DIFFERENTIAL FEMALE SOCIALITY IS LINKED WITH THE FINE-SCALE STRUCTURE OF SEXUAL INTERACTIONS IN REPLICATE GROUPS OF RED JUNGLEFOWL, *GALLUS GALLUS*

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Running head: Interrelated social and sexual structure

Recent work indicates that social structure has extensive implications for patterns of sexual selection and sexual conflict. However, little is known about the individual variation in social behaviours linking social structure to sexual interactions. Here, we use network analysis of replicate polygynandrous groups of red junglefowl (*Gallus gallus*) to show that the association between social structure and sexual interactions is underpinned by differential female sociality. Sexual dynamics are largely explained by a core group of highly social, younger females, which are more fecund and more polyandrous, and thus associated with more intense postcopulatory competition for males. In contrast, less fecund females from older cohorts, which tend to be socially dominant, avoid male sexual attention by clustering together and perching on branches, and preferentially reproduce with dominant males by more exclusively associating and mating with them. Collectively, these results indicate that individual females occupy subtly different social niches, and demonstrate that female sociality can be an important factor underpinning the landscape of intra-sexual competition and the emergent structure of animal societies.

1. Introduction

Animal groups are often characterised by non-random social structures that emerge from systematic variation in interactions and affiliations between individuals [1]. Social structure can have important fitness consequences by influencing access to resources, cooperative behaviours, and the spread of information and disease [2–6]. Social structure can also relate to the structure of sexual interactions, with potentially critical implications for patterns of sexual selection and sexual conflict [7–13].

Social and sexual structures may be related in complex ways in a population. In socially monogamous species, social structure may be determined by pair bonding and extra-pair sexual behaviour [14–16]. While in non-monogamous, more promiscuous systems, social structure may be organised by strategies among members of one sex to monopolise reproductive partners, such as cooperative coalitions or mate guarding [17–20]. While social structure can determine the structure of the network of intrasexual competitive interactions, these networks can in turn drastically change patterns of sexual selection [5,9,10,21,22]. For example, the strength of sexual selection may be intensified or relaxed depending on whether the most polygynous males tend to mate with the most or least polyandrous females in the population [21,22]. The structure of sexual interactions also has repercussions for female fitness and population viability because male competition often harms females, reducing their lifetime reproductive success [7,23–25].

Recent work has begun to reveal the importance of female social strategies in mediating the structure of sexual networks. Female sociality may emerge as a response to male sexual behaviour, e.g. when male harassment disrupts female aggregations and females alter space use, utilise refuges or modify habitat preferences to avoid males, as has been shown in a range of organisms, including cockroaches, *Diploptera punctata*

26 [26], water striders, *Aquarius remigis* [8,23], solitary bees, *Anthophora plumipes* [27],

27 guppies, *Poecilia reticulata* [28–30], mosquitofish, *Gambusia holbrooki* [31,32],

28 Columbian ground squirrels, *Urocitellus columbianus* [33], South American sea lions,

29 *Otaria flavescens* [34], and Sumatran orangutan, *Pongo pygmaeus abelii* [35]. Female

30 social strategies may regulate the level of male competition and sexual harassment

31 through behaviours consistent with social niche construction, e.g. by grouping together,

32 associating with other, relatively more attractive females or with males that provide

33 protection from harassment [26,29,31,34–36]. Little is known however, about the traits,

34 which underpin variation in female sociality. In guppies, receptive females are more

35 attractive to males than non-receptive females, and non-receptive females prefer to

36 group with receptive females to reduce sexual harassment by males, while receptive

37 females appear less socially discriminating [36]. In the rock hyrax, *Procavia capensis*,

38 a female's probability of mating is positively affected by her reproductive status and

39 social network position. Females that are central in the social network and those that

40 have central female competitors mate more frequently [37]. Such individual variation

41 in female sociality is expected to impact the structure of sexual networks, and thus

42 patterns of sexual selection in males. Critically however, little is known about the way

43 in which female sociality is linked to variation in individual male reproductive success,

44 e.g. the distribution of fertilizations across male and female phenotypes.

45   Here, we use network analysis to characterise the social structure of replicate

46 mixed-sex groups of red junglefowl,*Gallus gallus*. We identify female characteristics

47 that underpin variation in female social behaviour and show how patterns of female

48 sociality predict the structure of sexual interactions. In nature, red junglefowl and the

49 related domestic fowl, *G. domesticus*, form polygynandrous social groups with

50 overlapping generations, characterised by sex-specific dominance hierarchies [38–40].

51   Male sexual harassment of females is common and females resist the majority of male

52   sexual advances [41,42]. This harassment may result in costs to females, including

53   reduced feeding opportunities, and extended struggles that are energetically costly, and

54   which may reduce female fecundity and cause physical injury [42–45]. Male sexual

55   harassment can influence female spatial distribution [43], suggesting the potential for

56   female spatial and social structure to emerge as a response to male behaviour.

57   Specifically, both males and females may utilise perches to avoid social aggression

58   [39,46,47], and females may do so to avoid sexual harassment from males.

59   Female social status determines access to resources and high status is associated

60   with greater lifetime reproductive success [48,49]. Female age may be associated with

61   increased social and sexual experience, and is linked to changes in ornamentation and

62   fecundity, which can in turn affect the intensity of male sexual attention [50–53].

