Tobias, J. A., Sheard, C., Seddon, N., Meade, A., Cotton, A. J. and Nakagawa, S. (2016) Territoriality, Social
488 Bonds, and the Evolution of Communal Signaling in Birds. *Frontiers in Ecology and Evolution*, 4: 74. doi:
489 10.3389/fevo.2016.00074.

490 Tyler, S. J. and Ormerod, S. J. (1994) *The Dippers*. First. T & AD Poyser Ltd.

491 Villain, A. S., Mahamoud-Issa, M., Doligez, B. and Vignal, C. (2017) Vocal behaviour of mates at the nest in
492 the White-throated Dipper *Cinclus cinclus*: contexts and structure of vocal interactions, pair-specific acoustic
493 signature. *Journal of Ornithology* 158 (4): 897–910 1–14. doi: 10.1007/s10336-017-1449-4.

494 Ward, S., Lampe, H. M. and Slater, P. J. B. (2004) Singing is not energetically demanding for pied flycatchers,
495 *Ficedula hypoleuca*. *Behavioral Ecology* 15(3): 477–484, doi: 10.1093/beheco/arh038.

496 Yamaguchi, A. (1998) Can a sexually dimorphic learned birdsong be used for male-female recognition?
497 *Behaviour*, 135(7): 833–844.

498

499

500

501

502 **Figure Captions**

503

504 **Fig. 1.** Spectrograms of male Dipper song: a) full song; followed by sections of that song b) and c), which
505 represent the resolution at which songs were analysed (Avisoft settings as stated in methods). Syllables are
506 numbered, 1 and 5 showing how elements are grouped together to form syllables. Syllables can be repeated
507 straight away (e.g. 1) or appear later in the same song (e.g. 2). A spectrogram of female dipper song (d) is also
508 included for comparison.

509

510 **Fig. 2.** A comparison of song characteristics in male and female Dippers at different breeding stages: a) syllable
511 diversity, b) versatility, c) average syllables per second and d) song rate. Boxes show the median, first and third
512 quartiles; upper and lower whiskers extend to the highest and lowest values that are within 1.5 * the inter-
513 quartile range. Data beyond the end of the whiskers are outliers and plotted as individual points. Syllable
514 diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was
515 calculated by dividing the number of unique syllables found within one song by the total number of syllables
516 found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was
517 calculated by dividing the number of syllables found in each song by song length and then averaging over the 10
518 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period
519 of observation for each individual during which the bird sang at least once, starting at the time when the bird
520 was first observed singing. Sample sizes for each sex at each breeding stage are as follows: solo males (n = 10),
521 pre-breeding males (n = 14), breeding males (n = 10), solo females (n = 2), pre-breeding females (n = 8) and
522 breeding females (n = 1).

523

524 **Fig. 3.** The number of observations of female Dippers singing in different behavioural contexts during each
525 month of the breeding season. Within each month, observations correspond to different females because only
526 the first context in which a given female produced song is shown: "aggression" (black) describes females within
527 their own territory which sang in the presence of an intruder i.e. not their partner; "nest-building" (grey)
528 describes females recorded singing whilst prospecting or building a nest with their partner; and "other" (white)
529 describes females which sang in all other contexts.

530

531 **Fig. 4.** The proportion of observed individuals recorded singing for each month of the breeding season for male
532 and female Dippers. Proportions were calculated across all observed individuals per month according to whether

533 or not they were recorded singing at least once in that month. Sample sizes are denoted above the bars for each
534 sex in every month.

