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.

Keywords: *Gallus*; Polyandry; Sexual Networks; Sexual Selection; Social Networks; Social Niche Construction

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], water striders, *Aquarius remigis* [8,23], solitary bees, *Anthophora plumipes* [27], guppies, *Poecilia reticulata* [28–30], mosquitofish, *Gambusia holbrooki* [31,32], Columbian ground squirrels, *Urocitellus columbianus* [33], South American sea lions, *Otaria flavescens* [34], and Sumatran orangutan, *Pongo pygmaeus abelii* [35]. Female social strategies may regulate the level of male competition and sexual harassment through behaviours consistent with social niche construction, e.g. by grouping together, associating with other, relatively more attractive females or with males that provide protection from harassment [26,29,31,34–36]. Little is known however, about the traits, which underpin variation in female sociality. In guppies, receptive females are more attractive to males than non-receptive females, and non-receptive females prefer to group with receptive females to reduce sexual harassment by males, while receptive females appear less socially discriminating [36]. In the rock hyrax, *Procavia capensis*, a female's probability of mating is positively affected by her reproductive status and social network position. Females that are central in the social network and those that have central female competitors mate more frequently [37]. Such individual variation in female sociality is expected to impact the structure of sexual networks, and thus patterns of sexual selection in males. Critically however, little is known about the way in which female sociality is linked to variation in individual male reproductive success, e.g. the distribution of fertilizations across male and female phenotypes.

Here, we use network analysis to characterise the social structure of replicate mixed-sex groups of red junglefowl,*Gallus gallus*. We identify female characteristics that underpin variation in female social behaviour and show how patterns of female sociality predict the structure of sexual interactions. In nature, red junglefowl and the related domestic fowl, *G. domesticus*, form polygynandrous social groups with overlapping generations, characterised by sex-specific dominance hierarchies [38–40].

Male sexual harassment of females is common and females resist the majority of male sexual advances [41,42]. This harassment may result in costs to females, including reduced feeding opportunities, and extended struggles that are energetically costly, and which may reduce female fecundity and cause physical injury [42–45]. Male sexual harassment can influence female spatial distribution [43], suggesting the potential for female spatial and social structure to emerge as a response to male behaviour. Specifically, both males and females may utilise perches to avoid social aggression [39,46,47], and females may do so to avoid sexual harassment from males.

Female social status determines access to resources and high status is associated with greater lifetime reproductive success [48,49]. Female age may be associated with increased social and sexual experience, and is linked to changes in ornamentation and fecundity, which can in turn affect the intensity of male sexual attention [50–53]. Female age, social status and fecundity are therefore predicted to shape social and sexual interactions through their influence on both female behaviour and male mating preferences [49,53,54]. Using detailed observations of sexual interactions and social affiliation (based on proximity) we first characterise the structure of female-female and female-male social networks. Second, we determine the extent to which these social networks are related to the structure of sexual networks (i.e. networks linking individuals to their mating –rather than social- partners). We then show how individual variation in female characteristics (i.e. social status, age, fecundity) predicts female sociality and sexual behaviour. Finally, we present evidence that these female social phenotypes are associated with variation in sexual networks, with implications for patterns of male intrasexual competition, and differential intensity of male harassment of females.

2. Methods

We studied 18 groups of adult red junglefowl, each comprising of 10 males and 12 females, housed in outdoor pens at the University of Oxford field station in Wytham, UK (April-October, 2011-2013). The size and sex ratio of these groups fall within the range reported for social groups of red junglefowl or feral domestic fowl under natural conditions [38–40,55]. We monitored individual social and sexual behaviour and individual reproductive success throughout 13-day trials for each replicate group. The study system and methods have been described previously [55]. For a detailed description of empirical and analytical approaches adopted for this investigation see supplementary material. All analyses were conducted using R stat [56]. Mixed-effects models were conducted using package "lme4" [57], randomisations of social networks used package "tnet" [58] and randomisations of sexual networks used custom scripts.

3. Results

i) Social structure

Red junglefowl groups formed a single connected social network (figure 1A). Females had more social partners than males and were more social (degree: $\chi^2_1 = 15.705$, $p < 0.001$, strength: $\chi^2_1 = 150.38$, $p < 0.001$; figure 1B). Given that groups were female-biased, we expect focal males to have fewer male associates than females. However, for both males and females, the proportion of associates that were males was considerably lower than expectations based on group sex ratio (figure 1B). There was a non-significant tendency for males to associate with proportionally fewer males ($\chi^2_1 = 3.001$, $p = 0.083$; figure 1B).

ii) Social and sexual networks

The strength of the social association between a male and a female was positively correlated with the probability that they mated with each other. The magnitude of the correlation was more extreme than expected compared to null expectations generated from models using randomised versions of sexual networks ($p_{rand} = 0.002$; figures 1A, 1C & supplementary material figure S3). This suggests that controlling for any overall relationship between individual levels of sociality and propensity to mate, pairs that associate more strongly have a higher probability of mating with each other. The total number of copulations between pairs was also positively predicted by the strength of their social association. This relationship was again stronger than expected compared to null expectations generated from randomised sexual networks ($p_{rand} = 0.002$; figures 1A, 1C & supplementary material figure S4), as was the relationship between the strength of pairwise associations and number of copulation attempts received by females ($p_{rand} = 0.002$; figure 1C & supplementary material figure S5). Accordingly, a female's overall sociality with males, measured as either the proportion of her associates that were males, or the total strength of her association with males, positively and significantly predicted the number of her unique male partners (M), the number of copulations and copulation attempts that she received (Table S2).

iii) Female characteristics and socio-sexual structure

Older females were more dominant than younger females (figure 2A, supplementary material figure S6; $\chi_1^2 = 35.971$, $p < 0.001$). Controlling for social status, older females had lower reproductive success (T) than younger females ($\chi_1^2 = 15.293$, $p < 0.001$; figure 2A). Controlling for age, more dominant females showed a non-significant tendency to have higher reproductive success ($\chi_1^2 = 3.575$, $p = 0.059$; figure 2A). Older females also laid lighter eggs than younger females (Table S3).

Female characteristics were associated with female sociality. More dominant females were more social overall when controlling for their age (status: $\chi_1^2 = 16.062$, $p < 0.001$, age: $\chi_1^2 = 1.315$, $p = 0.251$; figures 1A & 2B). Older females consorted with a higher proportion of females and this relationship between female age and sex ratio bias was stronger than expected than null expectations generated from randomisations of social networks ($p_{rand} = 0.002$; figure 2C). In contrast, more dominant females consorted with a higher proportion of males (figure 2C), and this trend was marginally non-significantly stronger than null expectations based on randomisations of social networks ($p_{rand} = 0.054$).

Female-female associations were structured by female characteristics. Older females associated with on average older and more dominant females and in both cases the strength of the relationship was stronger than expected by chance compared to null expectations based on randomised social networks (age *vs* partner status, $p_{rand} = 0.002$, age *vs* partner age: $p_{rand} = 0.002$; figures 1A & 2D). We also confirmed the reverse: the social status of a female was positively correlated with the age and social status of her social partners, and these relationships were stronger than expected by chance compared to null expectations based on randomised social networks (status *vs* partner status $p_{rand} = 0.002$, status *vs* partner age: $p_{rand} = 0.002$; figure 1A & 2D). Older females and more dominant females associated with more dominant males, however only female age was more strongly associated with the status of male social partners than expected from randomised social networks (status: $p_{rand} = 0.262$; age: $p_{rand} = 0.002$; figure 1A & 2E). This suggests that the tendency of more dominant females to associate with more dominant males can be explained largely by the high overall sociality of dominant females. Older females, however, associated more with dominant males than expected based on their level of sociality alone.

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

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

Finally, we tested whether female characteristics determined the phenotypes of their sexual partners and the sires of their offspring. Binary networks revealed that older females on average mate with more dominant males. This tendency was marginally non-significantly stronger compared to random expectations (p_{rand} = 0.088; figure 3C). This suggests that, by virtue of mating infrequently, older females were more likely to mate randomly with dominant males because these males mate more frequently than subordinate males. The social status of a female was not associated with the average status of her sexual partners and this was consistent with expectations generated from randomised sexual networks ($p_{rand} = 0.751$; figure 3C). Similarly, taking into account repeated matings between male-female pairs using weighted sexual networks, revealed that female age was positively associated with the weighted social status of their sexual partners, and this relationship was not more extreme than expected from null expectations based on randomised sexual networks ($p_{rand} = 0.685$; figure 3C). Female social status was also positively associated with the weighted social status of her sexual partners, however, this relationship was stronger than null expectations based on randomised sexual networks ($p_{rand} = 0.004$; figure 3C). This suggests that more dominant females mate with more dominant males at a rate exceeding that expected based on their overall mating rate. Both older and more dominant females sired more offspring with more dominant males, however, in neither case was this relationship stronger than expected by chance assuming random paternity share across their sexual partners (status: $p_{rand} = 0.312$; age: $p_{rand} = 0.313$; figure 3C), suggesting that the higher social status of sires is largely driven by mating patterns themselves.

4. Discussion

We used detailed behavioural observations of replicate polygynandrous groups of red junglefowl to show that differential sociality across female characterisitcs is strongly associated with the fine-scale structure of sexual networks and an important factor in patterns of mating activity and sexual selection on males.

We found a clear sex difference in sociality. Females had more associates than males, and both sexes associated more with females. This is likely driven by sex differences in social tolerance. Aggression among males is likely more intense than among females, reducing male-male associations [39,59]. Moreover, the effect of female competition might be counteracted by the need for females to group together, e.g. to avoid male harassment [26,31,35].

Intersexual associations were closely related to patterns of sexual behaviour. Females were more likely to copulate with close male associates and copulated with these males more often. This establishes a link between the social and the sexual network. Relational data on physical proximity may therefore reflect a latent social network predisposing dyads to a higher probability of mating. This strong correlation between sexual contact patterns and social proximity may conflate sexual and social transmission routes of pathogens, parasites and microorganisms.

Female sociality varied across female characteristics. Females from older cohorts were more dominant than younger females, however female age and social status had contrasting relationships with sociality. More dominant females were overall more social, whereas older females associated more often with other older, more dominant females. The increased sociality of dominant females may reflect a lower tendency to avoid males, greater male sexual interest in dominant females or may emerge because dominant individuals are centrally positioned in groups [60]. The tight social clustering between older and more dominant females could mechanistically arise if females lower in the hierarchy are excluded from grouping with aggressive, dominant individuals [61]. Alternatively, this social clustering could reflect the strong propensity of older females to perch on branches away from males, thus spending more time in close proximity with each other. The overall outcome is that older females associated less often with males, proportionally more with females and received less sexual harassment. Female-female social clustering may therefore reflect an effective strategy to avoid harassment. Similar patterns in cockroaches, *D. punctata*, have led to the suggestion that females may engineer the sex ratio of their social environment, biasing it towards females to avoid costly male harassment [26]. Similarly, female eastern mosquitofish school closer together in the presence of males, which dilutes male harassment [32,62].

Older and more dominant females also consorted more with dominant males. This was more than expected by chance for older females. Previous work indicates that female fowl prefer to associate with dominant males, and that socially isolated females are harassed by peripheral, subordinate males [38,39,63]. Associating with dominant males may represent a strategy to attain high-quality mates and avoid harassment through protection by dominant males. In mallards, *Anas platyrhynchos*, a female's mate will aggressively interfere with copulation attempts from other males [64], while in primates females may incite mate guarding by specific males, potentially reducing harassment or the risk of infanticide [65]. Our results indicate that this potential strategy is not uniform across females but largely associated with female age.

Despite being less fecund and attracting less male sexual attention, older females, on average, secure more socially dominant mating partners. This is likely both because these males mate more frequently [66] and due to the effective social positioning of older females, potentially as a result of greater social experience. By comparison, younger, more fecund females were less discriminant and more polyandrous, mating more frequently and with more males. Older, more socially experienced female pied flycatchers, *Ficedula hypoleuca*, may have reduced rates of extra-pair young because they are better able to secure high-quality pair mates and avoid unwanted advances from extra-pair males [67]. Together, our characterisation of male-female and female-female social structure suggests that older females might use social niche construction to avoid sexual harassment and secure high-quality mates.

Differential female mating activity likely reflects a combination of male mating preferences and the necessity of more fecund females to mate more frequently. In line with this, previous findings in this population have shown that positive female Bateman gradients reflect a male preference for fecund females, rather than any fecundity benefits of polyandry to females [53]. It is however not clear how male preference for more fecund females is maintained, given that reproductive returns are likely eroded by the increased sperm competition. One possibility is that if variation in fecundity is partly additive, males may obtain genetic benefits by preferentially reproducing with more fecund females, through the production of more fecund daughters, which would result in a higher number of grand offspring. Second, males may produce more successful offspring if the higher egg mass of more fecund females [68] translates into increased offspring survival or performance. Third, mating with more fecund females may be less costly for males because these females have a higher propensity to mate and thus will resist male advances less. Alternatively, a male preference for more fecund females may not necessarily be adaptive to males, i.e. males may simply prefer more fecund females through a predisposition for phenotypes linked to female fecundity, e.g. larger comb [68].

Regardless of the adaptive significance of these patterns, the observed distribution of matings may favour an equilibrium state that can be likened to an ideal free distribution, in which males distribute their sexual effort across female partners proportionally to the number of eggs available for fertilisation, as has been argued for golden-orb web spider *Neuphila plumipes* [69]. Similar patterns were recently observed in *Drosophila melanogaster* where male mating effort was distributed across females proportional to their fecundity [70]. The increased sperm competition associated with more fecund females meant that males sired a similar number of offspring per mating with high- and low-fecundity females [70]. Thus, fecundity-dependent polyandry may erode any advantages of male preferences for more fecund females.

The offspring produced by dominant and older females were sired by, on average, more dominant males than those produced by younger and/or subordinate females. Previous work in smaller junglefowl groups, suggests that subordinate males are more likely to copulate with subordinate females, because dominant males intensely guard dominant females [46]. In the larger and more polyandrous groups of the present study, dominant females gain a greater share of their copulations from dominant partners. This suggests that dominant males may also protect paternity with dominant females by remating with them more frequently [66]. In line with this, we have previously shown that dominant, aggressive males, mate with more females, including the least polyandrous females largely because they are able to mate at an overall higher rate [66]. Similarly, by virtue of their low mating rate, subdominant males mate with fewer and more polyandrous females [66]. The extent to which these mating patterns reflect male-male competition or female preference remains unclear. Previous work suggests that female fowl prefer socially dominant males [46,71] and manipulate male-male competition in order to favour matings by these males [42]. The results of the present study indicate that differential female sociality may be an important -but so far neglected- factor underpinning the structure of sexual networks [21].

