Sociality beyond helpers at the nest: the number of strong associations predict reproductive trade-offs in a cooperative breeder

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SUMMARY

Individual social relationships can shape fitness across taxa, but in studies on cooperatively breeding species, the social environment relevant to reproduction is typically reduced to the number of helpers. We tested whether breeder sociality beyond helper number predicts reproductive performance in a colonial cooperative bird, the sociable weaver (*Philetairus socius*). Using long-term data and social networks built from foraging associations, we quantified individual sociality as the relative number of strong social bonds each individual maintained within its colony. We then tested whether this measure of sociality predicted multiple reproductive outcomes while accounting for helper number. Breeder sociality was unrelated to helper number, and its associations with reproductive performance differed between the sexes. While we found no evidence that sociality predicted breeding timing within the season, there was a tendency for chicks raised by high-sociality mothers to show higher fledging success. In breeding males, offspring of medium- and high-sociality fathers were heavier than those of low-sociality fathers. However, high-sociality males also initiated reproduction later in life than low-sociality males. These results show that cooperative breeding is embedded within multi-layered social structures beyond helper number, and that individual sociality may be linked to sex-specific life-history trade-offs.

INTRODUCTION

Recent studies on social species are revealing how individuals can experience markedly different social environments, reflecting variation in the number and strength of their associations with others. Such differences have been shown to predict fitness-related outcomes across a range of species [1,2]. In cooperatively breeding species, where non-breeding helpers assist breeders by provisioning nestlings, research has focused primarily on the number of helpers at the nest as the main social component experienced by breeders. This emphasis is logical given the well-established benefits of helpers, which can increase offspring number and survival [3–5]. Yet this helper-centred perspective may overlook the fact that cooperative interactions are embedded within a broader social context, where variation in social relationships beyond helping-at-the-nest may also influence reproductive outcomes.

Social interactions may shape reproduction through effects on social stress [6,7], access to resources [8,9], and coordination among individuals, including reproductive synchrony [10]. These processes may in turn reduce the energetic and physiological costs that constrain reproduction [11] and, in some cases, even lower predation risk (e.g. [12]). Consistent with this, empirical studies in non-cooperatively breeding species show that individual sociality can influence reproduction. For instance, in bottlenose dolphins (*Tursiops aduncus*), males with stable strong bonds sire more offspring [13], and in bighorn sheep (*Ovis canadensis*), socially central females show higher reproductive success [14]. Similar patterns have been reported in birds, where network position and bond strength predict access to breeding opportunities and reproductive output. For example, male manakins (*Pipra filicauda*) with higher centrality are more likely to attain breeding positions [15]. Likewise, female cowbirds (*Molothrus ater*) with stronger familiarity preferences laid more eggs across the breeding season [16], and great tits (*Parus major*) with stronger pair bonds laid earlier [17]. Together, these findings indicate that sociality can shape both mating opportunities and downstream reproductive outcomes such as breeding timing and offspring production.

Emerging evidence from cooperatively breeding species also suggests that reproductive performance may depend on a broader social context than helper number alone. In dwarf mongooses (*Helogale parvula*), social instability is associated with reduced reproductive success [18], and in greater anis (*Guira guira*), prior social associations between females synchronize reproduction and increase nest survival [10]. This raises the possibility that, in cooperative breeders, reproductive performance may depend not only on helper number but also on the broader social context in which helping occurs. However, the independent effects of breeder sociality and helper number remain largely unresolved. Evaluating both simultaneously is therefore essential to determine their relative contributions to reproductive performance.

To test whether breeder sociality predicts reproductive performance beyond the benefits of helper number, we used long-term individual-based data from a population of sociable weavers (*Philetairus socius*), a cooperative and colonial passerine with a well-defined hierarchical social structure [19]. Individuals live in relatively stable colonies centred around a large communal nest that is collectively built and maintained by all members [20]. Within colonies, birds form smaller breeding groups composed of breeders and non-breeding helpers that assist in chick provisioning [21], while also maintaining social associations outside the breeding context through repeated foraging and roosting interactions [22,23]. Crucially, this social organisation is shaped by strongly female-biased dispersal and male philopatry [24,25], such that males typically remain in their natal colony, often in the presence of kin, whereas females disperse into novel social environments. This sex-biased dispersal shapes the social context in which relationships are formed and maintained, potentially generating sex differences in the stability and fitness consequences of social bonds.

Within this social and demographic context, sociable weavers exhibit consistent individual differences in sociality, measured as the relative number of strong social bonds each individual maintains within its colony [26]. Because sociable weavers forage in highly cohesive flocks that often include most colony members [27], networks based on simple co-occurrence at RFID feeders can reflect general gregariousness rather than preferential social relationships [22]. In contrast, focusing on strong bonds (derived from time-overlapping foraging associations recorded at RFID feeders [22]) captures persistent, preferential associations among specific partners, with important implications for survival [26]. This distinction is critical, as recent theoretical work has highlighted that relationship quality (investment in specific partners) and relationship quantity (overall gregariousness) represent distinct dimensions of sociality that may have different adaptive consequences [2].

To examine whether breeder sociality predicts reproductive performance beyond the effects of number of helpers in a colonial cooperative system, we focused on colony-wide strong bonds (i.e. all strong bonds within the colony) in addition to helping associations. This allowed us to capture variation in the broader social environment experienced by breeders, beyond the immediate helping context and general group membership within the colony. Specifically, we tested whether parental sociality predicted fledging success and fledgling mass, and whether individual sociality predicted breeding timing within the season, the probability of attempting reproduction, and age at first reproduction, while statistically accounting for variation in helper number where relevant. We predicted that individuals with higher sociality would show higher fledging success, heavier fledglings, earlier breeding within the season, a higher probability of attempting reproduction, and an earlier age at first reproduction. Given the sex-biased dispersal in this species, we further expected these associations to be stronger in males than in females.

METHODS

Site and study species

We studied a population of sociable weavers (*Philetairus socius*) at Benfontein Nature Reserve, South Africa (28°52’S, 24°50’E), where a long-term research programme has been ongoing since

1993. Since 2008, the population has been regularly monitored through annual captures, and since 2010, breeding activity has been consistently monitored (see below).

Since 2017, all birds (adults and fledglings) at five focal colonies have been fitted with passive integrated transponder (PIT) tags enclosed in 3.3 mm plastic leg rings (Eccel Technology) to enable individual identification at RFID-equipped feeders (see below). In 2021, a fire destroyed two of these colonies. Their data were included up to the fire, and in 2022 an additional colony was PIT-tagged, resulting in four marked colonies contributing data after the fire (six colonies in total across the study period).