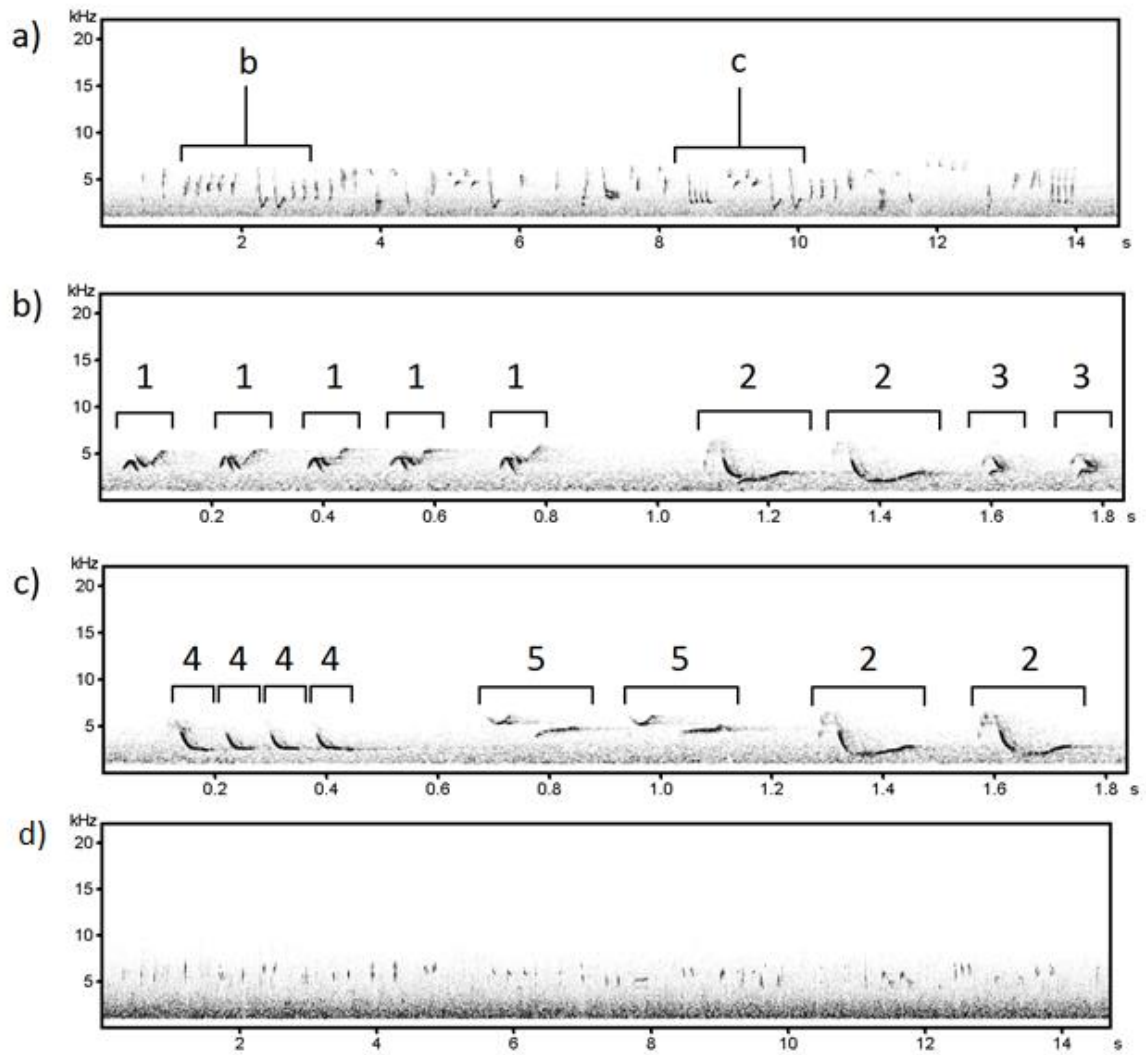


Fig. 1. Spectrograms of male Dipper song: a) full song; followed by sections of that song b) and c), which represent the resolution at which songs were analysed (Avisoft settings as stated in methods). Syllables are numbered, 1 and 5 showing how elements are grouped together to form syllables. Syllables can be repeated straight away (e.g. 1) or appear later in the same song (e.g. 2). A spectrogram of female dipper song (d) is also included for comparison.

