Social anxiety: how competition, sex, and dispersal affect our propensity to interact socially

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Abstract – Social interactions can be beneficial by allowing individuals to learn socially about their environment or collaborate to achieve outcomes that are otherwise unattainable. Social interactions can also be costly if individuals risk being exploited, attacked, or otherwise harmed as a result of the encounter. Individuals are expected to refrain from social interactions if the potential costs outweigh any benefits. We investigate when individuals are expected to reduce their social interactions, with a focus on sex, dispersal status and competition. Using a mathematical model, we find that competition and dispersal can reduce social interactions within a social group and, due to sexual selection, females are predicted to be less social than males. We then test whether sex and dispersal can shape social interactions in humans, using a standardized instrument to measure social anxiety and a novel behavioural game. Despite suggestions in our model and in the previous literature that women and immigrants are more likely to suffer from social anxiety, our empirical results did not support the theoretical expectations. We discuss potential reasons for this, including mechanisms counter to prior theories and methodological issues in the paradigm.

Keywords – inclusive fitness, kin selection, migration, sexual selection, social anxiety, social behaviours

Introduction

Social interactions have inherent trade-offs [1]. Through social interactions, individuals can learn about their environment by observing or imitating what others do, find a mating partner, and increase their chances of cooperating with social partners. But social interactions can also pose costs. Social interactions reduce the time available for other asocial activities – such as foraging, sleeping, or learning asocially – and social interactions can also be risky. For example, social interactions can expose individuals to parasites and disease [2] and, when social interactions involve investments, there is also the possibility that social partners will cheat [3] or fail to coordinate their actions effectively, thereby reducing the payoffs of interacting socially compared to alone [4,5]. Here, we investigate the issue of how humans balance their investments in social and asocial activities, and test these theoretical predictions using a self-report measure of social interaction anxiety and an experimental game.

The vast majority of primate species are social, but humans are seemingly unique among primates in the extent of our sociality [6,7]. Humans typically live in much larger groups than any other primate species, and we cooperate not only with relatives and friends, but also with people outside of our core social group and with strangers that we may never even meet [8-11]. Our propensity to cooperate with others is frequently touted as having been pivotal in our species' extraordinary ecological success: cooperation allowed us to prosper in nearly every habitat on Earth [7].

Given our social nature, individuals that have fewer social interactions might incur costs.

Indeed, lack of social interactions is known to raise the risk for developing a range of health

problems [12], ranging from dementia [13] and depression [14] to cardiovascular diseases [15] and decreased immune response [16]. The health risks associated with loneliness might even be comparable to those associated with smoking [17]. In ancestral human populations, a reduced tendency to interact socially could also have resulted in increased potential predation risk [18]; reduced food availability [19]; and reduced access to social information [20].

Individuals are expected to balance the potential costs and benefits associated with social interactions, although not all individuals will resolve this trade-off in the same way. Different social and biological scenarios may be consistently associated with higher costs arising from social interactions, which may favour individuals who recognise those scenarios and reduce their social interactions accordingly. From an evolutionary perspective, competition, dispersal, and sex are important determinants of several social behavioural traits. For example, competition can determine population structure in parasitoid wasps [21,22]; dispersal [23,24] and sex biases in dispersal [25] can affect the potential for altruism in social groups; and sex can affect how individuals interact with their social partners [26,27].

Social anxiety is defined by fear and avoidance of social interactions [28], and can range in severity from interpersonal concerns experienced by almost everyone to more severe worries that can become pathological [29]. The literature on human behaviour suggests that competition, sex, and dispersal are also important determinants of social anxiety: competitive environments are associated with increased social anxiety [30]; and women and immigrants report higher rates of social anxiety compared to men [31] and non-migrants [32,33]. However, we still lack a general theoretical framework for understanding whether and how social anxiety in humans has been and continues to be shaped by natural selection.

Here, we use social anxiety as a proxy for a reduced tendency to engage in social interactions. To study how such social strategies might evolve, we use an inclusive fitness approach [34,35]. According to the theory of inclusive fitness, an individual may pass on more copies of their genes by increasing their own reproductive success (direct fitness) and/or by increasing the reproductive success of other individuals with whom they share genes (indirect fitness) [34,35]. Social interactions can have both a direct benefit (if an individual cannot reproduce alone or some activities require cooperation) and an indirect benefit (if social partners, some of whom may be related to the behavioural actor, benefit from those same activities). Natural selection could have, therefore, shaped how individuals interact in a social group, with such interactions depending how related a focal individual is to their social partners. This in turn might explain why humans reduce social interactions in particular contexts, such as in environments of intense competition [30] or when they disperse to a new population [32,33]. The former reduces the benefit of relatedness to social partners and the latter reduces relatedness between an individual and her social partners. Ancestral human populations may have also been characterized by female-biased dispersal [36], which would have led women to be less related to their social partners.

Here we use an evolutionary theoretical approach to explore why and how competition, sex, and dispersal are expected to affect the payoffs accruing from social interactions and, therefore, individuals' tendency to interact with others. We combine our theoretical approach with empirical data, using a self-report social anxiety measurement and a novel economic game to measure social risk aversion. While self-report data can be useful, they are often biased and suffer from subjectivity [37]. Economic games can be useful in this regard, by reflecting relevant features of the real world and revealing participants' preferences in a way that self-report data may not [38]. Thus, we combine approaches from psychology,

economics, and evolutionary biology to have a multi-disciplinary understanding of human social behaviour.

Our theoretical approach generates predictions about how an individual's tendency to interact socially may be modulated by (i) the degree of genetic relatedness to their social partners and (ii) the extent of intragroup competition. We also explore the possibility that sex and dispersal-status drive specific social patterns in women and men, and in immigrants and non-migrants, respectively. Then, with our empirical approach, we survey a sample of individuals to measure sexual and migration patterns associated with self-reported anxiety about social interactions; and experimentally determine the willingness to interact socially in a task where payoffs are determined by the decisions of a partner. Our overall aim is to understand what drives patterns of social interaction from an evolutionary perspective.