RFID data collection and social network metrics

From 2018 to 2023 (excluding 2020), we systematically collected fine-scale association data in a foraging context using RFID-based feeding stations located 80–205 m from each colony (see [22] for details). Each station consisted of four feeding boxes, each equipped with four feeders and four perches fitted with RFID antennas (Priority1rfid, Melbourne, Australia) connected to data loggers. Feeders were designed to allow only one bird to feed at a time, and up to four birds can eat simultaneously in the same box (one for each perch). Data were collected every three days between April and June, a period selected for logistical feasibility and consistent data availability across years. For each colony-year, we constructed social networks based on the exact temporal overlap between individuals feeding simultaneously at the same feeding box. Following [22], association strength (edge weight) between two individuals was calculated as the total time they fed simultaneously, divided by the sum of the time each individual was present at any RFID feeder (i.e. a time-based formulation of the simple ratio index). Simultaneous feeding events shorter than 5 seconds were excluded to reduce the influence of brief overlaps, usually associated with aggressive interactions. This method captures fine-scale social structure in sociable weavers more accurately than simple co-occurrence approaches, as individuals often forage in cohesive flocks that include most colony members.

To identify strong social bonds (e.g. [28,29]), we followed [26] and ranked all pairwise association weights within each colony-year, classifying edges with values equal to or above the 80th percentile as strong bonds. In the same study system, the main downstream results were qualitatively robust to alternative strong-bond thresholds (70th and 90th percentiles [26]). This approach allows us to distinguish relatively high-quality bonds from more general gregarious associations [2] within each colony-year, while accounting for variation in colony size and overall network density. After identifying strong social bonds within each colony, we calculated how many each individual had. Finally, individuals were classified into three sociality categories (“Low”, “Medium”, “High”) by dividing the distribution of strong bond counts within each colony-year into terciles (33rd and 66th percentiles [26]). This relative classification captures variation in social bond number within each colony-year and was used as the predictor of sociality in subsequent analyses (see Table S1 for colony-year–specific ranges).

A large wildfire in September 2021 resulted in the destruction of several colonies and extensive movement of birds from collapsed to intact colonies [30]. Because this event occurred between the period in which sociality was quantified (April–June 2021) and the subsequent breeding season (2021/2022), substantially altering colony composition and social structure [30], the network positions recorded prior to the fire would not reliably reflect social relationships during breeding. We therefore excluded this breeding season from all analyses.

Reproduction monitoring

To monitor reproduction, during our study period (2018–2023), all nest chambers within each colony were checked every three days throughout the breeding season to detect new clutches [4,31]. This frequency allowed us to accurately estimate laying dates, as clutches typically consist of 3-4 eggs laid on consecutive days. Nestlings were ringed and blood-sampled at 9 days of age for individual identification and parentage analysis. Body mass was recorded at 17 days, close to fledging (typically from 20 days onwards [32]; unpublished data).

Breeder identification

Breeding individuals in this population have been routinely identified using a standardized protocol that integrates multiple complementary sources of information about each individual (see [31,33] for details). Across the entire dataset, each nest was video-recorded for a mean (± SD) total of 368 ± 274 min, typically across multiple days during incubation and nestling care, with behaviours automatically identified [34] and individuals visually identified via their unique colour-ring combinations. However, because sociable weavers are facultative cooperative breeders [21], individuals observed feeding nestlings may include helpers as well as the actual breeders. Therefore, our breeder identification relies on an integrative approach that combines information on genetic relatedness, age, breeding history, and nest visitation frequency within the breeding group with genetic parentage analysis (available when chicks hatch or survive to sampling age). Individuals were considered as helpers if seen visiting the brood at least 3 times, to avoid including prospecting non-helping visitors. A full description of the genetic analysis and the algorithm used for breeder identification is given in [31,33].

Statistical analysis

General procedures

All statistical analyses were conducted in R (v4.0.5) using generalized linear mixed models (GLMMs) implemented in the glmmTMB package (v1.1.7). The aim of our analyses was to examine how individual sociality (Low, Medium, High) related to several reproductive metrics, using model structures appropriate for the distribution and nature of each response variable (see below). To explicitly disentangle the effects of breeder sociality from those of helper number, the number of helpers at the nest was included as a covariate in all models where applicable. The only exception was the analysis of breeding probability. Because this response included both breeders and non-breeders, helper number at the nest could only be defined for individuals that actually initiated a breeding attempt, and therefore could not be included as a predictor in that model.

Depending on the response variable, the unit of analysis was either the breeding individual or the individual nestling. For reproductive metrics measured at the breeder level (e.g. breeding probability, age at first reproduction), models were fitted at the individual level. For offspring-related metrics (e.g. fledging success and fledgling mass), the unit of analysis was the chick. In breeder-level models, we included an interaction between the sociality category and sex, as the association between sociality and reproductive performance was expected to differ between males and females given the species' sex-biased dispersal. In chick-level analyses, datasets were restricted to broods for which the sociality category of both parents was known, allowing maternal and paternal sociality effects to be estimated simultaneously and conditionally on each other.

Because reproductive performance can vary with parental age, potentially reflecting differences in experience or condition [35], we included maternal and paternal age in offspring-level models, and individual age in breeder-level models where age was not itself the response variable. Exact age was known for 81% of individuals born in the study colonies through routine breeding monitoring. For individuals first captured as adults (19%), age was estimated by adding the average age at first dispersal to their first identification date. This average dispersal age was calculated separately for males and females based on the long-term capture–recapture dataset of migrating individuals with known age (males: 690 days; females: 727 days [36]). Number of helpers and age were mean-centred and scaled before analysis to aid interpretation and model convergence.

Differences between sociality categories were evaluated through Tukey-corrected pairwise comparisons based on estimated marginal means (*emmeans* package), with covariates held at their mean values. Because sociality categories were derived from social network analyses, which may violate independence assumptions [37], we validated all pairwise contrasts using permutation tests specifically designed for network-derived traits [38].

We randomised the underlying social networks and recalculated individual sociality for each permutation. Specifically, within each year × colony × sex block, we kept constant the total number of feeder co-occurrence events, the set of individuals involved, and the overall distribution of how often individuals appeared in co-occurrences. However, we randomly reassigned which individuals received each appearance count and which conspecifics they were associated with, thereby breaking the link between individuals and both their original interaction partners and their position within the network. This procedure preserves the marginal sampling structure of the data (year, colony, sex, and the distribution of appearance counts) while randomising the fine-scale association patterns that generate the observed social network.

From each permuted dataset, we rebuilt the social networks and estimated new individual sociality (see above). We then refitted the full model to each permuted dataset and recomputed the pairwise contrasts between sociality categories. For all analyses, we ran 10,000 permutations. Two-tailed p-values were calculated as the proportion of permuted contrasts whose absolute value was equal to or greater than that of the observed contrast.

Relationship between individual sociality and helper number

To verify that breeder sociality captured a dimension of the social environment distinct from the amount of help received at the nest, we conducted an exploratory analysis examining the association between the raw number of strong social bonds of breeding individuals and the number of helpers present at their nest for any breeding attempt. This analysis used the continuous count of strong bonds prior to any categorisation into sociality levels and was based on the complete dataset of breeding attempts, before applying the analytical restrictions described below. Associations were assessed using Spearman rank correlations and were conducted separately for males and females.

Fledgling survival

We tested whether parental sociality predicted chick survival until fledging, measured as the number of fledglings out of the number of hatched chicks within each brood. We modelled fledging success using a beta–binomial GLMM with the number of fledglings out of the number of hatched chicks as the response variable. Fixed effects included maternal and paternal sociality category, the scaled number of helpers at the nest, and the ages of the mother and father at laying. Random intercepts were included for maternal identity, paternal identity, colony and season.

Fledgling mass

We tested whether parental sociality predicted offspring body mass at day 17 post-hatching, a developmental stage close to fledging in sociable weavers. We used a Gaussian linear mixed-effects model with chick mass at day 17 as the response variable. Fixed effects included maternal and paternal sociality category, the scaled number of helpers at the nest, and the ages of the mother and father at laying. Random intercepts were included for paternal identity, maternal identity, brood identity (to account for shared early-life conditions among chicks from the same nest), season and colony.

Timing of reproduction within the season

We tested whether individual sociality predicted the timing of reproduction within the season (since laying earlier in the season is positively associated with reproductive output [39]), quantified as the number of days between an individual's first laying date and the earliest laying date recorded in its breeding colony (larger values indicating later breeding). Because the response variable showed overdispersion, we modelled timing of reproduction using a negative binomial GLMM. Fixed effects included individual sociality, sex and their interaction, the scaled number of helpers present at the individual's first breeding attempt, and age at the start of the breeding season. Age was calculated as the number of days between the individual's birth date and the earliest laying date recorded in its breeding colony. We included breeding colony, individual identity (ring) and season as random intercepts.

Probability of reproduction attempt

To assess whether individual sociality predicted the probability of attempting reproduction in a given breeding season. For each individual and season, we coded breeding status as 1 if the bird was identified as a breeder in at least one nest and 0 otherwise. Because sociality was measured during the preceding non-breeding period (April–June) and linked to the following breeding season (typically starting in September), sociality always preceded the reproductive outcome. To reduce potential bias due to sociality-dependent mortality [26], we restricted the dataset to individuals that were detected at feeders or during captures from the first laying date of the breeding season onwards, ensuring that all included individuals were alive and present at the onset of the breeding season. We modelled breeding status using a binomial GLMM with a logit link. Fixed effects included sociality category, sex and their interaction, as well as age at the midpoint of the breeding season. We included colony, individual identity (ring) and season as random intercepts.

Age at first reproduction attempt

We tested whether sociality category predicted age at first reproduction, defined as the number of days between an individual's hatching date and the laying date of its first recorded breeding attempt. For this analysis, we retained only individuals hatched in our study area for which exact age was known. For each individual, we identified the earliest laying date at which it was assigned as a breeder and included only those for which the first breeding attempt occurred after June 2017, when social network data were available.

We fitted a Gaussian linear mixed-effects model with age at first reproduction as the response variable. Fixed effects included sociality category, sex and their interaction, as well as the scaled number of helpers present at the individual's first breeding attempt. Colony and season were included as random intercepts.

RESULTS

Relationship between individual sociality and helper number

The raw number of strong social bonds was not correlated with the number of helpers present at the nest, either in males (n= 498; Spearman's $\rho = -0.02$, $p = 0.63$) or in females (n= 298; $\rho = -0.04$, $p = 0.45$).

Probability of chick fledging

We analysed fledging success in 145 broods. We found a tendency for chicks of high-sociality mothers to show higher fledging probabilities (0.69) than those of low- (0.51) or medium-sociality mothers (0.48), corresponding to absolute differences of 0.18 (High vs Low) and 0.21 (High vs Medium) (Table S2; Fig. 1). However, these differences did not reach statistical significance in the permutation tests (Low vs High: $p_{perm} = 0.104$; Medium vs High: $p_{perm} = 0.066$; Table S3). For paternal sociality, all contrasts were non-significant (all $p_{perm} \geq 0.442$). The number of helpers at the nest was positively associated with fledging probability. Because the reduced model excluding helper number failed to converge, likelihood-ratio tests could not be computed for this term. Nonetheless, the full model indicated a strong positive effect of helper number ($z = 3.83$, $p < 0.001$; Table S4; Fig. 1). Finally, age of the breeding parents did not influence the probability of fledging young (mother: LRT = 0.16, $p = 0.688$; father: LRT = 2.48, $p = 0.117$; Table S4).

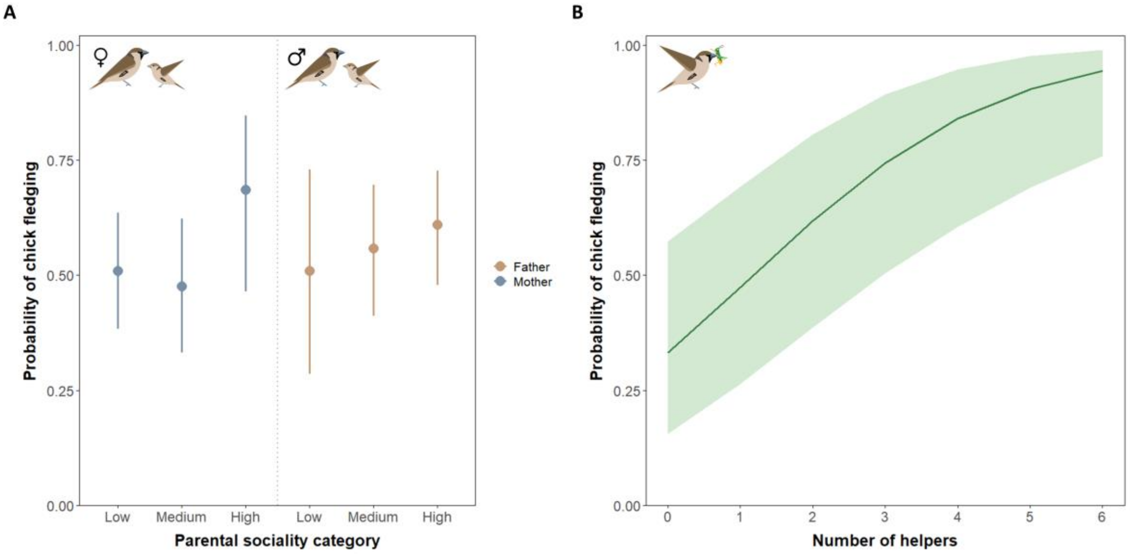

Figure 1. Fledging success in relation to parental sociality and number of helpers. A) Model predictions from the beta-binomial GLMM for the probability of chick fledging across maternal (blue) and paternal (brown) sociality categories. Points represent estimated means and vertical bars 95% confidence intervals. B) Model predictions from the same model showing the relationship between the number of helpers and the probability of chick fledging, with other covariates held constant. The solid line represents predicted values and the shaded area 95% confidence intervals.

Fledgling mass

We analysed fledgling mass at day 17 in 188 chicks from 88 broods. We found that chicks with medium- or high-sociality fathers were heavier than those with low-sociality fathers (Medium vs Low: 2.85 ± 1.19 g, $p_{perm} = 0.010$; High vs Low: 2.65 ± 1.12 g, $p_{perm} = 0.012$; Fig. 2; Table S5 and

S6). No significant difference was detected between medium- and high-sociality fathers (p_{perm} = 0.787). Maternal sociality showed no detectable association with fledgling mass (all $p_{perm} \geq$ 0.420). The number of helpers showed a positive association with fledgling mass (LRT = 8.41, p = 0.008; ; Table S7; Fig. 2). Finally, age of the breeding parents was not associated chick mass (mother: LRT = 0.58, p = 0.46; father: LRT = 1.70, p = 0.19; Table S7).

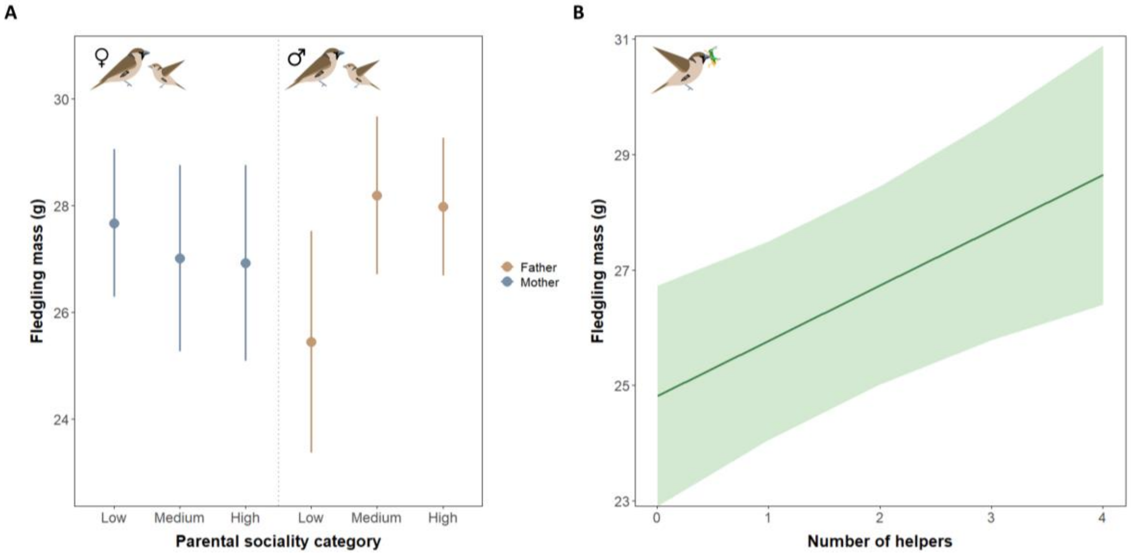

Figure 2. Fledgling mass in relation to parental sociality and number of helpers. A) Model predictions from the Gaussian LMM for fledgling mass at day 17 across maternal (blue) and paternal (brown) sociality categories. Points represent estimated means and vertical bars 95% confidence intervals. B) Model predictions from the same model showing the relationship between the number of helpers and fledgling mass, with other covariates held constant. The solid line represents predicted values and the shaded area 95% confidence intervals.

Timing of reproduction within the season

We analysed breeding timing in 288 breeding attempts. We found no evidence that individual sociality influenced breeding timing in either sex (Table S8; Fig. 3). All pairwise contrasts between sociality categories were non-significant for females (all $p_{perm} \geq 0.146$; Table S9) and for males (all $p_{perm} \geq 0.747$; Table S9). In contrast, older individuals bred earlier (LRT = 10.02, p = 0.0016), and birds with more helpers also initiated reproduction earlier (LRT = 8.97, p = 0.0027; Table S10; Fig. 3). The effect of sociality on reproductive timing did not differ between males and females (interaction: LRT = 1.58, p = 0.454; ; Table S10).

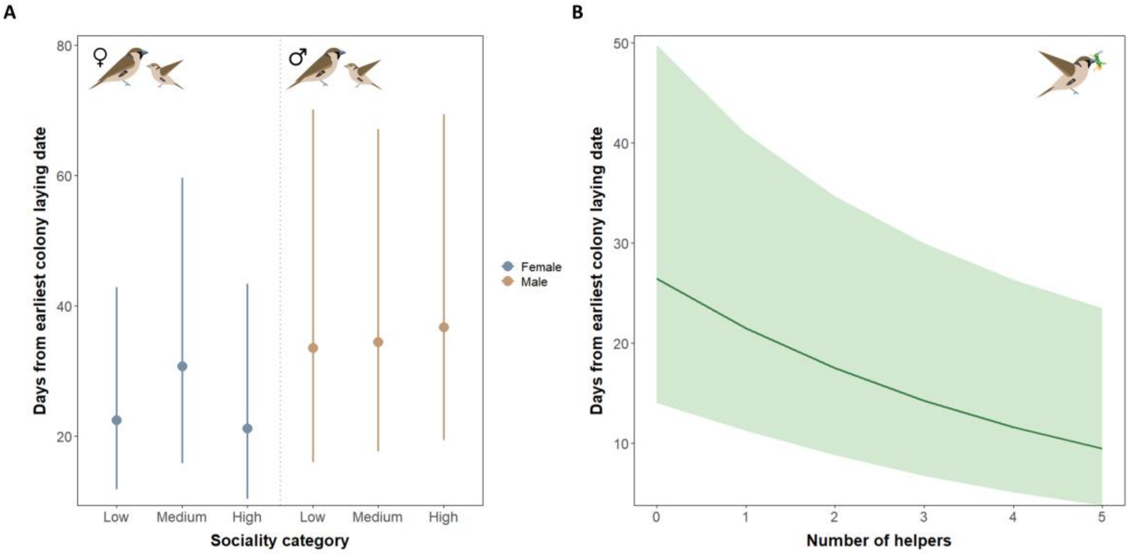

Figure 3. Timing of first breeding attempt within the season in relation to individual sociality and number of helpers. A) Model predictions from the negative binomial GLMM for the number of days between an individual's first laying date and the earliest laying date recorded in its colony for females (blue) and males (brown) across sociality categories. Points represent estimated means and vertical bars 95% confidence intervals. B) Model predictions from the same model showing the relationship between the number of helpers and the timing of first breeding attempt within the season, with other covariates held constant. The solid line represents predicted values and the shaded area 95% confidence intervals.

<u>Probability of attempting to reproduce</u>

We analysed breeding probability in 443 individual–season observations. We found a tendency for low-sociality males to show lower breeding probabilities (0.55) than medium- and high-sociality males (both 0.75; Table S11; Fig. 4), although these differences were not supported by permutation tests (Low vs Medium $p_{perm} = 0.125$; Low vs High: $p_{perm} = 0.116$; Table S12). In females, all pairwise contrasts between sociality categories were non-significant (all $p_{perm} \geq 0.619$; Table S12). There was no statistical support for a difference in the effect of sociality between males and females (interaction: LRT = 2.55, p = 0.279; Table S13). In contrast, age showed a strong positive association with breeding probability, with older individuals being more likely to attempt reproduction (LRT = 82.13, p < 0.001; Table S13).

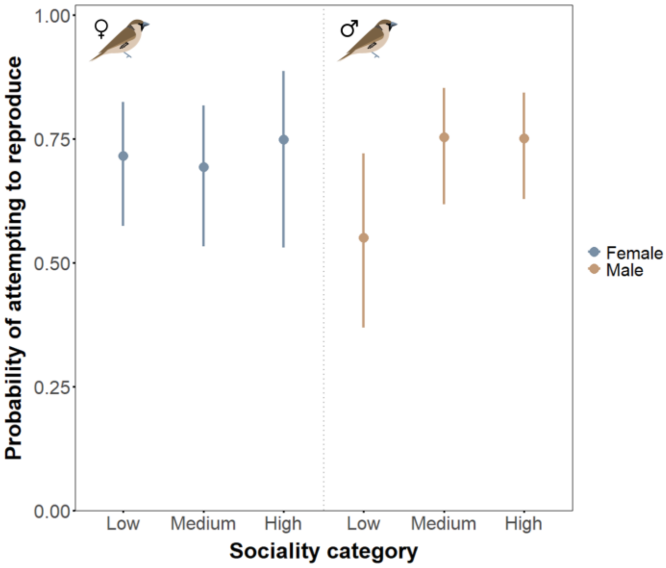

Figure 4. Probability of attempting to reproduce in relation to individual sociality. Model predictions (binomial GLMM) for the probability of attempting reproduction for females (blue) and males (brown) across sociality categories. Points represent estimated means and vertical bars their 95% confidence intervals.

<u>Age at first reproduction attempt</u>

We analysed age at first reproduction in 75 individuals. We found that high-sociality males initiated reproduction later than low-sociality males (175.8 ± 83.6 days, $p_{perm} = 0.048$; Fig. 5; Tables S14 and S15). Differences between low- and medium-sociality males (–119.7 ± 81.7 days,

$p_{perm} = 0.173$) and between medium- and high-sociality males (–56.1 ± 60.1 days, $p_{perm} = 0.361$) were not significant. In females, no contrasts between sociality categories were significant (all $p_{perm} \geq 0.153$). Helper number had no detectable effect (LRT = 0.15, p = 0.696). In addition, age at first reproduction showed sex-specific patterns in relation to sociality, with a near-significant interaction between sociality and sex (LRT = 5.37, p = 0.068; Table S16).

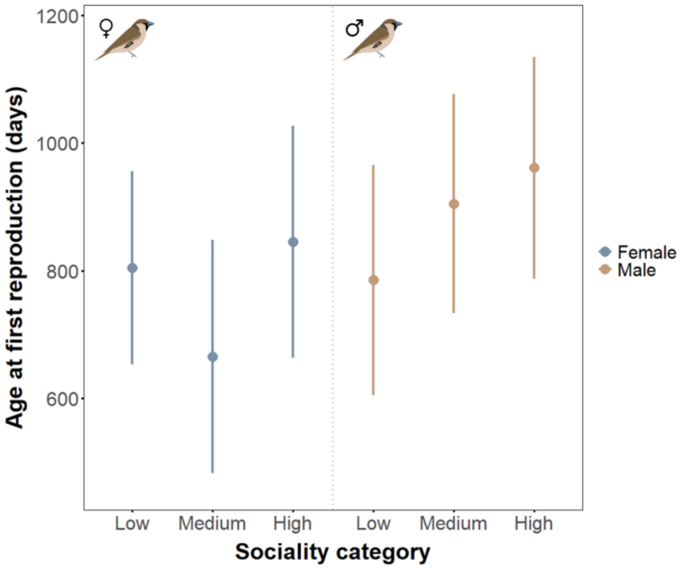

Figure 5. Age at first reproduction in relation to individual sociality. Model predictions (Gaussian GLMM) for age at first reproduction (days since hatching) for females (blue) and males (brown) across sociality categories. Points represent estimated means and vertical bars their 95% confidence intervals.

DISCUSSION

Our results suggest that individual sociality, beyond the number of helpers at the nest, is associated with multiple components of reproductive success in sociable weavers, although support varied across traits and between the sexes. At the offspring level, chicks raised by high-sociality breeding females tended to show higher fledging success than those raised by medium- and low-sociality females, although support for this pattern was only marginal. For breeding males, fledglings raised by medium- and high-sociality fathers were heavier than those raised by low-sociality fathers, and males with higher sociality also tended to show a higher probability of attempting reproduction, although this latter pattern did not reach statistical significance. In contrast, high-sociality males initiated reproduction later in life than low-sociality males. Together, these patterns reveal sex-specific effects and a potential male-specific life-history trade-off, whereby high-sociality males delay reproductive onset while producing heavier fledglings and tending to show higher breeding probability.

Importantly, these associations persisted after accounting for variation in helper number, indicating that individual sociality relates to reproductive performance beyond differences in breeding group size. While in non-cooperative species research linking social network metrics to reproductive success is well established (e.g. [40–43]), in cooperative systems the socially relevant structure influencing reproductive success is typically reduced to the number of helpers at the nest [44–46]. However, in our population, the number of strong social bonds an individual maintained within its colony was not related to the number of helpers present during breeding, and sociality based on those strong bonds was associated with several reproductive outcomes. Together, these results suggest that reducing cooperative social structure to helper number may overlook other biologically relevant dimensions of social organisation. Since many cooperatively breeding species are group-territorial, social associations beyond the immediate breeding group may often have been considered less relevant. However, even in such species, social structure can vary across the year (e.g. [47]), and individuals within the same social group can still differ in their social associations (e.g. [48]). More broadly, these observations, together with the results reported here, support the view that animal societies can be structured across multiple layers of interaction, each with potentially distinct fitness consequences [49].

We also found that helper number was consistently associated with reproductive performance and breeding timing, in line with previous work in sociable weavers [4,21,50] and other cooperative breeders (e.g., [51]). A higher number of helpers increased fledging probability and was positively associated with fledgling mass, which is consistent with evidence that helpers can increase provisioning and reduce parental workload during chick rearing [21,52]. In addition, individuals breeding in groups with more helpers initiated reproduction earlier in the season, a pattern also reported in other cooperative species [53,54] and potentially explained by reduced costs of breeding initiation [5].

The positive associations between sociality and different components of reproductive success, observed after controlling for helper number, were, for the most part, sex-specific, i.e. usually found for males, but seldom for females. This pattern is likely a result of the marked sex-biased dispersal system of sociable weavers, in which females typically disperse to breed in non-natal colonies whereas males are predominantly philopatric [25]. Because sociality was quantified prior to breeding, the social bonds measured for females that dispersed in a given year may not fully reflect the social environment they experience during reproduction in the new colony, potentially introducing greater variability in estimates of female sociality. More generally, immigrant females enter colonies where they lack prior social history and close kin, and may therefore have fewer opportunities to accumulate stable long-term bonds compared to philopatric males. In contrast, males remaining in their natal colonies can develop and maintain social connections across years within the same social environment, allowing the formation of strong bonds to influence their access to breeding roles and life-history trajectories.

While future work on the formation and maintenance of strong bonds will be needed to test these sex differences explicitly, several non-exclusive mechanisms could help explain the positive association between sociality and reproductive performance observed here. First, individuals with a higher number of strong bonds may benefit from enhanced information sharing within the colony [2]. Sociable weavers forage predominantly on the ground, typically in cohesive colony groups [20,27] and, during breeding, also in smaller groups foraging closer to the colony (Covas & Doutrelant, pers. obs.). Under these conditions, a higher number of strong bonds may facilitate information sharing within the colony [2], potentially improving access to socially acquired information about novel food patches, such as termite emergences, an important food source in this species [55]. Similar links between social associations and the discovery of novel food patches have been shown in other wild songbirds [56]. Higher sociality may also increase social tolerance and reduce contest competition during foraging [2,6], leading to fewer antagonistic interactions and potentially more efficient resource acquisition and chick provisioning. During the pre-breeding period, particularly in winter, sociality may further influence energetic state through communal roosting. In sociable weavers, roosting together reduces thermoregulatory costs, especially during cold nights [23]. Individuals maintaining more strong bonds may therefore experience improved energetic condition prior to reproduction, either because they gain more consistent access to communal roosting chambers or because they roost in larger groups, with potential carry-over effects on subsequent reproductive allocation and performance.

In addition, a larger number of strong bonds could be associated with greater social tolerance and reduced social stress [2], which may improve reproductive outcomes. Experimental work in passerines has shown that elevated glucocorticoid levels can alter parental provisioning behaviour and negatively affect brood survival [57]. Stress may also affect breeding condition, with consequences for reproductive allocation, chick condition and survival [58,59]. Finally, reduced social conflict within the colony may decrease aggressive interference around the nest, including the risk of infanticide [60]. These processes could help explain both the tendency for higher fledging success among chicks of high-sociality females and the greater fledgling mass of chicks raised by medium- and high-sociality males.

We found no evidence that individual sociality influenced breeding timing within the season. In arid and semi-arid environments, breeding is often opportunistic, closely tied to fluctuating resource availability [61] and highly variable in timing and length [62], which may limit the extent to which broader patterns of sociality influence seasonal reproductive timing. Instead, in this species, aligning reproduction with favourable breeding conditions may be more important. This may depend more strongly on breeder experience, which could explain why breeding timing was more closely associated with age, with older individuals initiating reproduction earlier, and with helper number. Advances in laying date with age are well documented in birds and are often attributed to increased breeding experience or improvements in individual performance, in line with maturation and learning hypotheses [63,64]. In sociable weavers specifically, longer pair-bond duration is also associated with earlier breeding [39], suggesting that the age effect detected here may partly reflect accumulated pair experience and partner familiarity.

We also detected a tendency for medium- and high-sociality males to show higher breeding probabilities, although this pattern did not reach significance in permutation tests and should therefore be interpreted with caution. Nonetheless, sociality may capture additional aspects of a male's social position within the colony that influence access to reproductive opportunities. A relatively greater number of strong bonds may increase exposure to reproductive cues from conspecifics and facilitate breeding activation when conditions are favourable [65,66]. It may also be associated with greater social tolerance and reduced conflict, potentially improving access to resources prior to the breeding season and helping meet the energetic demands associated with initiating reproduction [67]. At the same time, age remained a strong predictor of breeding probability: older individuals were significantly more likely to attempt reproduction, a pattern consistent with delayed entry into breeding roles typical of cooperative systems [68,69].

Finally, we found that age at first reproduction varied with sociality in males but not in females, with high-sociality males initiating reproduction approximately six months later than their low-sociality counterparts (roughly 26 vs 32 months). Although maximum recorded longevity in this species exceeds 15 years [70], average adult survival is approximately 0.66 [71], corresponding to an expected adult lifespan of roughly three years under constant survival. A six-month delay therefore represents a substantial fraction of expected adult life and likely constitutes a biologically meaningful shift in reproductive timing. This male-specific pattern is also consistent with the life-history structure of sociable weavers, where males are predominantly philopatric and typically remain in their natal colony as helpers before breeding [72]. In this species, as in other cooperative breeders, breeding reflects a trade-off between current reproductive benefits and the advantages of remaining in a non-breeding role, a balance that is sensitive to ecological conditions [67,73]. Within this framework, higher sociality may shift this balance—either by increasing the relative benefits of delayed breeding and helping close relatives, or by reinforcing socially mediated constraints on access to reproduction—thereby delaying reproductive onset. If strong bonds are predominantly formed among philopatric males, higher sociality may also increase exposure to intra-sexual competition and socially mediated constraints on breeding positions on the one hand (e.g. [74]), but offer increased possibilities of helping close kin or close social partners on the other, which would lead to increased inclusive fitness [75] or possibilities of being reciprocated in the future [76].

Although our results reveal consistent associations between individual sociality and multiple reproductive components, they do not allow us to determine whether social bonds themselves causally influence reproductive performance or instead reflect underlying individual differences that jointly shape both sociality and reproductive performance. Individuals that maintain more strong bonds could be in better physiological condition, healthier, or more competitive, and thus both more socially connected and more successful breeders. In this case, sociality would act as a proxy for individual quality rather than a direct driver of fitness differences. Alternatively, variation in sociality may relate to stable behavioural differences among individuals. Personality traits such as aggression or exploratory behaviour have been associated with reproductive success in birds, often through indirect pathways involving parental provisioning behaviour

[77,78]. In a densely connected colonial system such as that of sociable weavers, however, social positioning may not only reflect intrinsic traits but also influence access to information, tolerance during foraging, and energetic condition prior to reproduction. Under such conditions, social bonds could shape fitness trajectories through both direct and indirect pathways. Disentangling these alternatives will require experimental approaches. Manipulating social opportunities—for example by structuring feeding associations using automated feeders [79,80]—would provide stronger inference about whether social connectivity itself affects reproductive performance or instead covaries with underlying individual traits.

Taken together, these results suggest that cooperative breeding systems should not be understood solely through helping effort or breeding-group composition. Instead, cooperative breeders are likely embedded within multi-layered social structures [28,81] in which individual-level social network attributes can shape breeding opportunities and reproductive outcomes [82]. Incorporating social network metrics alongside helper number may therefore provide a more complete framework for understanding reproductive dynamics in cooperative societies. These findings align with growing comparative evidence that sociality predicts survival and reproductive success across taxa (e.g. [83]). Moreover, the marked sex differences observed here further highlight the importance of considering dispersal strategies and social structure when examining fitness consequences of social behaviour [84].

Finally, our results combined with earlier evidence that high- and medium-sociality sociable weavers show higher survival [26], suggest that individual sociality in males, while overall beneficial, may also be linked to life-history trade-offs [85,86] rather than to uniformly positive or negative fitness effects [2]. High-sociality males have higher survival and later onset of reproduction, but performed better in terms of reproductive output. Conversely, less social males reproduced earlier, which may partly compensate for reduced performance and survival later in life [86]. This pattern is consistent with the idea that alternative life-history trajectories may be shaped by social conditions, which may favour different patterns of allocation between reproduction and survival. Individual sociality in sociable weavers is moderately repeatable [26], and this temporal stability, together with the contrasting associations between sociality and different fitness components observed here, aligns with the social niche specialization hypothesis [87], whereby persistent individual differences can be maintained when alternative levels of sociality are linked to distinct life-history strategies. In this context, repeatability suggests that variation in sociality may be stable enough for different social trajectories to become associated with distinct life-history strategies. Further work encompassing lifetime reproductive success is required to further investigate this fascinating possibility.

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Sociality beyond helpers at the nest: the number of strong associations predict reproductive trade-offs in a cooperative breeder

SUPPLEMENTARY MATERIAL

Sociality levels classification

Table S1. Classification of sociality levels by year and colony. For each year-colony combination, the table shows the minimum and maximum numbers of strong social bonds observed within each category (see main text for classification criteria).

Year	Colony	Sociality level	Minimum strong bonds	Maximum strong bonds	Colony size at RFID-feeders
2018	11	Low	0	3	48
		Medium	4	7	
		High	8	16	
	20	Low	0	3	48
		Medium	4	7	
		High	8	16	
	27	Low	0	3	41
		Medium	4	8	
		High	9	16	
	43	Low	0	1	32
		Medium	2	6	
		High	7	11	
	71	Low	0	5	57
		Medium	6	9	
		High	11	24	
2019	11	Low	0	2	44
		Medium	3	6	
		High	7	12	
	20	Low	0	0	17
		Medium	1	1	
		High	3	4	
	27	Low	0	1	25
		Medium	2	3	
		High	4	9	
	43	Low	0	0	30
		Medium	1	1	
		High	2	6	
	71	Low	0	2	52
		Medium	3	4	
		High	5	12	
		Medium	7	8	
		High	9	19	
2022	11	Low	0	1	28
		Medium	2	5	
		High	6	11	

	20	Low	0	2	18
		Medium	3	3	
		High	4	6	
	21	Low	0	0	8
		Medium	1	1	
		High	2	2	
	71	Low	0	1	24
		Medium	2	4	
		High	5	10	
2023	11	Low	0	4	55
		Medium	5	12	
		High	13	23	
	20	Low	0	4	35
		Medium	5	7	
		High	9	20	
	21	Low	0	3	28
		Medium	4	5	
		High	6	9	
	71	Low	0	3	43
		Medium	4	7	
		High	10	15	

Table S2. Probability of chick fledging — Estimated marginal means. Estimated marginal means (probability scale) for chick fledging success from a beta–binomial generalized linear mixed model (GLMM). Probabilities are model predictions with parental age and number of helpers held at their mean values.

Parent	Category	Probability	95% CI
Mother	Low	0.510	0.383–0.635
Mother	Medium	0.476	0.333–0.623
Mother	High	0.686	0.464–0.846
Father	Low	0.510	0.286–0.730
Father	Medium	0.559	0.412–0.696
Father	High	0.610	0.479–0.727

Table S3. Probability of chick fledging — Pairwise contrasts. Pairwise contrasts between sociality categories for chick fledging probability based on estimated marginal means. Differences are expressed on the probability scale. The test statistic (t) corresponds to the observed contrast from the original model. Permutation p-values (pperm) were obtained from 10,000 network permutations and calculated as the proportion of permuted contrasts with absolute values equal to or greater than the observed statistic.

Parent	Contrast	Difference (prob)	t	p_{perm}
Mother	Low vs Medium	0.034	0.36	0.711
Mother	Low vs High	-0.176	-1.54	0.104
Mother	Medium vs High	-0.210	-1.69	0.066
Father	Low vs Medium	-0.049	-0.36	0.715
Father	Low vs High	-0.100	-0.80	0.442
Father	Medium vs High	-0.051	-0.56	0.575

Table S4. Probability of chick fledging — Fixed effects from a beta–binomial generalized linear mixed model (GLMM; family = betabinomial) with logit link modelling chick fledging success (number of fledglings out of the number of hatched chicks per brood). Random intercepts were included for maternal identity (variance = 1.95×10^{-9}), paternal identity (1.91×10^{-9}), colony (2.25×10^{-12}), and season (3.03×10^{-12}). The dispersion parameter was 1.42. Estimates are reported on the logit scale and significance was assessed using Wald z-tests. N = 145 broods.

	Estimate	SE	z	p
Intercept	-0.174	0.471	-0.370	0.712
Mother Medium	-0.137	0.383	-0.357	0.721
Mother High	0.741	0.483	1.536	0.125
Father Medium	0.198	0.545	0.362	0.717
Father High	0.409	0.510	0.801	0.423
Mother age (scaled)	0.082	0.205	0.401	0.688
Father age (scaled)	-0.291	0.186	-1.569	0.117
Number of helpers (scaled)	0.735	0.192	3.830	<0.001

Table S5. Fledgling mass (day 17) — Estimated marginal means. Estimated marginal means (g) for fledgling mass at day 17 from a Gaussian linear mixed model (LMM). Predicted values are model estimates with parental age and number of helpers held at their mean values.

Parent	Category	Predicted mass (g)	95% CI
Mother	Low	27.67	26.28-29.05
Mother	Medium	27.01	25.26-28.75
Mother	High	26.92	25.09-28.75
Father	Low	25.44	23.36-27.52
Father	Medium	28.18	26.70-29.66
Father	High	27.97	26.68-29.26

Table S6. Fledgling mass (day 17) — Pairwise contrasts. Pairwise contrasts between sociality categories for fledgling mass at day 17 based on estimated marginal means. Differences are expressed in grams. The test statistic (t) corresponds to the observed contrast from the original model. Permutation p-values (pperm) were obtained from 10,000 network permutations and calculated as the proportion of permuted contrasts with absolute values equal to or greater than the observed statistic.

Parent	Contrast	Difference (g)	t	p_{perm}
Mother	Low vs Medium	0.66	0.78	0.388
Mother	Low vs High	0.75	0.71	0.451
Mother	Medium vs High	0.08	0.07	0.942
Father	Low vs Medium	-2.74	-2.30	0.014
Father	Low vs High	-2.53	-2.26	0.016
Father	Medium vs High	0.21	0.24	0.787

Table S7. Fledgling mass (day 17) — Fixed effects. Fixed effects from a Gaussian linear mixed model (LMM) modelling fledgling mass at day 17 (g). Random intercepts were included for brood identity (variance = 5.875), paternal identity (1.012×10^{-9}), maternal identity (0), colony (0), and season (0). The residual variance was 3.985. Estimates are reported on the response scale (g). N = 188 chicks.

	Estimate	SE	z
Intercept	25.997	0.868	29.942
Father Medium	2.742	1.039	2.639
Father High	2.535	0.932	2.720
Mother Medium	-0.660	0.729	-0.906
Mother High	-0.745	0.827	-0.901
Father age (scaled)	-0.360	0.350	-1.029
Mother age (scaled)	0.064	0.409	0.157
Number of helpers (scaled)	1.105	0.347	3.187

Table S8. Timing within season — Estimated marginal means. Estimated marginal means (days) for the number of days from the first laying date in the colony from a negative binomial generalized linear mixed model (GLMM; family = nbinom2, log link). Predicted values are model estimates with age and number of helpers held at their mean values.

Sex	Category	Predicted days	95% CI
Female	Low	22.52	11.85–42.79
Female	Medium	30.76	15.86–59.65
Female	High	21.22	10.39–43.33
Male	Low	33.52	16.03–70.08
Male	Medium	34.43	17.66–67.10
Male	High	36.72	19.43–69.39

Table S9. Timing within season — Pairwise contrasts. Pairwise contrasts between sociality categories within each sex for the number of days from the first laying date in the colony based on estimated marginal means. Contrasts are expressed as ratios of expected days (log link). The test statistic (t) corresponds to the observed contrast from the original model. Permutation p-values (pperm) were obtained from 10,000 network permutations and calculated as the proportion of permuted contrasts with absolute values equal to or greater than the observed statistic.

Sex	Contrast	Ratio (expected days)	t	p_{perm}
F	Low vs Medium	0.732	-1.31	0.146
F	Low vs High	1.061	0.19	0.827
F	Medium vs High	1.450	1.20	0.182
M	Low vs Medium	0.974	-0.10	0.926
M	Low vs High	0.913	-0.37	0.747
M	Medium vs High	0.937	-0.34	0.767

Table S10. Timing within season — Fixed effects. Fixed effects from a negative binomial generalized linear mixed model (GLMM; family = nbinom2) with log link modelling the number of days from the first laying date in the colony. Random intercepts were included for breeding colony (variance = 0.428), individual identity (0.011), and season (0.095). The dispersion parameter was 0.927. Estimates are reported on the log. N = 288 observations.

	Estimate	SE	z
Intercept	3.108	0.326	9.522
Category Medium	0.312	0.238	1.311
Category High	-0.060	0.308	-0.194
Sex (M)	0.398	0.266	1.496
Age (scaled)	-0.227	0.071	-3.183
Number of helpers (scaled)	-0.211	0.070	-3.026
Category Medium* Sex (M)	-0.285	0.344	-0.828
Category High* Sex (M)	0.151	0.387	0.390

Table S11. Breeding probability — Estimated marginal means. Estimated marginal means (probability scale) for breeding probability from a binomial generalized linear mixed model (GLMM; logit link). Probabilities are model predictions with age held at its mean value.

Sex	Category	Predicted probability	95% CI
Female	Low	0.716	0.575–0.824
Female	Medium	0.694	0.534–0.818
Female	High	0.749	0.531–0.887
Male	Low	0.552	0.370–0.721
Male	Medium	0.754	0.618–0.853
Male	High	0.751	0.629–0.843

Table S12. Breeding probability — Pairwise contrasts. Pairwise contrasts between sociality categories within each sex for breeding probability based on estimated marginal means. Differences are expressed on the probability scale. The test statistic (t) corresponds to the observed contrast from the original model. Permutation p-values (pperm) were obtained from 10,000 network permutations and calculated as the proportion of permuted contrasts with absolute values equal to or greater than the observed statistic.

Sex	Contrast	Difference (prob)	t	p_{perm}
Female	Low vs Medium	0.022	0.23	0.829
Female	Low vs High	-0.034	-0.30	0.766
Female	Medium vs High	-0.055	-0.47	0.619
Male	Low vs Medium	-0.203	-1.84	0.125
Male	Low vs High	-0.200	-1.89	0.116
Male	Medium vs High	0.003	0.04	0.969

Table S13. Breeding probability — Fixed effects. Fixed effects from a binomial generalized linear mixed model (GLMM; logit link) modelling breeding probability. Random intercepts were included for colony (variance = 1.42×10^{-10}), individual identity (0.956), and season (6.13×10^{-10}). Estimates are reported on the logit scale and significance was assessed using Wald z-tests. N = 443 observations.

	Estimate	SE	z
Intercept	0.923	0.317	2.914
Category Medium	-0.104	0.442	-0.235
Category High	0.172	0.569	0.303
Sex (M)	-0.716	0.487	-1.472
Age (scaled)	1.387	0.217	6.380
Category Medium* Sex (M)	1.018	0.663	1.535
Category High* Sex (M)	0.726	0.742	0.979

Table S14. Age at first reproduction — Estimated marginal means. Estimated marginal means (days) for age at first reproduction from a Gaussian generalized linear mixed model (GLMM; identity link). Predicted values are model estimates with the number of helpers held at its mean value.

Sex	Category	Predicted probability	95% CI
Female	Low	804.6	653.6–955.6
Female	Medium	665.7	483.1–848.3
Female	High	844.8	663.1–1026.4
Male	Low	785.2	604.6–965.7
Male	Medium	904.9	733.3–1076.5
Male	High	961.0	787.3–1134.7

Table S15. Age at first reproduction — Pairwise contrasts. Pairwise contrasts between sociality categories within each sex for age at first reproduction based on estimated marginal means. Differences are expressed in days. The test statistic (t) corresponds to the observed contrast from the original model. Permutation p-values (pperm) were obtained from 10,000 network permutations and calculated as the proportion of permuted contrasts with absolute values equal to or greater than the observed statistic.

Sex	Contrast	Difference (prob)	t	p_{perm}
Female	Low vs Medium	138.9	1.76	0.153
Female	Low vs High	-40.2	-0.40	0.749
Female	Medium vs High	-179.1	-1.61	0.191
Male	Low vs Medium	-119.7	-1.47	0.173
Male	Low vs High	-175.8	-2.10	0.048
Male	Medium vs High	-56.1	-0.93	0.361

Table S16. Age at first reproduction — Fixed effects. Fixed effects from a Gaussian generalized linear mixed model (GLMM; identity link) modelling age at first reproduction (days). Random intercepts were included for colony (variance = 14,191) and season (5,019). The residual variance was 28,214 ($\sigma^2 = 2.82 \times 10^4$). Estimates are reported on the response scale (days). N = 75 observations.

	Estimate	SE	z
Intercept	804.622	75.617	10.641
Category Medium	-138.917	78.738	-1.764
Category High	40.148	99.806	0.402
Sex (M)	-19.442	80.718	-0.241
Number of helpers (scaled)	-8.605	21.949	-0.392
Category Medium* Sex (M)	258.632	109.259	2.367
Category High* Sex (M)	135.678	135.760	0.999