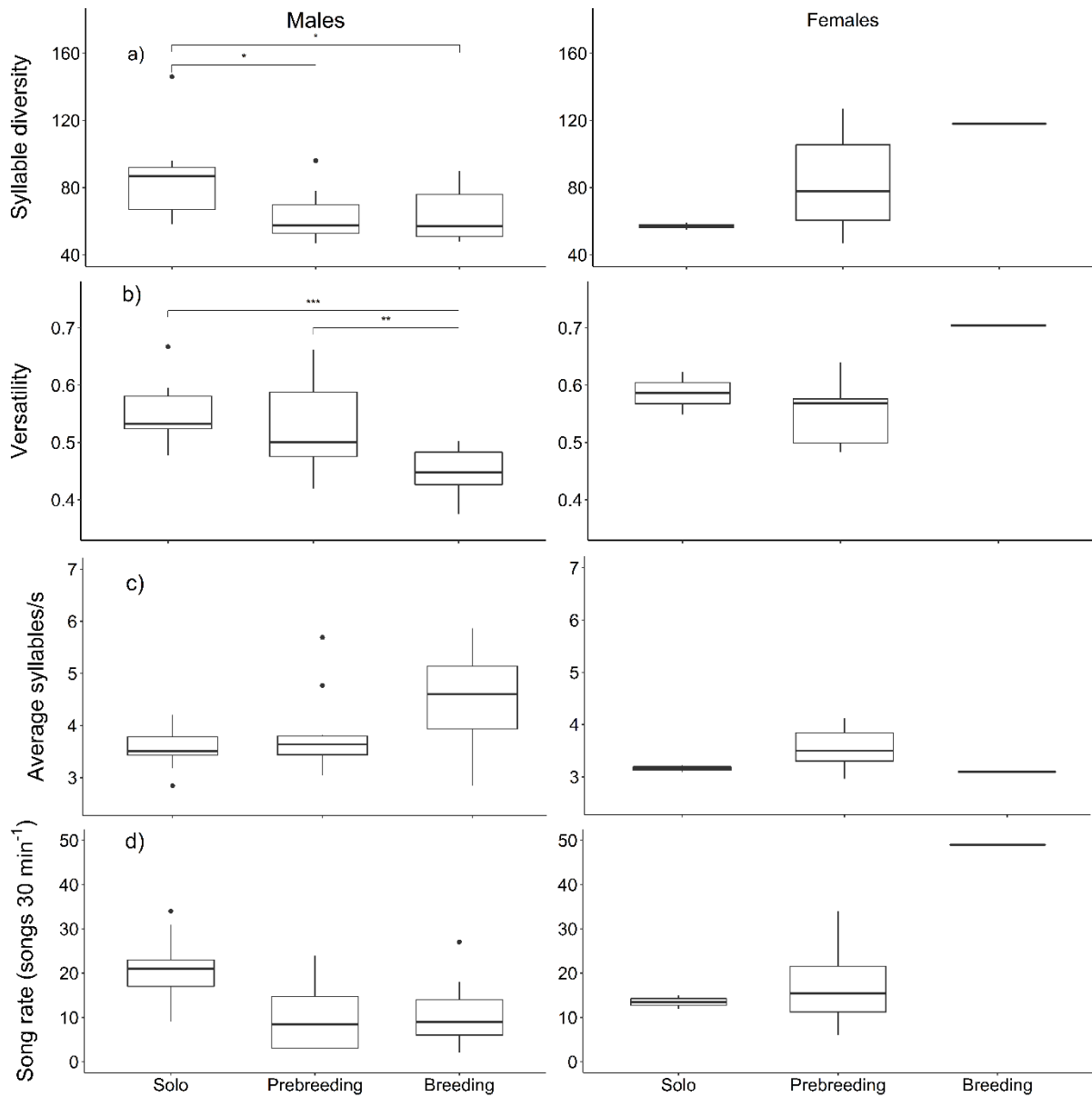


Fig. 2. A comparison of song characteristics in male and female Dippers at different breeding stages: a) syllable diversity, b) versatility, c) average syllables per second and d) song rate. Boxes show the median, first and third quartiles; upper and lower whiskers extend to the highest and lowest values that are within 1.5 * the interquartile range. Data beyond the end of the whiskers are outliers and plotted as individual points. Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird

was first observed singing. Sample sizes for each sex at each breeding stage are as follows: solo males (n = 10), pre-breeding males (n = 14), breeding males (n = 10), solo females (n = 2), pre-breeding females (n = 8) and breeding females (n = 1).