63   Female age, social status and fecundity are therefore predicted to shape social and

64   sexual interactions through their influence on both female behaviour and male mating

65   preferences [49,53,54]. Using detailed observations of sexual interactions and social

66   affiliation (based on proximity) we first characterise the structure of female-female and

67   female-male social networks. Second, we determine the extent to which these social

68   networks are related to the structure of sexual networks (i.e. networks linking

69   individuals to their mating –rather than social- partners). We then show how individual

70   variation in female characteristics (i.e. social status, age, fecundity) predicts female

71   sociality and sexual behaviour. Finally, we present evidence that these female social

72   phenotypes are associated with variation in sexual networks, with implications for

73   patterns of male intrasexual competition, and differential intensity of male harassment

74   of females.

75   ## 2. Methods

76   We studied 18 groups of adult red junglefowl, each comprising of 10 males and 12 females,

77   housed in outdoor pens at the University of Oxford field station in Wytham, UK (April-

78   October, 2011-2013). The size and sex ratio of these groups fall within the range reported for

79   social groups of red junglefowl or feral domestic fowl under natural conditions [38–40,55]. We

80   monitored individual social and sexual behaviour and individual reproductive success

81   throughout 13-day trials for each replicate group. The study system and methods have been

82   described previously [55]. For a detailed description of empirical and analytical approaches

83   adopted for this investigation see supplementary material. All analyses were conducted using

84   R stat [56]. Mixed-effects models were conducted using package "lme4" [57], randomisations

85   of social networks used package "tnet" [58] and randomisations of sexual networks used

86   custom scripts.

87

88   ## 3. Results

89   *i) Social structure*

90   Red junglefowl groups formed a single connected social network (figure 1A). Females

91   had more social partners than males and were more social (degree: $\chi^2_1 = 15.705$, p <

92   0.001, strength: $\chi^2_1 = 150.38$, p < 0.001; figure 1B). Given that groups were female-

93   biased, we expect focal males to have fewer male associates than females. However,

94   for both males and females, the proportion of associates that were males was

95   considerably lower than expectations based on group sex ratio (figure 1B). There was

96   a non-significant tendency for males to associate with proportionally fewer males

97   ($\chi^2_1 = 3.001$, p = 0.083; figure 1B).

98

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100

101   *ii) Social and sexual networks*

102 The strength of the social association between a male and a female was positively

103 correlated with the probability that they mated with each other. The magnitude of the

104 correlation was more extreme than expected compared to null expectations generated

105 from models using randomised versions of sexual networks (p_{rand} = 0.002; figures 1A,

106 1C & supplementary material figure S3). This suggests that controlling for any overall

107 relationship between individual levels of sociality and propensity to mate, pairs that

108 associate more strongly have a higher probability of mating with each other. The total

109 number of copulations between pairs was also positively predicted by the strength of

110 their social association. This relationship was again stronger than expected compared

111 to null expectations generated from randomised sexual networks (p_{rand} = 0.002; figures

112 1A, 1C & supplementary material figure S4), as was the relationship between the

113 strength of pairwise associations and number of copulation attempts received by

114 females (p_{rand} = 0.002; figure 1C & supplementary material figure S5). Accordingly, a

115 female's overall sociality with males, measured as either the proportion of her

116 associates that were males, or the total strength of her association with males, positively

117 and significantly predicted the number of her unique male partners (*M*), the number of

118 copulations and copulation attempts that she received (Table S2).

119

120 *iii) Female characteristics and socio-sexual structure*

121 Older females were more dominant than younger females (figure 2A, supplementary

122 material figure S6; $\chi_1^2 = 35.971$, p < 0.001). Controlling for social status, older

123 females had lower reproductive success (*T*) than younger females ($\chi_1^2 = 15.293$, p <

124 0.001; figure 2A). Controlling for age, more dominant females showed a non-

125 significant tendency to have higher reproductive success ($\chi_1^2 = 3.575$, p = 0.059; figure

126 2A). Older females also laid lighter eggs than younger females (Table S3).

127   Female characteristics were associated with female sociality. More dominant

128   females were more social overall when controlling for their age (status: $\chi^2_1 = 16.062$,

129    $p < 0.001$, age: $\chi^2_1 = 1.315$, $p = 0.251$; figures 1A & 2B). Older females consorted with

130   a higher proportion of females and this relationship between female age and sex ratio

131   bias was stronger than expected than null expectations generated from randomisations

132   of social networks ($p_{rand} = 0.002$; figure 2C). In contrast, more dominant females

133   consorted with a higher proportion of males (figure 2C), and this trend was marginally

134   non-significantly stronger than null expectations based on randomisations of social

135   networks ($p_{rand} = 0.054$).

136   Female-female associations were structured by female characteristics. Older

137   females associated with on average older and more dominant females and in both cases

138   the strength of the relationship was stronger than expected by chance compared to null

139   expectations based on randomised social networks (age vs partner status, $p_{rand} = 0.002$,

140   age vs partner age: $p_{rand} = 0.002$; figures 1A & 2D). We also confirmed the reverse: the

141   social status of a female was positively correlated with the age and social status of her

142   social partners, and these relationships were stronger than expected by chance

143   compared to null expectations based on randomised social networks (status vs partner

144   status $p_{rand} = 0.002$, status vs partner age: $p_{rand} = 0.002$; figure 1A & 2D). Older females

145   and more dominant females associated with more dominant males, however only

146   female age was more strongly associated with the status of male social partners than

147   expected from randomised social networks (status: $p_{rand} = 0.262$; age: $p_{rand} = 0.002$;

148   figure 1A & 2E). This suggests that the tendency of more dominant females to associate

149   with more dominant males can be explained largely by the high overall sociality of

150   dominant females. Older females, however, associated more with dominant males than

151   expected based on their level of sociality alone.