Our study also has important implications for male harm of females and population viability. Male intrasexual competition can harm females, often through intense sexual harassment [25]. This can severely impact the viability and growth rate of populations through a process similar to the Tragedy of the Commons [72]. In water striders females locally disperse to avoid male harassment [8,23]. The resulting patterns of female aggregation both determines sexual selection on male traits [8] and may also mediate group productivity, by ameliorating the costs of sexual conflict to females [73]. Broadly similar patterns have been confirmed for a diverse range of species [8,23,27–33,35,37]. Our results build on this work by showing that individual variation in female sociality and fecundity is associated with the intensity of harassment that females receive. Population growth rate will be more severely impacted when social structure exposes the most fecund subset of females to more intense harassment [74,75]. The negative impact of male harm on group productivity will instead be buffered when the most productive females are sheltered from harm. Our results indicate that red junglefowl groups fall in the former scenario because younger, more fecund females attract more sexual attention than older, less fecund females. Previous work in similar groups of fowl demonstrates that females resist the majority of male copulation attempts [41,42]. Resistance can be energetically costly [25] and, in fowl, associated with the risk of injuries (e.g. rupture of hard-shelled egg within the female oviduct [42]). In other species, the avoidance of male harassment has also been shown to drive females to forage suboptimally [27]. In our study population, females exposed to higher rates of coerced mating attempts tend to lose more body mass over time [45]. In the present study, we observed that older females have lower fecundity and avoid males by spending more time perching. It is possible that longer perching times may limit feeding by older females. While it is likely that older females feed less because reduced fecundity exacts lower nutritional demands, it is also possible that, in the absence of male harassment, older females might feed more or more optimally, which might marginally improve their fecundity. Conversely, the higher fecundity of younger females, will exact greater energetic demands and will require more continuous access to food [33]. Such demands may place limits on the ability of younger fecund females to avoid male harassment by perching when compared to less fecund older females

[27]. In commercial flocks of fowl, male sexual harassment impacts female foraging behaviour and space use, resulting in a reduction of female fecundity and flock productivity, and changes in sexual behaviour can reduce female stress and increase reproductive performance [43]. Thus, in applied settings, management of flock social structure may be utilised to simultaneously influence sexual behaviour to increase fertility, productivity and welfare.

An important caveat of our study is that our data are largely cross-sectional rather than longitudinal. Thus, we cannot completely disentangle the effect of female age from other cohort effects. While females mix freely in the general population between breeding seasons, females from the same cohort will likely have had more interactions with each other. Moreover, early development in our population is spent in close association largely within a single cohort. However, such potential effects are biologically relevant, particularly in philopatric groups where older females are likely be more familiar with each other, more socially experienced and potentially more socially dominant than other younger birds [61]. Another important consideration concerns the ecological relevance of our study. While the group size and sex ratio used here are within the range found in populations under natural conditions [38], it is likely that captivity may influence the patterns described. First, relatively high population density may increase the rate of social and sexual interactions. Second, life expectancy can be considerably higher in captive versus natural populations [76] and may accentuate age-dependent patterns. Therefore, while the results of our study present a proof-of-concept demonstration of the importance of female sociality in modulating the structure of sexual networks, future studies should seek to determine the extent to which the patterns observed here apply to natural populations of red junglefowl.

In conclusion, we use a replicated set up to confirm previous findings that female sociality is strongly linked with patterns of inter-sexual dynamics, with more fecund females attracting more sexual attention. We further show that female sociality differs with female characteristics and that such differential sociality has important repercussions for the intensity of sexual harassment suffered by females, the intensity of intrasexual competition faced by males and the phenotype of the males reproducing with females occupying different socio-sexual niches. Future studies should unravel the feedback between these processes. In this context, manipulations of the relationships between female age, status, social experience and sexual attractiveness will provide a key tool in dissecting the complex mechanisms through which social, sexual and phenotypic structures interrelate within animal groups.

Ethics. Research was conducted according to United Kingdom home office legislation (Home office licenses 30/2418 and 30/2931) following approval by the Departmental Animal Welfare Ethical Review Body (AWERB).

Data accessibility. We will deposit supporting data in Dryad Digital Repository on acceptance.

Competing interests. We have no competing interests.

Author contributions. G.C.M. and T.P. conceived the study. G.C.M. conducted the field work and analysed the data. L.G. S., E.A.F., D.S.R. performed molecular analyses for parentage assignment. G.C.M. and T.P. wrote the manuscript.

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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.