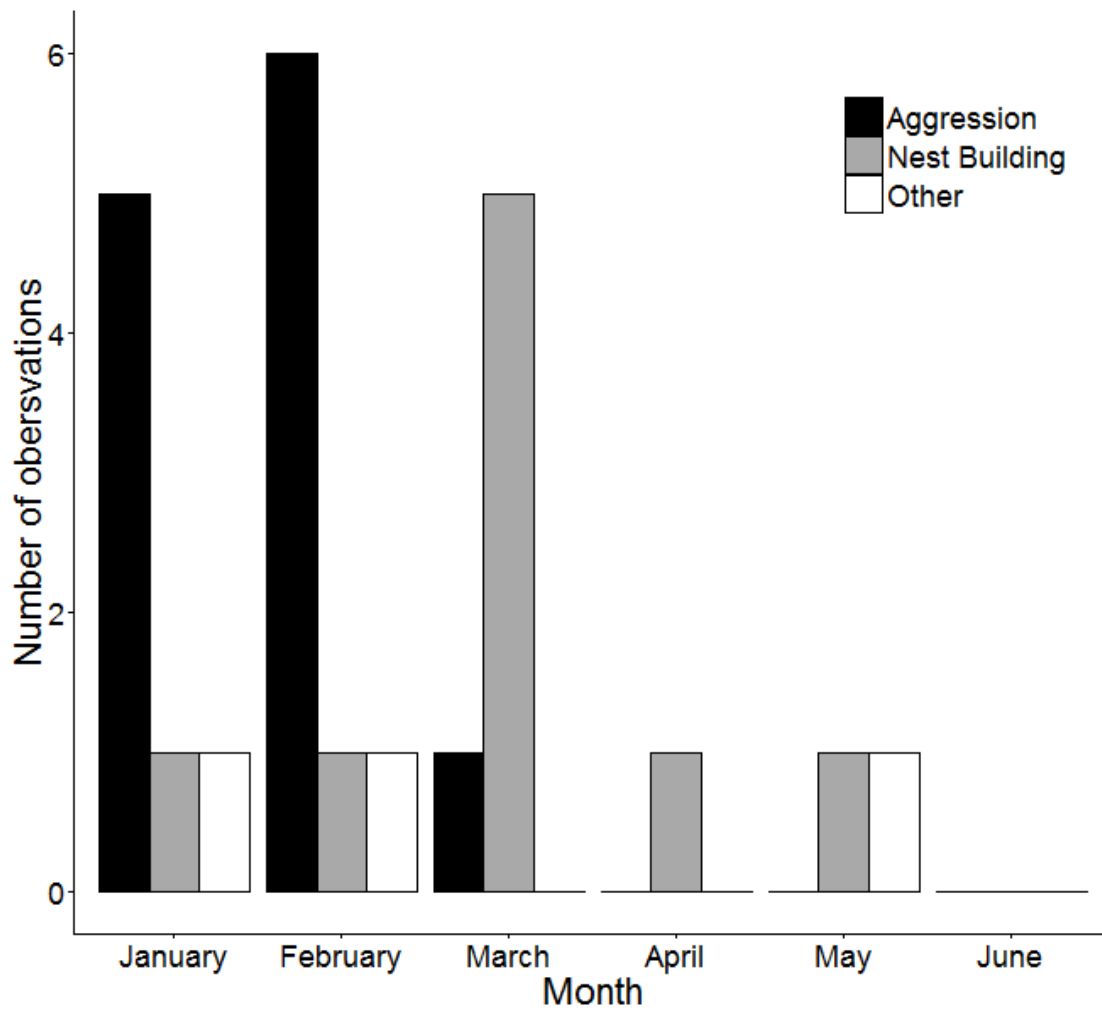
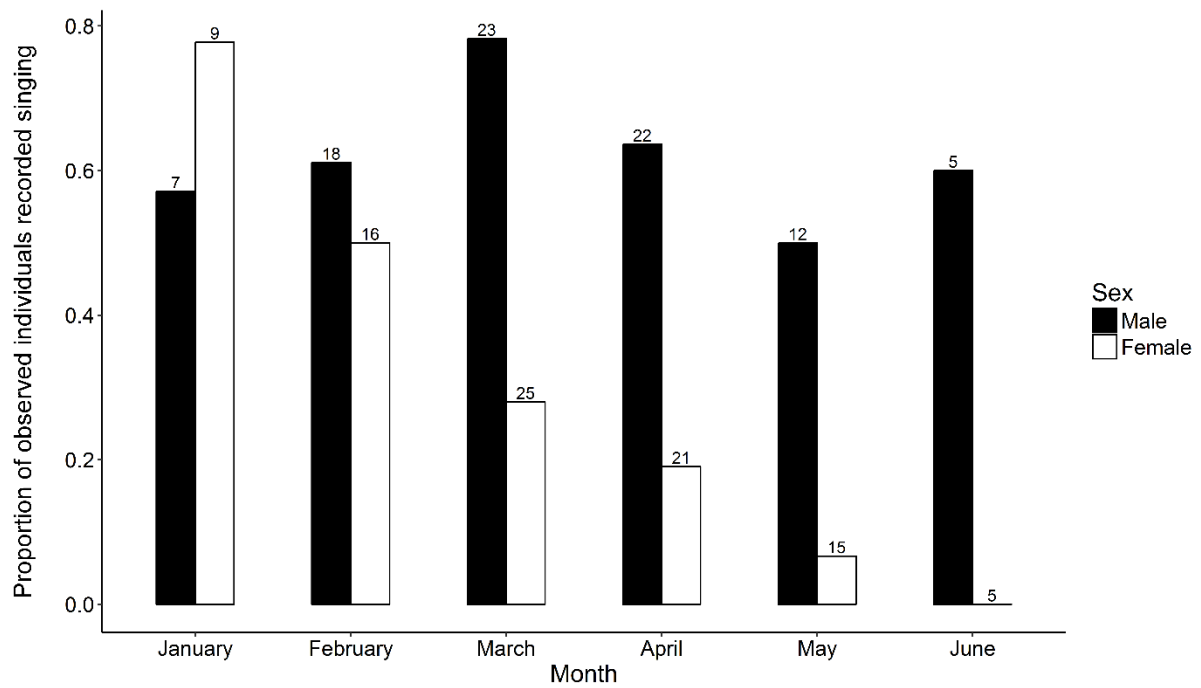