152   Overall rates of female sexual interactions were related to female
153 characteristics. Females with higher reproductive success (T) were courted more often
154 by males ($\chi^2_1 = 6.515$, p = 0.012; figure 3A), and males attempted to copulate with
155 them more often ($\chi^2_1 = 22.849$, p < 0.001; figure 3A). These females also mated with
156 more males ($\chi^2_1 = 18.625$, p < 0.001), mated with those males more often ($\chi^2_1 =$
157 24.764, p < 0.001; figure 3A) and were more likely to solicit copulation at least once
158 ($\chi^2_1 = 12.175$, p < 0.001). Due to the relationships of female age and status with T, we
159 investigated the relationship between rates of female sexual interactions and female age
160 and social status. Controlling for their social status, older females received significantly
161 less courtship, fewer mating attempts and had fewer mates (M) (supplementary material
162 table S4, figure S7). Controlling for female age, female social status tended to show the
163 opposite pattern; dominant females had higher M, received more mating attempts and
164 courtship, however these relationships were not significant (supplementary material
165 table S4, figure S7).

166   We assessed whether differential exposure to male sexual interest across
167 females was associated with female perching behaviour. Females perched above the
168 ground more often than males ($\chi^2_1 = 47.251$, p < 0.001) and older females were
169 observed perching more often than younger females ($\chi^2_1 = 12.902$, p < 0.001), whereas
170 status was not associated with perching ($\chi^2_1 = 1.588$, p = 0.208, figure 3B).

171   Finally, we tested whether female characteristics determined the phenotypes of
172 their sexual partners and the sires of their offspring. Binary networks revealed that older
173 females on average mate with more dominant males. This tendency was marginally
174 non-significantly stronger compared to random expectations ($p_{rand} = 0.088$; figure 3C).
175 This suggests that, by virtue of mating infrequently, older females were more likely to
176 mate randomly with dominant males because these males mate more frequently than

177   subordinate males. The social status of a female was not associated with the average

178   status of her sexual partners and this was consistent with expectations generated from

179   randomised sexual networks (p_{rand} = 0.751; figure 3C). Similarly, taking into account

180   repeated matings between male-female pairs using weighted sexual networks, revealed

181   that female age was positively associated with the weighted social status of their sexual

182   partners, and this relationship was not more extreme than expected from null

183   expectations based on randomised sexual networks (p_{rand} = 0.685; figure 3C). Female

184   social status was also positively associated with the weighted social status of her sexual

185   partners, however, this relationship was stronger than null expectations based on

186   randomised sexual networks (p_{rand} = 0.004; figure 3C). This suggests that more

187   dominant females mate with more dominant males at a rate exceeding that expected

188   based on their overall mating rate. Both older and more dominant females sired more

189   offspring with more dominant males, however, in neither case was this relationship

190   stronger than expected by chance assuming random paternity share across their sexual

191   partners (status: p_{rand} = 0.312; age: p_{rand} = 0.313; figure 3C), suggesting that the higher

192   social status of sires is largely driven by mating patterns themselves.

193

194   ## 4. Discussion

195   We used detailed behavioural observations of replicate polygynandrous groups of red

196   junglefowl to show that differential sociality across female characterisitcs is strongly

197   associated with the fine-scale structure of sexual networks and an important factor in

198   patterns of mating activity and sexual selection on males.

199   We found a clear sex difference in sociality. Females had more associates than

200   males, and both sexes associated more with females. This is likely driven by sex

201   differences in social tolerance. Aggression among males is likely more intense than

202 among females, reducing male-male associations [39,59]. Moreover, the effect of

203 female competition might be counteracted by the need for females to group together,

204 e.g. to avoid male harassment [26,31,35].

205 Intersexual associations were closely related to patterns of sexual behaviour.

206 Females were more likely to copulate with close male associates and copulated with

207 these males more often. This establishes a link between the social and the sexual

208 network. Relational data on physical proximity may therefore reflect a latent social

209 network predisposing dyads to a higher probability of mating. This strong correlation

210 between sexual contact patterns and social proximity may conflate sexual and social

211 transmission routes of pathogens, parasites and microorganisms.

212 Female sociality varied across female characteristics. Females from older

213 cohorts were more dominant than younger females, however female age and social

214 status had contrasting relationships with sociality. More dominant females were overall

215 more social, whereas older females associated more often with other older, more

216 dominant females. The increased sociality of dominant females may reflect a lower

217 tendency to avoid males, greater male sexual interest in dominant females or may

218 emerge because dominant individuals are centrally positioned in groups [60]. The tight

219 social clustering between older and more dominant females could mechanistically arise

220 if females lower in the hierarchy are excluded from grouping with aggressive, dominant

221 individuals [61]. Alternatively, this social clustering could reflect the strong propensity

222 of older females to perch on branches away from males, thus spending more time in

223 close proximity with each other. The overall outcome is that older females associated

224 less often with males, proportionally more with females and received less sexual

225 harassment. Female-female social clustering may therefore reflect an effective strategy

226 to avoid harassment. Similar patterns in cockroaches, *D. punctata*, have led to the

227 suggestion that females may engineer the sex ratio of their social environment, biasing

228 it towards females to avoid costly male harassment [26]. Similarly, female eastern

229 mosquitofish school closer together in the presence of males, which dilutes male

230 harassment [32,62].