Model

Methods

We built a model of social strategies using the Taylor-Frank approach [23,39] to kin selection. We consider an infinite diploid population divided into social groups [40] with n_f adult females and n_m adult males in an even sex-ratio. Regardless of their sex, individuals spend some of their time alone (e.g. feeding, sleeping, exploring the environment) and some of their time interacting socially (e.g. mating, learning with social partners, cooperating). Crucially, regardless of their strategy, individuals need to have social and asocial interactions to have reproductive success. Specifically, pay-offs are determined by:

$$f_{i|A} = (1 - x_{i|A})x_{i|A}((y) - (1 - y)),$$

where: i refers to the sex of the focal individual; A refers to the migration status of the focal individual; $x_{i|A}$ is the probability that the focal individual interacts with their social partners; and y is the probability that the focal individual's social partners interact socially. Accordingly, the payoff that the focal individual gets by themselves is determined by their own behaviour $(1 - x_{i|A})$. If an individual is interacting socially ($x_{i|A}$), there is a probability that social partners also decide to act socially (y), in which case both the focal individual and the social partner receive a benefit ($x_{i|A} y$). But the social partner may not act socially $(1 - y)$, in which case the focal individual pays a cost ($x_{i|A} (-(1 - y))$). In other words, the payoffs of interacting socially are equivalent to the stag-hunt game [4].

After such asocial and social activities, males compete among themselves for a share of the offspring produced by the females in the social group. Males with higher total payoff relative to the other males have higher reproductive success. Each female then produces a large number of offspring with an even sex-ratio and in proportion to her fecundity (see supplementary material for details). Adults then die. Juveniles in the same social group then compete for reproductive resources in proportion to a (the degree of intragroup competition, with $a = 0$ representing competition exclusively between groups and $a = 1$ representing competition exclusively within groups). After intragroup competition, juveniles can disperse individually between social groups. Female and male juveniles may disperse at different rates. Following dispersal, juveniles of both sexes survive within each social group to adulthood, returning the population to the beginning of the life cycle. Using this mathematical approach, we consider three different scenarios: 1) no potential for sexual or migration-status differences in social interactions; 2) potential for sexual differences but no potential for migration-status differences in social interactions; 3) potential for dispersal-

status differences but no potential for sexual differences in social interactions. See
Supplementary Material for full details of the model.

Results

Scenario 1: No sexual or dispersal-status differences in social behaviour. Under this scenario, we find that a higher dispersal rate and increased intragroup competition independently disfavour the tendency to interact socially (Figure 1a). Increased dispersal rate leads to lower genetic relatedness between an individual and her social partners, reducing the potential for an actor to increase her indirect fitness through interacting with her social partners [34,35]. Similarly, increased intragroup competition disvalues relatedness of an individual to their social partners, as the latter are more likely to be competitors for resources.

Scenario 2: Sexual differences but no dispersal-status differences in social behaviour. In this scenario, females are generally selected to have a lower propensity to interact socially than males (Figure 1b,c). This can be understood in terms of sexual selection: male fecundity is always relative to the fecundity of the other males while female fecundity is independent of the fecundity of the other females. This favours risky strategies in males (such as tendency to seek social interactions). Males become less likely to interact socially when there is strong male-biased dispersal (Figure 1c). At that point, relatedness between a male and his social partners is so low that their sociality decreases beyond the level of sociality observed in the females.

Scenario 3: Dispersal-status differences but no sexual differences in social behaviour. Here, we find that non-dispersers are consistently favoured to be more social than dispersers (Figure 2). Nevertheless, as dispersal increases, relatedness among non-dispersers decreases

and, consequently, their tendency to interact socially also decreases (Figure 2). Increased intragroup competition reduces the differences between non-dispersers and dispersers but reduces sociality in both (Figure 2) due to its effect of eroding the value of relatedness between an individual and her social partners.

Experimental study

Methods

This project was approved by the University College London ethics board (project ID:3720/002). All data were collected in June 2020 using Prolific (www.prolific.co), an online crowd-sourcing platform. All data and analysis scripts are available online (www.github.com/GSFaria-wasp/Sociality). Prior to taking part in the study, participants were informed that their participation was voluntary, and were required to tick a box giving consent for the authors to use their anonymous data for research purposes. We included participants who were fluent in English. Specific preregistered predictions for this study can be found here (<http://aspredicted.org/blind.php?x=b65w8>).

We recruited 1005 participants (407 females, 584 males, 11 non-binary, and 2 that preferred not to say). All participants were first asked to complete the Social Interaction Anxiety Scale [41], a 20-item instrument that measures how comfortable participants are with social interactions. For each question, participants are asked to indicate the degree to which they feel the statement is characteristic or true of them (where 0 = not at all and 4 = extremely). The degree of social interaction anxiety is obtained by summing the scores provided (with items 5, 9, and 11 being reversed): higher scores indicate higher levels of social anxiety. At the end of this survey, we asked participants to provide basic demographic information, including age and gender, and whether they currently lived in the region in which they grew

up. The latter question served as a proxy for dispersal status to map onto our theoretical model results. We used the demographic data to ask whether women and ‘dispersers’ were more likely to experience social interaction anxiety.

After a four-day interval, participants were recalled to play an economic game, with the economic game providing a behavioural measure of social risk sensitivity. We successfully recalled 941 of the original 1005 participants (382 females, 546 males, 11 non-binary, and 2 that preferred not say). Participants played two kinds of game: an asocial and a social game. In each game the participant could choose to receive a lower, guaranteed payoff or could choose to gamble to achieve a higher, but riskier, payoff. In the asocial game, the participant could choose to get a secure payoff of £0.50 or could opt for a risky payoff (from £0.50 to £1.00, in £0.10 increments). In the risky trials, the participant had a 50% chance to win the higher payoff but a 50% chance to get nothing. This probability was not communicated to the participants. The social game had the same incentive structure as the asocial game, but the risky game was framed as a social risk: participants could choose to play a solo game (for a fixed payoff of £0.50) or could choose to play with a co-player (for a payoff of £0.50 to £1.00, in £0.10 increments). The player only got the payoff in the social game if the partner also chose to interact socially in that round. Thus, the game has the same incentive structure as a stag-hunt game. The participants were asked to play 11 rounds, with an incremented reward for the riskier option. With this game we could measure participants’ general risk sensitivity, and also their socially-specific risk sensitivity.