Fig. 3. The number of observations of female Dippers singing in different behavioural contexts during each month of the breeding season. Within each month, observations correspond to different females because only the first context in which a given female produced song is shown: “aggression” (black) describes females within their own territory which sang in the presence of an intruder i.e. not their partner; “nest-building” (grey) describes females recorded singing whilst prospecting or building a nest with their partner; and “other” (white) describes females which sang in all other contexts.



1

2 **Fig. 4.** The proportion of observed individuals recorded singing for each month of the breeding season for male
 3 and female Dippers. Proportions were calculated across all observed individuals per month according to whether
 4 or not they were recorded singing at least once in that month. Sample sizes are denoted above the bars for each
 5 sex in every month.

Table 1. A comparison of the means (\pm SD) of a range of complexity, frequency and temporal characteristics of song in male (N = 14) and female (N = 8) Dippers. Data are for individuals recorded in the ‘pre-breeding’ stage only.

Measure	Male	Female	Test statistic (t or W)	p
Syllable diversity	61.5 \pm 15.7	82.5 \pm 29.3	t = -1.88	0.091
Versatility	0.52 \pm 0.07	0.55 \pm 0.054	t = -0.90	0.379
Maximum peak frequency (kHz)	8.08 \pm 0.52	7.85 \pm 0.28	W = 47.5	0.585
Minimum peak frequency (kHz)	1.59 \pm 0.36	1.54 \pm 0.46	t = -0.26	0.797
Average peak frequency (kHz)	4.91 \pm 0.19	4.93 \pm 0.19	t = 0.21	0.836
Average song length (s)	6.39 \pm 1.79	8.02 \pm 3.87	W = 47.0	0.570
Average syllables per second	3.77 \pm 0.69	3.53 \pm 0.43	W = 64.5	0.585
Song rate (songs 30 min ⁻¹)	9.79 \pm 7.02	16.8 \pm 9.32	W = 30.5	0.092

Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual’s 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing.

Table 2. A comparison of the means (\pm SD) of a range of complexity, frequency and temporal characteristics of songs produced by male Dippers at different breeding stages. Sample sizes are given in parentheses; significant differences ($p < 0.05$) are shown in bold. P values are provided before and after adjustment using the Benjamini–Hochberg false discovery rate procedure to control for multiple testing.

Measure	Male songs			Test Statistic	p	p adjusted
	Solo (10)	Pre-breeding (14)	Breeding (10)			
Syllable diversity	85.4 \pm 25.1	61.5 \pm 15.7	61.2 \pm 17.8	F = 5.40	0.010	0.039
Versatility	0.55 \pm 0.053	0.52 \pm 0.07	0.45 \pm 0.05	F = 8.38	0.001	0.010
Maximum peak frequency (kHz)	8.42 \pm 0.68	8.08 \pm 0.52	8.01 \pm 0.49	$\chi^2 = 2.13$	0.346	0.461
Minimum peak frequency (kHz)	1.52 \pm 0.50	1.59 \pm 0.36	1.40 \pm 0.42	F = 0.60	0.553	0.553
Average peak frequency (kHz)	4.89 \pm 0.42	4.91 \pm 0.19	4.75 \pm 0.30	F = 0.85	0.438	0.500
Average song length (s)	8.33 \pm 3.00	6.39 \pm 1.79	6.08 \pm 2.10	$\chi^2 = 4.44$	0.106	0.168
Average syllables/s	3.51 \pm 0.37	3.77 \pm 0.69	4.50 \pm 0.93	$\chi^2 = 6.84$	0.033	0.066
Song rate (songs 30 min ⁻¹)	19.4 \pm 9.05	9.79 \pm 7.02	10.7 \pm 7.57	$\chi^2 = 7.32$	0.026	0.066

Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing.