



25 **SUMMARY**

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

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## 48 INTRODUCTION

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

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

74 Emerging evidence from cooperatively breeding species also suggests that reproductive  
75 performance may depend on a broader social context than helper number alone. In dwarf  
76 mongooses (*Helogale parvula*), social instability is associated with reduced reproductive success  
77 [18], and in greater anis (*Guira guira*), prior social associations between females synchronize  
78 reproduction and increase nest survival [10]. This raises the possibility that, in cooperative  
79 breeders, reproductive performance may depend not only on helper number but also on the  
80 broader social context in which helping occurs. However, the independent effects of breeder  
81 sociality and helper number remain largely unresolved. Evaluating both simultaneously is  
82 therefore essential to determine their relative contributions to reproductive performance.

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

96 Within this social and demographic context, sociable weavers exhibit consistent individual  
97 differences in sociality, measured as the relative number of strong social bonds each individual  
98 maintains within its colony [26]. Because sociable weavers forage in highly cohesive flocks that

99 often include most colony members [27], networks based on simple co-occurrence at RFID  
100 feeders can reflect general gregariousness rather than preferential social relationships [22]. In  
101 contrast, focusing on strong bonds (derived from time-overlapping foraging associations  
102 recorded at RFID feeders [22]) captures persistent, preferential associations among specific  
103 partners, with important implications for survival [26]. This distinction is critical, as recent  
104 theoretical work has highlighted that relationship quality (investment in specific partners) and  
105 relationship quantity (overall gregariousness) represent distinct dimensions of sociality that may  
106 have different adaptive consequences [2].

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

119

## 120 **METHODS**

### 121 **Site and study species**

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

124 1993. Since 2008, the population has been regularly monitored through annual captures, and  
125 since 2010, breeding activity has been consistently monitored (see below).

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

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### 133 **RFID data collection and social network metrics**

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

148 sociable weavers more accurately than simple co-occurrence approaches, as individuals often  
149 forage in cohesive flocks that include most colony members.

150 To identify strong social bonds (e.g. [28,29]), we followed [26] and ranked all pairwise  
151 association weights within each colony-year, classifying edges with values equal to or above the  
152 80th percentile as strong bonds. In the same study system, the main downstream results were  
153 qualitatively robust to alternative strong-bond thresholds (70th and 90th percentiles [26]). This  
154 approach allows us to distinguish relatively high-quality bonds from more general gregarious  
155 associations [2] within each colony-year, while accounting for variation in colony size and overall  
156 network density. After identifying strong social bonds within each colony, we calculated how  
157 many each individual had. Finally, individuals were classified into three sociality categories  
158 (“Low”, “Medium”, “High”) by dividing the distribution of strong bond counts within each  
159 colony-year into terciles (33rd and 66th percentiles [26]). This relative classification captures  
160 variation in social bond number within each colony-year and was used as the predictor of  
161 sociality in subsequent analyses (see Table S1 for colony-year–specific ranges).

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

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### 169 **Reproduction monitoring**

170 To monitor reproduction, during our study period (2018–2023), all nest chambers within each  
171 colony were checked every three days throughout the breeding season to detect new clutches  
172 [4,31]. This frequency allowed us to accurately estimate laying dates, as clutches typically consist

173 of 3-4 eggs laid on consecutive days. Nestlings were ringed and blood-sampled at 9 days of age  
174 for individual identification and parentage analysis. Body mass was recorded at 17 days, close  
175 to fledging (typically from 20 days onwards [32]; unpublished data).

## 176 **Breeder identification**

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

190

## 191 **Statistical analysis**

### 192 General procedures

193 All statistical analyses were conducted in R (v4.0.5) using generalized linear mixed models  
194 (GLMMs) implemented in the glmmTMB package (v1.1.7). The aim of our analyses was to  
195 examine how individual sociality (Low, Medium, High) related to several reproductive metrics,  
196 using model structures appropriate for the distribution and nature of each response variable

197 (see below). To explicitly disentangle the effects of breeder sociality from those of helper  
198 number, the number of helpers at the nest was included as a covariate in all models where  
199 applicable. The only exception was the analysis of breeding probability. Because this response  
200 included both breeders and non-breeders, helper number at the nest could only be defined for  
201 individuals that actually initiated a breeding attempt, and therefore could not be included as a  
202 predictor in that model.

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

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

221 helpers and age were mean-centred and scaled before analysis to aid interpretation and model  
222 convergence.

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

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

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

243

244

245 Relationship between individual sociality and helper number

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

254 Fledgling survival

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

262 Fledgling mass

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

270 Timing of reproduction within the season

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

281 Probability of reproduction attempt

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

294

295 Age at first reproduction attempt

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

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

306

307 **RESULTS**

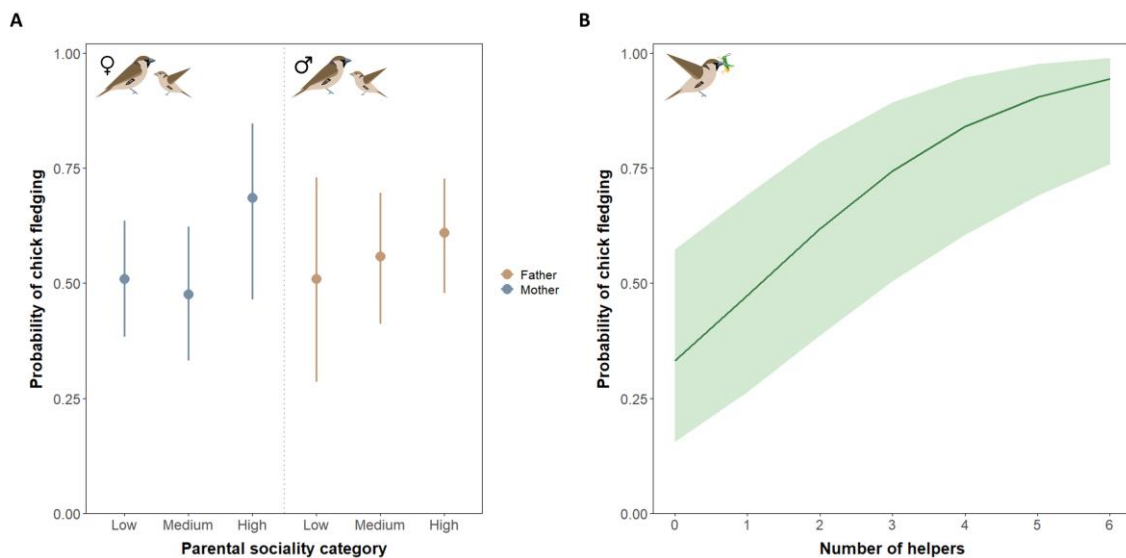
308 Relationship between individual sociality and helper number

309 The raw number of strong social bonds was not correlated with the number of helpers present  
310 at the nest, either in males ( $n = 498$ ; Spearman's  $\rho = -0.02$ ,  $p = 0.63$ ) or in females ( $n = 298$ ;  $\rho =$   
311  $-0.04$ ,  $p = 0.45$ ).

312 Probability of chick fledging

313 We analysed fledging success in 145 broods. We found a tendency for chicks of high-sociality  
314 mothers to show higher fledging probabilities (0.69) than those of low- (0.51) or medium-  
315 sociality mothers (0.48), corresponding to absolute differences of 0.18 (High vs Low) and 0.21  
316 (High vs Medium) (Table S2; Fig. 1). However, these differences did not reach statistical  
317 significance in the permutation tests (Low vs High:  $p_{\text{perm}} = 0.104$ ; Medium vs High:  $p_{\text{perm}} = 0.066$ ;  
318 Table S3). For paternal sociality, all contrasts were non-significant (all  $p_{\text{perm}} \geq 0.442$ ). The number

319 of helpers at the nest was positively associated with fledging probability. Because the reduced  
 320 model excluding helper number failed to converge, likelihood-ratio tests could not be computed  
 321 for this term. Nonetheless, the full model indicated a strong positive effect of helper number ( $z$   
 322 = 3.83,  $p < 0.001$ ; Table S4; Fig. 1). Finally, age of the breeding parents did not influence the  
 323 probability of fledging young (mother: LRT = 0.16,  $p = 0.688$ ; father: LRT = 2.48,  $p = 0.117$ ; Table  
 324 S4).



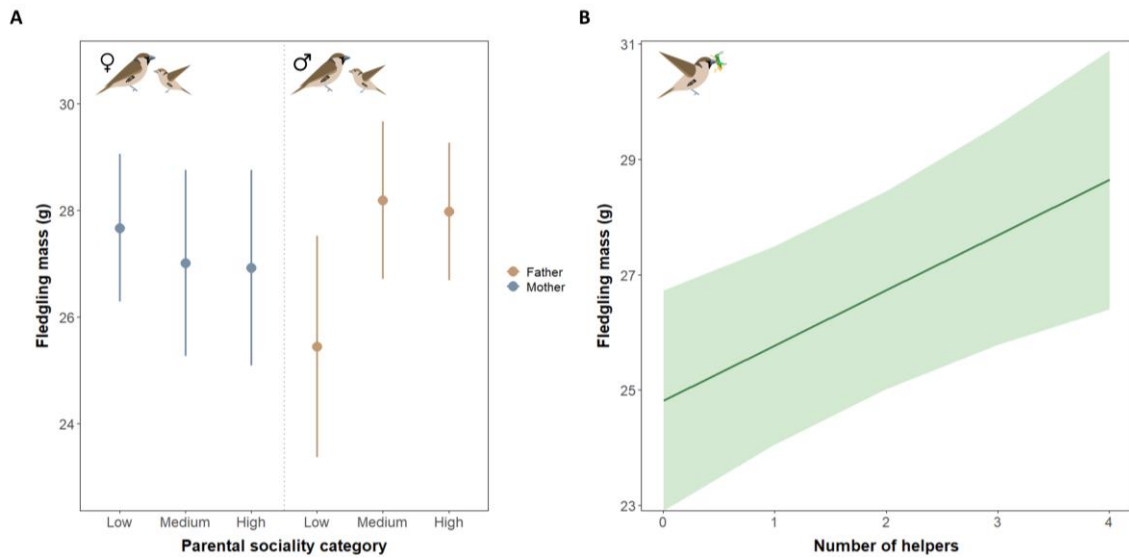
325

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

### 333 Fledgling mass

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

337 S6). No significant difference was detected between medium- and high-sociality fathers ( $p_{perm} =$   
 338 0.787). Maternal sociality showed no detectable association with fledgling mass (all  $p_{perm} \geq$   
 339 0.420). The number of helpers showed a positive association with fledgling mass (LRT = 8.41,  $p$   
 340 = 0.008; ; Table S7; Fig. 2). Finally, age of the breeding parents was not associated chick mass  
 341 (mother: LRT = 0.58,  $p = 0.46$ ; father: LRT = 1.70,  $p = 0.19$ ; Table S7).



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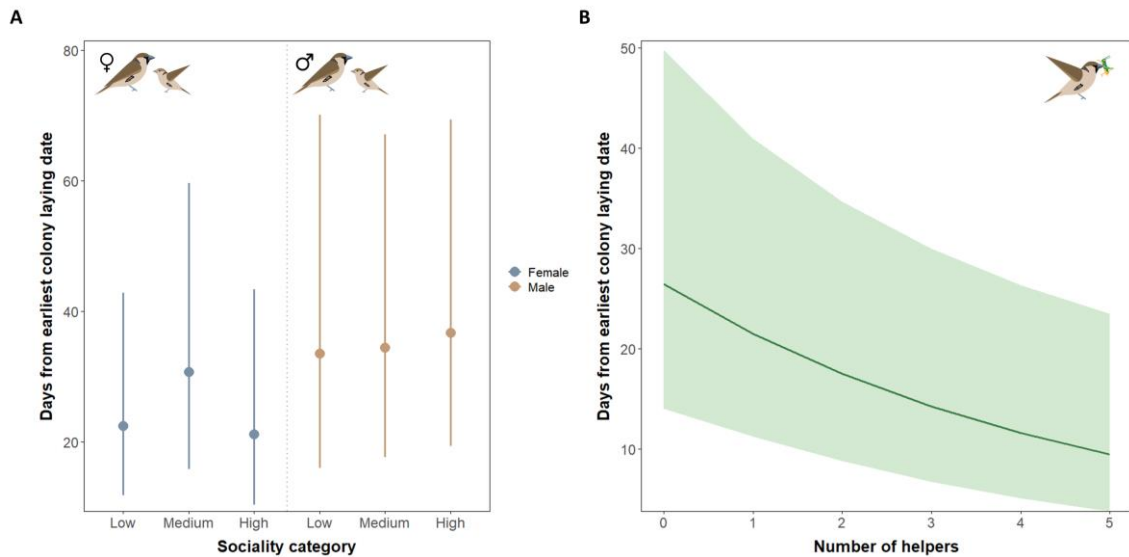
343 **Figure 2. Fledgling mass in relation to parental sociality and number of helpers.** A) Model  
 344 predictions from the Gaussian LMM for fledgling mass at day 17 across maternal (blue) and  
 345 paternal (brown) sociality categories. Points represent estimated means and vertical bars 95%  
 346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

349

### 350 Timing of reproduction within the season

351 We analysed breeding timing in 288 breeding attempts. We found no evidence that individual  
 352 sociality influenced breeding timing in either sex (Table S8; Fig. 3). All pairwise contrasts  
 353 between sociality categories were non-significant for females (all  $p_{perm} \geq 0.146$ ; Table S9) and for

354 males (all  $p_{perm} \geq 0.747$ ; Table S9). In contrast, older individuals bred earlier (LRT = 10.02,  $p =$   
 355 0.0016), and birds with more helpers also initiated reproduction earlier (LRT = 8.97,  $p = 0.0027$ ;  
 356 Table S10; Fig. 3). The effect of sociality on reproductive timing did not differ between males  
 357 and females (interaction: LRT = 1.58,  $p = 0.454$ ; ; Table S10).



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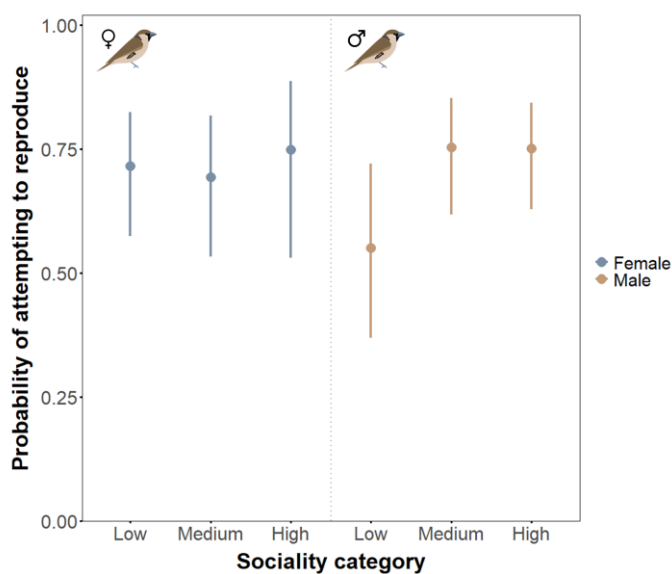
359 **Figure 3. Timing of first breeding attempt within the season in relation to individual sociality**  
 360 **and number of helpers.** A) Model predictions from the negative binomial GLMM for the number  
 361 of days between an individual's first laying date and the earliest laying date recorded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

367

368 Probability of attempting to reproduce

369 We analysed breeding probability in 443 individual–season observations. We found a tendency  
 370 for low-sociality males to show lower breeding probabilities (0.55) than medium- and high-

371 sociality males (both 0.75; Table S11; Fig. 4), although these differences were not supported by  
372 permutation tests (Low vs Medium  $p_{\text{perm}} = 0.125$ ; Low vs High:  $p_{\text{perm}} = 0.116$ ; Table S12). In  
373 females, all pairwise contrasts between sociality categories were non-significant (all  $p_{\text{perm}} \geq$   
374 0.619; Table S12). There was no statistical support for a difference in the effect of sociality  
375 between males and females (interaction: LRT = 2.55,  $p = 0.279$ ; Table S13). In contrast, age  
376 showed a strong positive association with breeding probability, with older individuals being  
377 more likely to attempt reproduction (LRT = 82.13,  $p < 0.001$ ; Table S13).