Participants in this task were playing against real co-players. We achieved this by having the participants make these same social decisions at the end of the survey task four days prior, and then matching participant decisions to those that had previously been made by another

individual ex-post at random. We used data from the economic game to determine whether women and ‘dispersers’ tended to have a higher threshold for accepting the risk of a social interaction.

(iii) Statistical analysis

We analysed the data using multi-model selection with model averaging [42,43] to compare the explanatory power of different variables. The Akaike information criterion (AIC) was used to evaluate models, with lower AIC values indicating a better fit [43]. With this approach, we specified a global model containing all fixed effects and interactions specified in our pre-registered predictions (<http://aspredicted.org/blind.php?x=bg65w8>). All possible model combinations were compared resulting in a top model set, which contained all the models that were within 2 AICc units of the best model. Parameter estimates were obtained through averaging across the top model set. This approach incorporates the uncertainty over the true parameter estimate when many models have similar levels of support. All estimates reported below are full model averages, which provide conservative estimates for terms that are not included in all the top models.

For model 1, we used the sum of the score in the Social Interaction Anxiety Scale as our dependent variable and gender, age, and dispersal-status (based on city) as independent variables. Binary input variables were centred. As the response term was normally distributed, we use a linear-regression model instead of an ordered logistic regression as described in the pre-registration. We excluded from the analysis participants who did not identify themselves as female or male (n =13).

For model 2, we used the difference between the threshold risk (i.e. the reward value at which point the participant starts choosing the riskier option) in the social game and in the asocial game to measure how prone individuals are to take risks when the risk source was social. Accordingly, negative values mean that participants were risk-prone for social interactions and positive values mean that participants were risk-averse for social interactions. This social risk-sensitivity variable was continuous, ranging from -11 to 11. In line with our pre-registration, we excluded 20 participants that failed to pass the comprehension questions and 71 participants who displayed at least two non-transitive responses (i.e. participants who accepted a low-value risky gamble but rejected a higher-value risky gamble). Following exclusions, the total sample number was 837 (346 females, 491 males). The data were normally distributed and, therefore, we used a linear-regression model.

Results

Social Interaction Anxiety Scale scores ranged from 0 to 74, with a mean of 34.1 ($\pm$ 0.49; skewness 0.17). Older participants were less socially-anxious (estimate -0.31; 95% CI: -0.42, -0.20). Neither gender (estimate -1.39; 95% CI: -3.70, 0.92) or dispersal status (estimate 0.15; 95% CI: -1.10, 1.40) had significant effects on self-reported social anxiety.

In the economic game, the risk threshold difference ranged from -11 to 11, with a mean of -0.99 ($\pm$ 0.15; skewness 0.21), meaning that participants were slightly socially risk prone. Participants that were risk averse in the asocial task were also risk averse in the social task (estimate -0.95; 95% CI: -1.01, -0.88). In contrast to the predictions of the theoretical model, sex (estimate -0.09; 95% CI: -0.43, 0.26) and dispersal-status (estimate -0.01; 95% CI: -0.20, 0.18) had no detectable effect on the risk threshold difference. We also found no effect of age on risk threshold difference (estimate -0.01; 95% CI: -0.03, 0.02).

299

300 *Discussion*

301 Our theoretical model showed that relatedness, intragroup competition, and sex can shape
302 how likely individuals are to attempt to interact socially with others. Accordingly, natural
303 selection could have favoured individuals to decrease their baseline of sociality whenever: a)
304 there is decreased relatedness; b) there is increased intragroup competition; c) and the
305 individual is a female. However, neither the data from the self-report survey nor our
306 behaviour experiment supported the predictions made by the theoretical model. We first
307 discuss the predictions of the theoretical model in light of existing empirical findings, before
308 addressing the discrepancy between the theoretical predictions and the empirical results
309 obtained in this study.

310

311 Our theoretical model revealed a key role for relatedness in driving patterns of social
312 interaction. Nevertheless, given how many of our social interactions occur outside of the
313 family in modern populations [44,45], it could be argued that relatedness plays a diminishing
314 role in defining our social interactions in current populations. To address this potential
315 concern, we note that relatedness is simply a vector of information that informs a focal
316 individual about her social partners' behaviour [23,34,35]. If a focal individual favours those
317 with the same behaviour, whatever that behaviour might be, then this allows that behaviour to
318 increase in the population. Genealogical kinship, and therefore genetics, is an important
319 source of information, given that genetically related individuals are more likely to share the
320 same genes and, therefore, have the same behaviour. But genetic relatedness is not the only
321 source of information. Any cue – such as cultural traits or even past interactions with specific
322 individuals – that allows a focal individual to identify social partners with a similar behaviour
323 will increase relatedness [23]. Accordingly, natural selection could have selected individuals

to act socially whenever relatedness is high (e.g. same culture, past positive interactions, same family) and not act socially whenever relatedness is low (e.g. different culture, past negative interactions, different family) [23,34,35]. While the word relatedness can be used in all of these contexts, we refer to contextual similarity to refer to all cases of non-genetic relatedness to avoid confusion. Based on the results of our model, we therefore expect any factor that contributes to contextual similarity between social partners to promote social interactions between them. In contrast, factors that reduce the contextual similarity between social partners will reduce social interactions between them.

Focusing on intragroup competition, we find that intragroup competition disvalues the importance of genetic relatedness (or contextual similarity), therefore decreasing sociality. As such, intragroup competition could have shaped our proclivity for social interactions. Furthermore, natural selection could have selected individuals to reduce or increase social interactions depending on the value of intragroup competition that they encounter in their environment. This finding has some support from previous empirical studies, which have shown that individuals living in more competitive environments tend to have a higher level of social anxiety [30].

Our theoretical results offer a new perspective on patterns of social anxiety relating to sex and immigration status that have been observed in the empirical literature. For example, women are more prone to social anxiety than men [31]. Both female-biased dispersal (likely to have been present in ancestral populations; [36]) and sexual selection (with men in ancestral populations being more social to increase their mating success) might have contributed to these patterns, as explored by our model. Empirical work also supports the patterns suggested by our models on dispersal-status, with immigrants being more likely to

experience loneliness and social isolation [32,33]. According to our theoretical framework, this reflects a decreased perceived contextual similarity between immigrants and their social partners, and perhaps a decreased tendency to be involved in social interactions. Dense immigrant populations [32,46] and general social support [47] reduce the likelihood of the negative outcomes mentioned above. In our theoretical framework, this would be equivalent with increased perceived contextual similarity between immigrants and their social partners, given their similar society status, conditions, or positive past interactions with non-immigrants.

Discrepancy between theory and empirical results

Despite suggestions of our theoretical model and the literature that women and immigrants should manifest higher levels of social anxiety, our empirical results do not support these expectations. Previous research using the Social Interaction Anxiety Scale (SIAS) has shown that women self-report experiencing higher social anxiety than men [48], although this study only involved individuals that had already reported experiencing social anxiety raising the possibility that the sample was non-representative. Our study, by contrast, drew a sample from a large online population and we did not record whether participants had previously been diagnosed with any mental health disorders, including social anxiety. We also found no relationship between immigrant status and score on the SIAS, despite the fact that previous work has reported higher social anxiety among immigrants [32,33]. It is possible that our proxy for immigration (whether a participant currently lives in the country or city where they grew up) was insufficient to capture the aspects of immigration that are conceivably linked to social anxiety. Participants might have immigrated with their family, have a support community that they can rely on, or could have immigrated to a country with a similar culture and/or language to their country of origin [47]. Indeed, all of these factors could have

contributed to increase contextual similarity between immigrants and their social partners, as suggested by our theoretical framework.

Our behavioural study also revealed no associations between sex or immigrant status on the tendency to avoid social interactions. More importantly, there was no correlation between being socially anxious in the Social Interaction Anxiety Scale and being socially risk averse in the economic game. One possibility for this discrepancy is that our experimental paradigm did not adequately capture social anxiety. Notably, the paradigm focused on social risk in terms of economic loss and involved small stakes, which could have been insufficient to induce social anxiety. Moreover, it may be that paradigms incorporating the potential for social rather than economic harm (e.g. loss of status or negative social evaluation) would have been more relevant for capturing social anxiety. In our study, people interacted with anonymous partners via the internet, meaning that the potential for social harm was minimal. In future studies, it would be helpful to explore whether scores on the SIAS positively predict social anxiety in behavioural settings involving social rather than economic costs.

We did find an effect of age on the Social Interaction Anxiety Scale, with older participants having lower levels of social anxiety. Nevertheless, age did not affect social risk preferences in the economic game. While we did not account for the effect of age in our theoretical model, older individuals are likely to have more stable and positive social relationships [49]. Accordingly, using our theoretical framework, this could be either because intragroup competition is stronger at a younger age or contextual similarity and/or genetic relatedness increases between an individual and their social partners (for instance, due to constant positive long-term interactions with the same social partners and/or through the development of a family).

399

400 **Conclusion**

401 Our study focused on the factors underlying social behaviour in humans, with both a
402 theoretical and an empirical approach. Our mathematical models highlight the importance of
403 biological and demographic factors in predicting patterns of social interaction, although we
404 were unable to verify these predictions with either self-report survey data or with the results
405 of a behavioural game. We suggest that future work exploring social anxiety might need to
406 incorporate more nuanced measures of immigration status, as well as including games that
407 incorporate social costs of interactions.

408

409 **Data accessibility.** Data is available here <https://github.com/GSFaria-wasp/Sociality>

410

411 **Ethics statement.** This project has been approved by the UCL Ethics Board, project ID:
412 3720/002.

413

414 **Authors' contributions.** G.S.F., V.B., and N.R. designed the study and wrote the
415 manuscript. G.S.F. led the mathematical analysis. G.S.F. and N.R. ran the statistical analysis.

416

417 **Competing interests.** We declare we have no competing interests.

418

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Figure legends

Figure 1 | How social an individual is depends on the relatedness between the individual and her social partners. Individuals are more social when relatedness is higher, which is the case when female dispersal is lower (a), and when intragroup competition is lower (a). When sociality can evolve independently in females (dark red) and males (light green), females and males may favour different levels of sociality (b; dashed line represents the level of sociality

when sociality does not evolve independently in females and males). Specifically, regardless of sex-biased dispersal, males are expected to be more social than females (b). The following parameter values were used for both panels: number of adult females and males $n_f = n_m = 4$; and male dispersal $d_m = 0$. Additionally, in panel (b) intragroup competition $a = 0$.

Figure 2 | How social an individual is depends on her dispersal status. Individuals are more social when they do not disperse from their natal patch (a-c). Individuals that disperse are less social (a-c). In both cases, sociality decreases as intragroup competition increases. However, individuals that disperse increase their sociality as dispersal increases in contrast with individuals that do not disperse, whose sociality decreases as dispersal increases (a-c). The following parameter values were used in all panels: number of adult females and males $n_f = n_m = 4$; and female and male dispersal $d_f = d_m = 0.25$ (a); 0.50 (b); 0.75 (c).

————— increased dispersal increases sociality in dispersers and decreases sociality in non-dispersers —————>

Electronic supplementary material

1

2 1. Basic model of the evolution of sociality and inclusive fitness predictions

3

4 Natural selection favours any gene that is associated with greater individual relative
5 fitness, $dW/dg_{i|A} > 0$ where W is the relative fitness of the individual carrying the gene
6 and g is the genic value of a gene picked at random from the population (Taylor 1996).
7 We assume that the population is divided into social groups with an equal number of
8 females and males, meaning that the gene can be picked from a random female ($i = f$)
9 or from a random male ($i = m$). Moreover, the gene can be picked from an individual
10 that is a native ($A = N$) or a non-native ($A = D$) to the social group. The relative
11 fitness needs to be averaged across females and males, i.e. $W = v_f W_{f|A} + v_m W_{m|A}$,
12 where: $W_{f|A}$ is the relative fitness of the female carrying the gene; $W_{m|A}$ is the relative
13 fitness of the male carrying the gene; v_f is the reproductive value of the females; and v_m
14 is the reproductive value of the males. The relative fitness of a female may be written
15 as $W_{f|A}(x_{f|A}, y_A, z_A)$, where $x_{f|A}$ is the level of sociality of the focal female, $y_A = (y_{f|A}$
16 $+ y_{m|A})/2$ is the average level of sociality of the individuals in the social group, $y_{f|A}$ is
17 the average level of sociality of the females in the social group, $y_{m|A}$ is the average level
18 of sociality of the males in the social group, $z_A = (z_{f|A} + z_{m|A})/2$ is the average level of
19 sociality of the individuals in the population, $z_{f|A}$ is the average level of sociality of the
20 females in the population, and $z_{m|A}$ is the average level of sociality of the males in the
21 population. Similarly, the relative fitness of a male may be written as $W_{m|A}(x_{m|A}, y_A,$
22 $z_A)$, where $x_{m|A}$ is the level of sociality of the focal male. Values range from 0 to 1.

23

24 Following the personal fitness approach of Taylor & Frank (1996) for a class-structured
25 population, we may write $dW/dg_{i|A} = v_f(dW_{f|A}/dg_{f|A}) + v_m(dW_{m|A}/dg_{m|A}) =$
26 $v_f((\partial W_{f|A}/\partial x_{f|A})(dx_{f|A}/dG_{f|A})(dG_{f|A}/dg_{f|A}) +$
27 $(\partial W_{f|A}/\partial y_{f|A})(dy_{f|A}/dG_{f|A}') (dG_{f|A}'/dg_{f|A}) +$
28 $(\partial W_{f|A}/\partial y_{m|A})(dy_{m|A}/dG_{m|A}') (dG_{m|A}'/dg_{f|A})) +$

29 $v_m((\partial W_{m|A}/\partial x_{m|A})(dx_{m|A}/dG_{m|A})(dG_{m|A}/dg_{m|A}) +$
 30 $(\partial W_{m|A}/\partial y_{m|A})(dy_{m|A}/dG_{m|A}')(dG_{m|A}'/dg_{m|A}) +$
 31 $(\partial W_{m|A}/\partial y_{f|A})(dy_{f|A}/dG_{f|A}')(dG_{f|A}'/dg_{m|A}))$, where: $G_{f|A}$ is the focal female's breeding
 32 value; $G_{f|A}'$ is the average breeding value of the females in the social group; $dx_{f|A}/dG_{f|A}$
 33 $= dy_{f|A}/dG_{f|A}' = \gamma_{f|A}$ is the mapping between genotype and phenotype in the females;
 34 $dG_{f|A}/dg_{f|A} = p_{f|A}$ is the consanguinity of the gene in the focal female to the female
 35 herself; $dG_{f|A}'/dg_{f|A} = p_{ff|A}$ is the consanguinity of the gene in the focal female with a
 36 randomly-chosen female on her social group (including herself); $dG_{m|A}'/dg_{f|A} = p_{fm|A}$ is
 37 the consanguinity of the gene in the focal female and a randomly-chosen male on her
 38 social group; $G_{m|A}$ is the focal male's breeding value; $G_{m|A}'$ is the average breeding
 39 value of the males in the social group; $dx_{m|A}/dG_{m|A} = dy_{m|A}/dG_{m|A}' = \gamma_{m|A}$ is the
 40 mapping between genotype and phenotype in the males; $dG_{m|A}/dg_{m|A} = p_{m|A}$ is the
 41 consanguinity of the gene in the focal male to the male himself; $dG_{m|A}'/dg_{m|A} = p_{mm|A}$
 42 is the consanguinity of the gene in the focal male with a randomly-chosen male on his
 43 social group (including himself); and $dG_{f|A}'/dg_{m|A} = p_{mf|A}$ is the consanguinity of the
 44 gene in the focal male with a randomly-chosen female on his social group. The
 45 consanguinity between a gene to its carrier is the same no matter the sex that we are
 46 considering or the nativity status of the individual in the social group and, therefore,
 47 $p_{f|A} = p_{m|A} = p$. We divide all terms of the right side of the equation by p to get the
 48 kin-selection coefficients of relatedness (Bulmer 1994), specifically whole-group
 49 coefficients of relatedness (Pepper 2000).

50

51 If sociality cannot evolve independently in females and males, then $\gamma_{f|A} = \gamma_{m|A} = 1$. In
 52 this scenario, all derivatives are evaluated at $x_{f|A} = x_{m|A} = y_{f|A} = y_{m|A} = z_{f|A} = z_{m|A} =$
 53 z_A . Accordingly, natural selection favours an increase in the level of sociality in females
 54 and males if:

55

$$\begin{aligned}
 &v_f(-C_f(z_A) + B_{ff}(z_A)r_{ff|A} + B_{fm}(z_A)r_{fm|A}) + \\
 &v_m(-C_m(z_A) + B_{mm}(z_A)r_{mm|A} + B_{mf}(z_A)r_{mf|A}) > 0
 \end{aligned} \tag{A1}$$

57

58 where: $-C_f(z_A) = \partial W_{f|A}/\partial x_{f|A}$; $B_{ff}(z_A) = \partial W_{f|A}/\partial y_{f|A}$; $B_{fm}(z_A) = \partial W_{f|A}/\partial y_{m|A}$;
 59 $-C_m(z_A) = \partial W_{m|A}/\partial x_{m|A}$; $B_{mm}(z_A) = \partial W_{m|A}/\partial y_{m|A}$; $B_{mf}(z_A) = \partial W_{m|A}/\partial y_{f|A}$; $r_{ff|A}$
 60 $= p_{ff|A}/p$; $r_{fm|A} = p_{fm|A}/p$; $r_{mm|A} = p_{mm|A}/p$; and $r_{mf|A} = p_{mf|A}/p$. If sociality can
 61 evolve independently in females and males, then $\gamma_{f|A} = 1$ and $\gamma_{m|A} = 0$ when analysing
 62 sociality in females and $\gamma_{f|A} = 0$ and $\gamma_{m|A} = 1$ when analysing sociality in males. In this
 63 scenario, all derivatives are evaluated at $x_{f|A} = y_{f|A} = z_{f|A}$ and at $x_{m|A} = y_{m|A} = z_{m|A}$.
 64 Accordingly, natural selection favours an increase in the level of sociality in females if:

65

$$66 \quad v_f(-C_f(z_{f|A}) + B_{ff}(z_{f|A})r_{ff|A}) + v_m(B_{mf}(z_{f|A})r_{mf|A}) > 0 \quad (A2)$$

67

68 and an increase in the level of sociality in males if:

69

$$70 \quad v_f(B_{fm}(z_{m|A})r_{fm|A}) + v_m(-C_m(z_{m|A}) + B_{mm}(z_{m|A})r_{mm|A}) > 0 \quad (A3)$$

71

72 2.1 Demographic model when dispersal status is unknown

73

74 *Life cycle* – We consider an infinite diploid ($v_f = v_m = 1/2$) population divided into
 75 social groups (Wright 1931) containing n_f females and n_m males. Individuals in the
 76 social group have to spend some of their time alone – feeding, sleeping, exploring the
 77 environment –, but they also have to interact socially – mating, learning with social
 78 partners, cooperating. Crucially, regardless of their strategy, they need to do both to
 79 have reproductive success. That is, an individual that spends all her time alone will not
 80 be able to reproduce. Conversely, an individual that spends all her time interacting
 81 socially will not be able to perform basic biological functions and, therefore, will not
 82 survive. Specifically, a female's fecundity is:

83

$$84 \quad f_f = (1 - x_f)x_f((y) - (1 - y)) \quad (A4)$$

85

86 where: $(1 - x_f)$ is the success that the focal female gets by acting alone; and $x_f((y) -$
 87 $(1 - y))$ is the success that the focal female gets by acting socially. Specifically, the
 88 focal female can only be successful by acting socially if she acts socially (x_f) and if her
 89 social partners act socially (y). However, by acting socially, she incurs a risk of her
 90 social partners deciding not to act socially ($1 - y$), in which case she pays a cost for an
 91 unsuccessful social interaction. Similarly, a male's fecundity is:

92

$$93 \quad f_m = (1 - x_m)x_m((y) - (1 - y)) \quad (A5)$$

94

95 where: $(1 - x_m)$ is the success that the focal male gets by acting alone; and $x_m((y) -$
 96 $(1 - y))$ is the success that the focal male gets by acting socially. After such asocial and
 97 social activities, each female produces a large number of offspring, with an even
 98 sex-ratio and in proportion to her fecundity. Adults then die. Juveniles in the same
 99 social group then compete as a group with other groups of individuals from other social
 100 groups in proportion to $1 - a$ and compete among themselves with probability a . After
 101 competing, juveniles can disperse individually between social groups, with female
 102 juveniles dispersing with probability d_f and male juveniles dispersing with probability
 103 d_m to a random social group or else remaining in their current social group. Following
 104 dispersal, n_f females and n_m males survive at random within each social group to
 105 adulthood, returning the population to the beginning of the life cycle.

106

107 *Natural selection* – Female relative fitness in this model is:

108

$$109 \quad W_f = \frac{f_f}{aF_f + (1 - a)\bar{F}_f} \quad (A6)$$

110

111 where: $F_f = f_f|_{x_f=y_f}$; and $\bar{F}_f = f_f|_{x_f=y_f=z_f, y_m=z_m}$. Likewise, male relative fitness in this
 112 model is given by:

113

$$114 \quad W_m = \frac{f_m}{F_m} W_F \quad (A7)$$

115

116 where: $W_F = W_f|_{f_f = F_f}$, $F_m = f_m|_{x_m = y_m}$. We can now use the inequalities derived in
 117 section 1 to reach the marginal fitness equations for the evolution of sociality and,
 118 consequently, to derive the optimal level of sociality (see below).

119

120 *Relatedness* – The relatedness between the focal female and a randomly-chosen female
 121 in her social group (including the focal female herself) is:

122

$$123 \quad r_{ff} = \frac{1}{n_f} + \frac{n_f - 1}{n_f} (1 - d_f)^2 r \quad (A8)$$

124

125 where: with probability $1/n_f$ the randomly chosen female is the focal female herself, in
 126 which case relatedness is 1; and with probability $(n_f - 1)/n_f$ is a different female, in
 127 which case they are only related if they are both locals $(1 - d_f)^2$ and, if so, their
 128 relatedness is defined by the relatedness between juveniles born in the same social group
 129 (r). The relatedness between the focal female and a randomly-chosen male in her social
 130 group is:

131

$$132 \quad r_{fm} = (1 - d_f)(1 - d_m)r \quad (A9)$$

133

134 and they are only related if they are both locals $(1 - d_f)(1 - d_m)$ and, if so, their
 135 relatedness is defined by the relatedness between juveniles born in the same social group
 136 (r). The relatedness between the focal male and a randomly-chosen male in his social
 137 group (including the focal male himself):

138

$$139 \quad r_{mm} = \frac{1}{n_m} + \frac{n_m - 1}{n_m} (1 - d_m)^2 r \quad (A10)$$

140

141 where: with probability $1/n_m$ the randomly chosen male is the focal male himself, in
 142 which case relatedness is 1; and with probability $(n_m - 1)/n_m$ is a different male, in
 143 which case they are only related if they are both locals $(1 - d_m)^2$ and, if so, their
 144 relatedness is defined by the relatedness between juveniles born in the same social group
 145 (r). The relatedness between the focal male and a randomly-chosen female in his social
 146 group is:

147

$$148 \quad r_{mf} = (1 - d_m)(1 - d_f)r \quad (A11)$$

149

150 and they are only related if they are both locals $(1 - d_m)(1 - d_f)$ and, if so, their
 151 relatedness is defined by the relatedness between juveniles born in the same social group
 152 (r). Note that $r_{fm} = r_{mf}$ and, therefore, we use r_{fm} to represent both throughout the
 153 rest of the electronic supplementary material.

154

155 Relatedness between two juveniles born in the same social group is then given by $r =$
 156 p'/p , where p' is the consanguinity between two individuals born in the same social
 157 group and is defined by picking a gene at random from one of the two individuals and a
 158 gene at random from the same locus from the other individual and calculating the
 159 probability that these two genes are identical by descent (Bulmer 1994). Assuming that
 160 consanguinities are at their neutral-equilibrium, appropriate if the selection is weak
 161 (Gardner et al. 2011), we write:

162

$$163 \quad p' = \frac{1}{4} \left(\frac{1}{n_f} p + \frac{n_f - 1}{n_f} (1 - d_f)^2 p' \right) + \frac{1}{4} \left(\frac{1}{n_m} p + \frac{n_m - 1}{n_m} (1 - d_m)^2 p' \right) + \frac{1}{2} (1 - d_f)(1 - d_m) p', \quad (A12)$$

164

165 where: with probability $1/4$ we may have drawn the maternal gene from both
 166 individuals, in which case with probability $1/n_f$ they share the same mother giving
 167 consanguinity p , or else with probability $(n_f - 1)/n_f$ they have different mothers who
 168 are consanguineous only to the extent that both are locals $(1 - d_f)^2$ and, if so, their
 169 consanguinity is p' ; with probability $1/4$ we may have drawn the paternal gene from

both individuals, in which case with probability $1/n_m$ they share the same father giving consanguinity p , or else with probability $(n_m - 1)/n_m$ they have different fathers who are consanguineous only to the extent that both are locals $(1 - d_m)^2$ and, if so, their consanguinity is p' ; and with probability $1/2$, we have drawn the maternal gene from one and the paternal gene from the other, in which case they are consanguineous only to the extent that both of their parents are locals $(1 - d_f)(1 - d_m)$ and, if so, their consanguinity is p' . Rearranging, we get:

$$p' = \frac{n_f + n_m}{(1 - d_f)^2 n_m + (1 - d_m)^2 n_f + (4 - d_f - d_m)(d_f + d_m) n_m n_f} p, \quad (\text{A13})$$

and the relatedness between two random individuals born in the same social group is then given by $r = p'/p$ (Bulmer 1994). Rearranging, we obtain:

$$r = \frac{n_f + n_m}{(1 - d_f)^2 n_m + (1 - d_m)^2 n_f + (4 - d_f - d_m)(d_f + d_m) n_m n_f}. \quad (\text{A14})$$

No sex differences – Assuming that there are no sex differences, we can use the derivatives of the left side of the inequality (A1) and obtain the marginal fitness equation for the present model:

$$\frac{(2 + r_{fm} - a(r_{ff} + r_{fm}) - r_{mm})(1 - 2z^*)}{(1 - z^*)z^*} - \frac{(1 - a)(r_{ff} + 2r_{fm} + r_{mm})}{1 - 2z^*} = 0. \quad (\text{A15})$$

Now, and using the relatedness coefficients defined by equations (A8-11), we can solve equation (A15) for z^* to obtain the optimal level of sociality, represented in Figure 1A. Note that we obtain two optimal levels of sociality, but only one results in positive levels of fecundity for the individuals and, therefore, that is the only solution that follows the assumptions of the model.

Sex differences – Assuming that there are sex differences, we can use the derivatives of

the left side of the inequalities (A2-3) and obtain the marginal fitness equation for females

200

$$\frac{(1 + r_{\text{fm}} - a(r_{\text{ff}} + r_{\text{fm}}))(1 - 2z_{\text{f}}^*)}{(1 - z_{\text{f}}^*)z_{\text{f}}^*} - \frac{(1 - a)(r_{\text{ff}} + r_{\text{fm}})}{1 - z_{\text{f}}^* - z_{\text{m}}^*} = 0, \quad (\text{A16})$$

202

and for males

204

$$\frac{(1 - r_{\text{mm}})(1 - 2z_{\text{m}}^*)}{(1 - z_{\text{m}}^*)z_{\text{m}}^*} - \frac{(1 - a)(r_{\text{ff}} + r_{\text{fm}})}{1 - z_{\text{f}}^* - z_{\text{m}}^*} = 0. \quad (\text{A17})$$

206

Now we can solve the system of equations (A16-17) to get the optimal levels of sociality for both females and males represented in Figure 1B. As before, there are two solutions, but only one results in positive levels of fecundity for the individuals, therefore being the only solution that follows the assumptions of the model.

211

2.2 Demographic model when dispersal status is known without sex differences

213

Life cycle – The life cycle of this model is the same as the one considered in section 2.1, except that now individuals know if they dispersed or if they stayed in their natal social group. Accordingly, the fecundity of the focal female that does not disperse is

217

$$f_{\text{f|N}} = (1 - x_{\text{f|N}})x_{\text{f|N}}((y) - (1 - y)); \quad (\text{A18})$$

219

the fecundity of the focal female that disperses is

221

$$f_{\text{f|D}} = (1 - x_{\text{f|D}})x_{\text{f|D}}((y) - (1 - y)); \quad (\text{A19})$$

223

the fecundity of the focal male that does not disperse is

225

$$226 \quad f_{m|N} = (1 - x_{m|N})x_{m|N}((y) - (1 - y)); \quad (A20)$$

227

228 and the fecundity of the focal male that disperses is

229

$$230 \quad f_{m|D} = (1 - x_{m|D})x_{m|D}((y) - (1 - y)); \quad (A21)$$

231

232 and

233

$$234 \quad y = \frac{1}{2}((1 - d_f)y_{f|N} + d_f y_{f|D} + (1 - d_m)y_{m|N} + d_m y_{m|D}); \quad (A22)$$

235

236 where: $x_{f|N}$ is the level of sociality of the focal female that does not disperse; $x_{f|D}$ is the
 237 level of sociality of the focal female that disperses; $x_{m|N}$ is the level of sociality of the
 238 focal male that does not disperse; $x_{m|D}$ is the level of sociality of the focal male that
 239 disperses; $y_{f|N}$ is the average level of sociality of females that do not disperse; $y_{f|D}$ is the
 240 average level of sociality of the females that disperse; $y_{m|N}$ is the average level of
 241 sociality of the males that do not disperse; and $y_{m|D}$ is the average level of sociality of
 242 the males that disperse.

243

244 *Natural selection* – Female relative fitness in this model is:

245

$$246 \quad W_f = \frac{(1 - d_f)f_{f|N} + d_f f_{f|D}}{a((1 - d_f)F_{f|N} + d_f F_{f|D}) + (1 - a)((1 - d_f)\bar{F}_{f|N} + d_f \bar{F}_{f|D})} \quad (A23)$$

247

248 where: $F_{f|N} = f_{f|N}|_{x_{f|N}=y_{f|N}}$; $F_{f|D} = f_{f|D}|_{x_{f|D}=y_{f|D}}$; $\bar{F}_{f|N} =$

249 $f_{f|N}|_{x_{f|N}=y_{f|N}=z_{f|N}, x_{f|D}=y_{f|D}=z_{f|D}, x_{m|N}=y_{m|N}=z_{m|N}, x_{m|D}=y_{m|D}=z_{m|D}}$; and $\bar{F}_{f|D} =$

250 $f_{f|D}|_{x_{f|N}=y_{f|N}=z_{f|N}, x_{f|D}=y_{f|D}=z_{f|D}, x_{m|N}=y_{m|N}=z_{m|N}, x_{m|D}=y_{m|D}=z_{m|D}}$. Likewise, male relative fitness

251 in this model is given by:

252

253

$$W_m = \frac{(1 - d_m)f_{m|N} + d_m f_{f|D}}{(1 - d_m)F_{m|N} + d_m F_{f|D}} W_F \quad (A24)$$

254

255 where: $W_F = W_f | f_{f|N} = F_{f|N}, f_{f|D} = F_{f|D}$; $F_{m|N} = f_{m|N} | x_{m|N} = y_{m|N}$; and $F_{m|D} =$

256 $f_{m|D} | x_{m|D} = y_{m|D}$. We can now use the inequalities derived in section 1 to reach the

257 marginal fitness equations for the evolution of sociality and, consequently, to derive the

258 optimal level of sociality for when individuals are natives and for when they are

259 non-natives (see below).

260

261 *Relatedness* – The relatedness between the focal female that does not disperse and a

262 randomly-chosen female in her social group (including the focal female herself) is:

263

264

$$r_{ff|N} = \frac{1}{n_f} + \frac{n_f - 1}{n_f} (1 - d_f) r \quad (A25)$$

265

266 where: with probability $1/n_f$ the randomly chosen female is the focal female herself, in

267 which case relatedness is 1; and with probability $(n_f - 1)/n_f$ is a different female, in

268 which case they are only related if that female is local $(1 - d_f)$ and, if so, their

269 relatedness is defined by the relatedness between juveniles born in the same social group

270 (r). The relatedness between the focal female that does not disperse and a

271 randomly-chosen male in her social group is:

272

273

$$r_{fm|N} = (1 - d_m) r \quad (A26)$$

274

275 and they are only related if the male is local $(1 - d_m)$ and, if so, their relatedness is

276 defined by the relatedness between juveniles born in the same social group (r). The

277 relatedness between the focal male that does not disperse and a randomly-chosen male

278 in his social group (including the focal male himself):

279

280

$$r_{mm|N} = \frac{1}{n_m} + \frac{n_m - 1}{n_m}(1 - d_m)r \quad (\text{A27})$$

281

282 where: with probability $1/n_m$ the randomly chosen male is the focal male himself, in
283 which case relatedness is 1; and with probability $(n_m - 1)/n_m$ is a different male, in
284 which case they are only related if that male is local $(1 - d_m)$ and, if so, their
285 relatedness is defined by the relatedness between juveniles born in the same social group
286 (r). The relatedness between the focal male that does not disperse and a
287 randomly-chosen female in his social group is:

288

289

$$r_{mf|N} = (1 - d_f)r \quad (\text{A28})$$

290

291 and they are only related if the female is local $(1 - d_f)$ and, if so, their relatedness is
292 defined by the relatedness between juveniles born in the same social group (r). Note
293 that $r_{fm|N} = r_{mf|N}$ and, therefore, we use $r_{fm|N}$ to represent both throughout the rest of
294 the electronic supplementary material. The relatedness between the focal female that
295 disperses and a randomly-chosen female in her social group (including the focal female
296 herself) is:

297

298

$$r_{ff|D} = \frac{1}{n_f} \quad (\text{A29})$$

299

300 where: with probability $1/n_f$ the randomly chosen female is the focal female herself, in
301 which case relatedness is 1; and she is not related to the other females in the social
302 group. The relatedness between the focal female that disperses and a randomly-chosen
303 male in her social group is:

304

305

$$r_{fm|D} = 0 \quad (\text{A30})$$

306

and this means that she is not related to the males in the social group. The relatedness between the focal male that disperses and a randomly-chosen male in his social group (including the focal male himself):

310

$$r_{mm|D} = \frac{1}{n_m} \quad (A31)$$

312

where: with probability $1/n_m$ the randomly chosen male is the focal male himself, in which case relatedness is 1; and he is not related to the other males in the social group. The relatedness between the focal male that disperses and a randomly-chosen female in his social group is:

317

$$r_{mf|D} = 0 \quad (A32)$$

319

and this means that he is not related to the females in the social group. Note that $r_{fm|D} = r_{mf|D}$ and, therefore, we use $r_{fm|D}$ to represent both throughout the rest of the electronic supplementary material. Relatedness between two juveniles born in the same social group is given by equation (A14), defined in section 2.1.

324

Result – We assume no sex differences. Accordingly, we can use the derivatives of the left side of the inequality (A1) for when $A = N$ and for when $A = D$. Such approach results in two marginal fitness equations, which create a system of equations that can be solved for z_N^* and z_D^* . As in previous sections, there are two solutions, but only one results in positive levels of fecundity for the individuals, therefore being the only solution that follows the assumptions of the model. The solution is represented in Figure 2.

332

333 3. References

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