231   Older and more dominant females also consorted more with dominant males.

232 This was more than expected by chance for older females. Previous work indicates that

233 female fowl prefer to associate with dominant males, and that socially isolated females

234 are harassed by peripheral, subordinate males [38,39,63]. Associating with dominant

235 males may represent a strategy to attain high-quality mates and avoid harassment

236 through protection by dominant males. In mallards, *Anas platyrhynchos*, a female's

237 mate will aggressively interfere with copulation attempts from other males [64], while

238 in primates females may incite mate guarding by specific males, potentially reducing

239 harassment or the risk of infanticide [65]. Our results indicate that this potential strategy

240 is not uniform across females but largely associated with female age.

241   Despite being less fecund and attracting less male sexual attention, older

242 females, on average, secure more socially dominant mating partners. This is likely both

243 because these males mate more frequently [66] and due to the effective social

244 positioning of older females, potentially as a result of greater social experience. By

245 comparison, younger, more fecund females were less discriminant and more

246 polyandrous, mating more frequently and with more males. Older, more socially

247 experienced female pied flycatchers, *Ficedula hypoleuca*, may have reduced rates of

248 extra-pair young because they are better able to secure high-quality pair mates and

249 avoid unwanted advances from extra-pair males [67]. Together, our characterisation of

250 male-female and female-female social structure suggests that older females might use

251 social niche construction to avoid sexual harassment and secure high-quality mates.

252   Differential female mating activity likely reflects a combination of male mating

253   preferences and the necessity of more fecund females to mate more frequently. In line

254   with this, previous findings in this population have shown that positive female Bateman

255   gradients reflect a male preference for fecund females, rather than any fecundity

256   benefits of polyandry to females [53]. It is however not clear how male preference for

257   more fecund females is maintained, given that reproductive returns are likely eroded by

258   the increased sperm competition. One possibility is that if variation in fecundity is

259   partly additive, males may obtain genetic benefits by preferentially reproducing with

260   more fecund females, through the production of more fecund daughters, which would

261   result in a higher number of grand offspring. Second, males may produce more

262   successful offspring if the higher egg mass of more fecund females [68] translates into

263   increased offspring survival or performance. Third, mating with more fecund females

264   may be less costly for males because these females have a higher propensity to mate

265   and thus will resist male advances less. Alternatively, a male preference for more

266   fecund females may not necessarily be adaptive to males, i.e. males may simply prefer

267   more fecund females through a predisposition for phenotypes linked to female

268   fecundity, e.g. larger comb [68].

269   Regardless of the adaptive significance of these patterns, the observed

270   distribution of matings may favour an equilibrium state that can be likened to an ideal

271   free distribution, in which males distribute their sexual effort across female partners

272   proportionally to the number of eggs available for fertilisation, as has been argued for

273   golden-orb web spider *Neuphila plumipes* [69]. Similar patterns were recently observed

274   in *Drosophila melanogaster* where male mating effort was distributed across females

275   proportional to their fecundity [70]. The increased sperm competition associated with

276   more fecund females meant that males sired a similar number of offspring per mating

277   with high- and low-fecundity females [70]. Thus, fecundity-dependent polyandry may

278   erode any advantages of male preferences for more fecund females.

279   The offspring produced by dominant and older females were sired by, on

280   average, more dominant males than those produced by younger and/or subordinate

281   females. Previous work in smaller junglefowl groups, suggests that subordinate males

282   are more likely to copulate with subordinate females, because dominant males intensely

283   guard dominant females [46]. In the larger and more polyandrous groups of the present

284   study, dominant females gain a greater share of their copulations from dominant

285   partners. This suggests that dominant males may also protect paternity with dominant

286   females by remating with them more frequently [66]. In line with this, we have

287   previously shown that dominant, aggressive males, mate with more females, including

288   the least polyandrous females largely because they are able to mate at an overall higher

289   rate [66]. Similarly, by virtue of their low mating rate, subdominant males mate with

290   fewer and more polyandrous females [66]. The extent to which these mating patterns

291   reflect male-male competition or female preference remains unclear. Previous work

292   suggests that female fowl prefer socially dominant males [46,71] and manipulate male-

293   male competition in order to favour matings by these males [42]. The results of the

294   present study indicate that differential female sociality may be an important -but so far

295   neglected- factor underpinning the structure of sexual networks [21].

296   Our study also has important implications for male harm of females and

297   population viability. Male intrasexual competition can harm females, often through

298   intense sexual harassment [25]. This can severely impact the viability and growth rate

299   of populations through a process similar to the Tragedy of the Commons [72]. In water

300   striders females locally disperse to avoid male harassment [8,23]. The resulting patterns

301   of female aggregation both determines sexual selection on male traits [8] and may also

302   mediate group productivity, by ameliorating the costs of sexual conflict to females [73].

303   Broadly similar patterns have been confirmed for a diverse range of species [8,23,27–

304   33,35,37]. Our results build on this work by showing that individual variation in female

305   sociality and fecundity is associated with the intensity of harassment that females

306   receive. Population growth rate will be more severely impacted when social structure

307   exposes the most fecund subset of females to more intense harassment [74,75]. The

308   negative impact of male harm on group productivity will instead be buffered when the

309   most productive females are sheltered from harm. Our results indicate that red

310   junglefowl groups fall in the former scenario because younger, more fecund females

311   attract more sexual attention than older, less fecund females. Previous work in similar

312   groups of fowl demonstrates that females resist the majority of male copulation

313   attempts [41,42]. Resistance can be energetically costly [25] and, in fowl, associated

314   with the risk of injuries (e.g. rupture of hard-shelled egg within the female oviduct

315   [42]). In other species, the avoidance of male harassment has also been shown to drive

316   females to forage suboptimally [27]. In our study population, females exposed to higher

317   rates of coerced mating attempts tend to lose more body mass over time [45]. In the

318   present study, we observed that older females have lower fecundity and avoid males by

319   spending more time perching. It is possible that longer perching times may limit feeding

320   by older females. While it is likely that older females feed less because reduced

321   fecundity exacts lower nutritional demands, it is also possible that, in the absence of

322   male harassment, older females might feed more or more optimally, which might

323   marginally improve their fecundity. Conversely, the higher fecundity of younger

324   females, will exact greater energetic demands and will require more continuous access

325   to food [33]. Such demands may place limits on the ability of younger fecund females

326   to avoid male harassment by perching when compared to less fecund older females

327 [27]. In commercial flocks of fowl, male sexual harassment impacts female foraging

328 behaviour and space use, resulting in a reduction of female fecundity and flock

329 productivity, and changes in sexual behaviour can reduce female stress and increase

330 reproductive performance [43]. Thus, in applied settings, management of flock social

331 structure may be utilised to simultaneously influence sexual behaviour to increase

332 fertility, productivity and welfare.

333 An important caveat of our study is that our data are largely cross-sectional

334 rather than longitudinal. Thus, we cannot completely disentangle the effect of female

335 age from other cohort effects. While females mix freely in the general population

336 between breeding seasons, females from the same cohort will likely have had more

337 interactions with each other. Moreover, early development in our population is spent in

338 close association largely within a single cohort. However, such potential effects are

339 biologically relevant, particularly in philopatric groups where older females are likely

340 be more familiar with each other, more socially experienced and potentially more

341 socially dominant than other younger birds [61]. Another important consideration

342 concerns the ecological relevance of our study. While the group size and sex ratio used

343 here are within the range found in populations under natural conditions [38], it is likely

344 that captivity may influence the patterns described. First, relatively high population

345 density may increase the rate of social and sexual interactions. Second, life expectancy

346 can be considerably higher in captive versus natural populations [76] and may

347 accentuate age-dependent patterns. Therefore, while the results of our study present a

348 proof-of-concept demonstration of the importance of female sociality in modulating the

349 structure of sexual networks, future studies should seek to determine the extent to which

350 the patterns observed here apply to natural populations of red junglefowl.

351   In conclusion, we use a replicated set up to confirm previous findings that

352   female sociality is strongly linked with patterns of inter-sexual dynamics, with more

353   fecund females attracting more sexual attention. We further show that female sociality

354   differs with female characteristics and that such differential sociality has important

355   repercussions for the intensity of sexual harassment suffered by females, the intensity

356   of intrasexual competition faced by males and the phenotype of the males reproducing

357   with females occupying different socio-sexual niches. Future studies should unravel the

358   feedback between these processes. In this context, manipulations of the relationships

359   between female age, status, social experience and sexual attractiveness will provide a

360   key tool in dissecting the complex mechanisms through which social, sexual and

361   phenotypic structures interrelate within animal groups.

References

1. Krause J, James R, Franks D, Croft D, editors. 2014 *Animal Social Networks*. Oxford, UK: Oxford University Press.

2. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.* **279**, 4199–4205. (doi:10.1098/rspb.2012.1591)

3. Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014 The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* **29**, 326–335. (doi:10.1016/j.tree.2014.04.002)

4. Fisher DN, McAdam AG. 2017 Social traits, social networks and evolutionary biology. *J. Evol. Biol.* **30**, 2088–2103. (doi:10.1111/jeb.13195)

5. McDonald GC, Farine DR, Foster KR, Biernaskie JM. 2017 Assortment and the analysis of natural selection on social traits. *Evolution* **71**, 2693–2702. (doi:10.1111/evo.13365)

6. Sah P, Mann J, Bansal S. 2018 Disease implications of animal social network structure: A synthesis across social systems. *J. Anim. Ecol.* **87**, 546–558. (doi:10.1111/1365-2656.12786)

7. Le Galliard J-F, Fitze PS, Ferrière R, Clobert J. 2005 Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 18231–18236. (doi:10.1073/pnas.0505172102)

8. Eldakar OT, Wilson DS, Dlugos MJ, Pepper JW. 2010 The role of multilevel selection in the evolution of sexual conflict in the water strider *Aquarius remigis*. *Evolution* **64**, 3183–3189. (doi:10.1111/j.1558-5646.2010.01087.x)

9. Oh KP, Badyaev AV. 2010 Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *Am. Nat.* **176**, E80–9. (doi:10.1086/655216)

10. McDonald GC, James R, Krause J, Pizzari T. 2013 Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 1–10.

11. Cardoso SD, Faustino AI, Costa SS, Valério F, Gonçalves D, Oliveira RF. 2017 Social network predicts loss of fertilizations in nesting males of a fish with alternative reproductive tactics. *Acta Ethologica* **20**, 59–68. (doi:10.1007/s10211-016-0249-9)

12. Wacker S, Ness MH, Östlund-Nilsson S, Amundsen T. 2017 Social structure affects mating competition in a damselfish. *Coral Reefs* **36**, 1279–1289. (doi:10.1007/s00338-017-1623-4)

13. Bebbington K, Kingma SA, Fairfield EA, Dugdale HL, Komdeur J, Spurgin LG, Richardson DS. 2017 Kinship and familiarity mitigate costs of social conflict between Seychelles warbler neighbors. *Proc. Natl. Acad. Sci.* **114**, E9036–E9045. (doi:10.1073/pnas.1704350114)

14. Cohas A, Allainé D. 2009 Social structure influences extra-pair paternity in socially monogamous mammals. *Biol. Lett.* , rsbl.2008.0760. (doi:10.1098/rsbl.2008.0760)

15. Schlicht L, Valcu M, Kempenaers B. 2014 Spatial patterns of extra-pair paternity: beyond paternity gains and losses. *J. Anim. Ecol.* (doi:10.1111/1365-2656.12293)

16. Maldonado-Chaparro AA, Montiglio P-O, Forstmeier W, Kempenaers B, Farine DR. 2018 Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. *Biol. Rev.* **93**, 1558–1577. (doi:10.1111/brv.12408)

17. Ridley MW, Hill DA. 1987 Social organization in the pheasant (*Phasianus colchicus*): harem formation, mate selection and the role of mate guarding. *J. Zool.* **211**, 619–630. (doi:10.1111/j.1469-7998.1987.tb04475.x)

18. Ryder TB, McDonald DB, Blake JG, Parker PG, Loiselle BA. 2008 Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proc. R. Soc. B Biol. Sci.* **275**, 1367–1374. (doi:10.1098/rspb.2008.0205)

19. Pizzari T, Biernaskie JM, Carazo P. 2015 Inclusive fitness and sexual conflict: how population structure can modulate the battle of the sexes. *BioEssays* **37**, 155–166. (doi:10.1002/bies.201400130)

20. Qi X-G *et al.* 2017 Male cooperation for breeding opportunities contributes to the evolution of multilevel societies. *Proc. R. Soc. B Biol. Sci.* **284**. (doi:10.1098/rspb.2017.1480)

21. McDonald GC, Pizzari T. 2018 Structure of sexual networks determines the operation of sexual selection. *Proc. Natl. Acad. Sci. U. S. A.* **115**, E53–E61. (doi:10.1073/pnas.1710450115)

22. Muniz DG, Guimarães PR, Buzatto BA, Machado G. 2015 A sexual network approach to sperm competition in a species with alternative mating tactics. *Behav. Ecol.* **26**, 121–129. (doi:10.1093/beheco/aru166)

23. Eldakar OT, Dlugos MJ, Wilcox RS, Wilson DS. 2009 Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behav. Ecol. Sociobiol.* **64**, 25–33. (doi:10.1007/s00265-009-0814-6)

24. Parker GA. 2006 Sexual conflict over mating and fertilization: an overview. *Philos. Trans. R. Soc. B Biol. Sci.* **361**, 235–259. (doi:10.1098/rstb.2005.1785)

25. Arnqvist G, Rowe L. 2005 *Sexual Conflict*. Princeton, NJ: Princeton University Press.

26. Stanley CR, Williams HL, Preziosi RF. 2018 Female clustering in cockroach aggregations—A case of social niche construction? *Ethology* **0**. (doi:10.1111/eth.12799)

27. Stone GN. 1995 Female foraging responses to sexual harassment in the solitary bee *Anthophora plumipes*. *Anim. Behav.* **50**, 405–412.

28. Darden SK, James R, Ramnarine IW, Croft DP. 2009 Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proc. R. Soc. B Biol. Sci.* **276**, 2651–2656. (doi:10.1098/rspb.2009.0087)

29. Darden SK, Watts L. 2012 Male sexual harassment alters female social behaviour towards other females. *Biol. Lett.* **8**, 186–188. (doi:10.1098/rsbl.2011.0807)

30. Darden SK, Croft DP. 2008 Male harassment drives females to alter habitat use and leads to segregation of the sexes. *Biol. Lett.* **4**, 449–451. (doi:10.1098/rsbl.2008.0308)

31. Pilastro A, Benetton S, Bisazza A. 2003 Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish *Gambusia holbrooki*. *Anim. Behav.* **65**, 1161–1167. (doi:10.1006/anbe.2003.2118)

32. Dadda M, Pilastro A, Bisazza A. 2005 Male sexual harassment and female schooling behaviour in the eastern mosquitofish. *Anim. Behav.* **70**, 463–471.

33. MacWhirter RB. 1991 Effects of reproduction on activity and foraging behaviour of adult female Columbian ground squirrels. *Can. J. Zool.* **69**, 2209–2216.

34. Cappozzo HL, Túnez JI, Cassini MH. 2008 Sexual harassment and female gregariousness in the South American sea lion, *Otaria flavescens*. *Naturwissenschaften* **95**, 625–630. (doi:10.1007/s00114-008-0363-2)

35. Fox EA. 2002 Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behav. Ecol. Sociobiol.* **52**, 93–101. (doi:10.1007/s00265-002-0495-x)

36. Brask JB, Croft DP, Thompson K, Dabelsteen T, Darden SK. 2012 Social preferences based on sexual attractiveness: a female strategy to reduce male sexual attention. *Proc. Biol. Sci.* **279**, 1748–1753. (doi:10.1098/rspb.2011.2212)

37. Ziv EB, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L. 2016 Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. *Behav. Ecol. Sociobiol.* **70**, 901–912. (doi:10.1007/s00265-016-2112-4)

38. Collias NE, Collias EC, Hunsaker D, Minning L. 1966 Locality fixation, mobility and social organization within an unconfined population of red jungle fowl. *Anim. Behav.* **14**, 550–9. (doi:10.1016/S0003-3472(66)80059-3)

39. McBride G, Parer IP, Foenander F. 1969 The social organization and behaviour of the feral domestic fowl. *Anim. Behav. Monogr.* **1**, 125–181.

40. Collias NE, Collias EC. 1996 Social organization of a red junglefowl, *Gallus gallus*, population related to evolution theory. *Anim. Behav.* **51**, 1337–1354. (doi:10.1006/anbe.1996.0137)

41. Løvlie H, Cornwallis CK, Pizzari T. 2005 Male mounting alone reduces female promiscuity in the fowl. *Curr. Biol.* **15**, 1222–1227. (doi:10.1016/j.cub.2005.05.060)

42. Pizzari T. 2001 Indirect partner choice through manipulation of male behaviour by female fowl, *Gallus gallus domesticus*. *Proc. R. Soc. B Biol. Sci.* **268**, 181–186. (doi:10.1098/rspb.2000.1348)

43. Leone EH, Estévez I. 2008 Economic and welfare benefits of environmental enrichment for broiler breeders. *Poult. Sci.* **87**, 14–21. (doi:10.3382/ps.2007-00154)

44. Løvlie H, Pizzari T. 2007 Sex in the morning or in the evening? Females adjust daily mating patterns to the intensity of sexual harassment. *Am. Nat.* **170**, E1–E13. (doi:10.1086/518201)

45. Carleial R, McDonald GC, Pizzari T. In press Dynamic phenotypic correlates of social status and mating effort in male and female red junglefowl, *Gallus gallus*. *J. Evol. Biol*. (doi:10.1111/jeb.13541)

46. Johnsen TS, Zuk M, Fessler EA. 2001 Social dominance, male behaviour and mating in mixed-sex flocks of red Junglefowl. *Behaviour* **138**, 1–18.

47. Morejohn GV. 1968 Breakdown of isolation mechanisms in mwo species of captive junglefowl (*Gallus gallus* and *Gallus sonneratii*). *Evolution* **22**, 576–582. (doi:10.2307/2406881)

48. Banks EM. 1956 Social Organization in Red Jungle Fowl Hens (*Gallus Gallus* Subsp.). *Ecology* **37**, 239–248. (doi:10.2307/1933136)

49. Collias N, Collias E, Jennrich RI. 1994 Dominant red junglefowl (*Gallus Gallus*) hens in an unconfined flock rear the most young over their lifetime. *The Auk* **111**, 863–872. (doi:10.2307/4088818)

50. Hutt FB. 1949 *Genetics of the fowl*. New York, NY: McGraw-Hill.

51. Holmes DJ, Thomson SL, Wu J, Ottinger MA. 2003 Reproductive aging in female birds. *Exp. Gerontol.* **38**, 751–756.

52. Cornwallis CK, Dean Rebecca, Pizzari T. 2014 Sex-specific patterns of aging in sexual ornaments and gametes. *Am. Nat.* **184**, E66–E78. (doi:10.1086/677385)

53. Collet JM, Dean RF, Worley K, Richardson DS, Pizzari T. 2014 The measure and significance of Bateman's principles. *Proc. R. Soc. B Biol. Sci.* **281**, 20132973. (doi:10.1098/rspb.2013.2973)

54. Cornwallis CK, Birkhead TR, Blows AEMW, Geber EMA. 2007 Changes in sperm quality and numbers in response to experimental manipulation of male social Status and female attractiveness. *Am. Nat.* **170**, 758–770. (doi:10.1086/521955)

55. Sullivan MS. 1991 Flock structure in red junglefowl. *Appl. Anim. Behav. Sci.* **30**, 381–386. (doi:10.1016/0168-1591(91)90143-L)

56. R Core Team. 2014 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.

57. Bates D, Maechler M, Bolker BM, Walker S. 2014 lme4: Linear mixed-effects models using Eigen and S4. *J. Stat. Softw.*

58. Opsahl T. 2009 *Structure and Evolution of Weighted Networks*. London, UK: University of London (Queen Mary College). See http://toreopsahl.com/publications/thesis/.

59. Guhl AM. 1968 Social Behavior of the Domestic Fowl. *Trans. Kans. Acad. Sci. 1903-* **71**, 379–384. (doi:10.2307/3627156)

60. Hemelrijk CK. 2000 Towards the integration of social dominance and spatial structure. *Anim. Behav.* **59**, 1035–1048. (doi:10.1006/anbe.2000.1400)

61. Kim T, Zuk M. 2000 The effects of age and previous experience on social rank in female red junglefowl, *Gallus gallus spadiceus*. *Anim. Behav.* **60**, 239–244. (doi:10.1006/anbe.2000.1469)

62. Dadda M, Pilastro A, Bisazza A. 2008 Innate responses to male sexual harassment in female mosquitofish. *Behav. Ecol. Sociobiol.* **63**, 53–62. (doi:10.1007/s00265-008-0635-z)

63. Graves HB, Hable CP, Jenkins TH. 1985 Sexual selection in *gallus*: Effects of morphology and dominance on female spatial behavior. *Behav. Processes* **11**, 189–197. (doi:10.1016/0376-6357(85)90060-9)

64. Barash DP. 1977 Sociobiology of Rape in Mallards (Anas platyrhynchos): Responses of the Mated Male. *Science* **197**, 788–789. (doi:10.1126/science.197.4305.788)

65. Palombit RA. 2015 Infanticide as Sexual Conflict: Coevolution of Male Strategies and Female Counterstrategies. *Cold Spring Harb. Perspect. Biol.* **7**, a017640. (doi:10.1101/cshperspect.a017640)

66. McDonald GC, Spurgin LG, Fairfield EA, Richardson DS, Pizzari T. 2017 Pre- and postcopulatory sexual selection favor aggressive, young males in polyandrous groups of red junglefowl. *Evolution* **71**, 1653–1669. (doi:10.1111/evo.13242)

67. Moreno J, Martínez JG, González-Braojos S, Cantarero A, Ruiz-de-Castañeda R, Precioso M, López-Arrabé J. 2015 Extra-pair paternity declines with female age and wing length in the pied flycatcher. *Ethology* **121**, 501–512. (doi:10.1111/eth.12364)

68. Pizzari T, Cornwallis CK, Løvlie H, Jakobsson S, Birkhead TR. 2003 Sophisticated sperm allocation in male fowl. *Nature* **426**, 70–74. (doi:10.1038/nature02004)

69. Jordan LA, Kokko H, Kasumovic M, Adkins-Regan AEE, Bronstein EJL. 2014 Reproductive Foragers: male spiders choose mates by selecting among competitive environments. *Am. Nat.* **183**, 638–649. (doi:10.1086/675755)

70. Morimoto J, Pizzari T, Wigby S. 2016 Developmental environment effects on sexual selection in male and female *Drosophila melanogaster*. *PLOS ONE* **11**, e0154468. (doi:10.1371/journal.pone.0154468)

71. Pizzari T, Birkhead TR. 2000 Female feral fowl eject sperm of subdominant males. *Nature* **405**, 787–789. (doi:10.1038/35015558)

72. Holman L, Kokko H. 2013 The consequences of polyandry for population viability, extinction risk and conservation. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 20120053. (doi:10.1098/rstb.2012.0053)

73. Eldakar OT, Gallup AC. 2011 The group-level consequences of sexual conflict in multigroup populations. *PLoS ONE* **6**, e26451. (doi:10.1371/journal.pone.0026451)

74. Long T, Pischedda A, Stewart A, Rice W. 2009 A cost of sexual attractiveness to high-fitness females. *PLoS Biol.* **7**. (doi:10.1371/journal.pbio.1000254)

75. Chenoweth SF, Appleton NC, Allen SL, Rundle HD. 2015 Genomic evidence that sexual selection impedes adaptation to a novel environment. *Curr. Biol.* **25**, 1860–1866. (doi:10.1016/j.cub.2015.05.034)

76. Ricklefs RE, Scheuerlein A. 2001 Comparison of aging-related mortality among birds and mammals. *Exp. Gerontol.* **36**, 845–857. (doi:10.1016/S0531-5565(00)00245-X)

77. Farine DR. 2014 Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Anim. Behav.* **89**, 141–153. (doi:10.1016/j.anbehav.2014.01.001)

Figure 1. The social and sexual structure of red junglefowl groups. (A) Social (top) and sexual networks (bottom) of 18 groups of males (blue) and females (orange). Node size is scaled to social status. The intensity of female node colour increases with female age. Orange edges connect female pairs that associated, blue edges connect male-female pairs and edge width indicates the strength of social associations. Male-male edges are not shown. Grey edges connect male and female pairs that copulated and edge width indicates the number of repeat copulations between pairs. Node position in sexual networks is the same as social networks for ease of comparison. Estimates of assortment by female characteristics on female-female social networks are shown using weighted network assortativity for female social status (r_{Stat}) and female age (r_{Age}) [77]. (B) The total number of edges (degree), sum of edge weights (strength) and the proportion of male associates weighted by edge weights from social networks is shown for males and females. Dotted lines show null expectations for the sex ratios of the associates of focal females (orange) and males (blue), (C) estimated slopes from mixed-effects models between the social network association index between male and female pairs with either the total number of male copulation attempts, the probability that the pair mated, or the number of times the pair copulated. Grey points show observed estimates; white circles and black vertical lines show the mean and 95% range of estimates calculated from randomised networks.

Figure 2. Female characteristics define the social structure of red junglefowl groups. (A) The relationship between female social status and age in years. The intensity of orange colour and the size of points reflect female age and total reproductive success (*T*) respectively. (B) The relationship between female social status and the sum of a female's edge weights from social networks (strength). The estimated relationship from mixed-effects models between female age and female social status with: (C) proportion of male associates weighted by edge weights from social networks, (D) the weighted average age and social status of female social partners, and (E) the weighted average social status of male social partners. Grey points show observed estimates; white circles and black vertical lines show the mean and 95% range of estimates calculated from randomised social networks.

Figure 3. Female characteristics define the sexual structure of red junglefowl groups. (A) Boxplots show the relationship between female reproductive success (*T*) and the total number of times females were courted, the total number of times males attempted to copulate with them and the total number of times females copulated. White points show raw data. (B) The relationship between female age and the proportion of scans they were observed perching. The intensity of orange colour reflects female age. (C) Estimated slopes from mixed-effects models between female age and status with either the average social status of females' sexual partners, the weighted average status of females' sexual partners and the weighted average status of their offspring's sires. Grey points show observed estimates; white circles and black vertical lines show the mean and 95% range of estimates calculated from randomised sexual networks.