378

379 **Figure 4. Probability of attempting to reproduce in relation to individual sociality.**

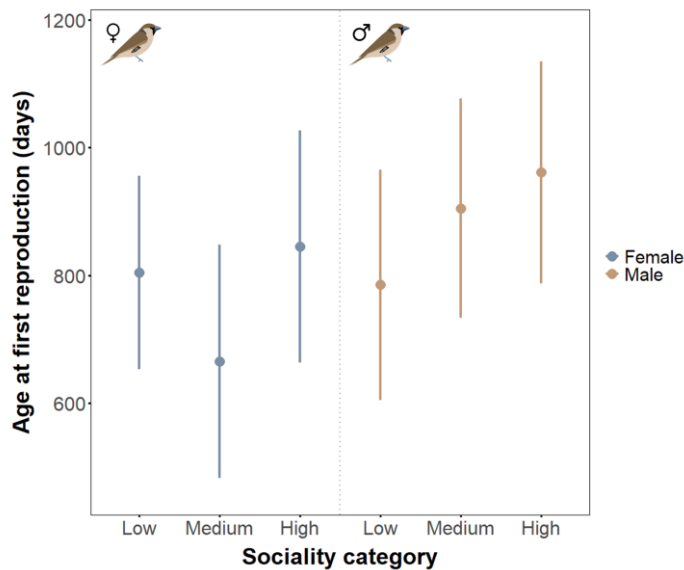
380 Model predictions (binomial GLMM) for the probability of attempting reproduction for females  
381 (blue) and males (brown) across sociality categories. Points represent estimated means and  
382 vertical bars their 95% confidence intervals.

383

384 Age at first reproduction attempt

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

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



393

394 **Figure 5. Age at first reproduction in relation to individual sociality.** Model predictions  
395 (Gaussian GLMM) for age at first reproduction (days since hatching) for females (blue) and males  
396 (brown) across sociality categories. Points represent estimated means and vertical bars their  
397 95% confidence intervals.

398

## 399 DISCUSSION

400 Our results suggest that individual sociality, beyond the number of helpers at the nest, is  
401 associated with multiple components of reproductive success in sociable weavers, although  
402 support varied across traits and between the sexes. At the offspring level, chicks raised by high-  
403 sociality breeding females tended to show higher fledging success than those raised by medium-  
404 and low-sociality females, although support for this pattern was only marginal. For breeding

405 males, fledglings raised by medium- and high-sociality fathers were heavier than those raised by  
406 low-sociality fathers, and males with higher sociality also tended to show a higher probability of  
407 attempting reproduction, although this latter pattern did not reach statistical significance. In  
408 contrast, high-sociality males initiated reproduction later in life than low-sociality males.  
409 Together, these patterns reveal sex-specific effects and a potential male-specific life-history  
410 trade-off, whereby high-sociality males delay reproductive onset while producing heavier  
411 fledglings and tending to show higher breeding probability.

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

428 We also found that helper number was consistently associated with reproductive performance  
429 and breeding timing, in line with previous work in sociable weavers [4,21,50] and other

430 cooperative breeders (e.g., [51]). A higher number of helpers increased fledging probability and  
431 was positively associated with fledging mass, which is consistent with evidence that helpers can  
432 increase provisioning and reduce parental workload during chick rearing [21,52]. In addition,  
433 individuals breeding in groups with more helpers initiated reproduction earlier in the season, a  
434 pattern also reported in other cooperative species [53,54] and potentially explained by reduced  
435 costs of breeding initiation [5].

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

449 While future work on the formation and maintenance of strong bonds will be needed to test  
450 these sex differences explicitly, several non-exclusive mechanisms could help explain the  
451 positive association between sociality and reproductive performance observed here. First,  
452 individuals with a higher number of strong bonds may benefit from enhanced information  
453 sharing within the colony [2]. Sociable weavers forage predominantly on the ground, typically in  
454 cohesive colony groups [20,27] and, during breeding, also in smaller groups foraging closer to

455 the colony (Covas & Doutrelant, pers. obs.). Under these conditions, a higher number of strong  
456 bonds may facilitate information sharing within the colony [2], potentially improving access to  
457 socially acquired information about novel food patches, such as termite emergences, an  
458 important food source in this species [55]. Similar links between social associations and the  
459 discovery of novel food patches have been shown in other wild songbirds [56]. Higher sociality  
460 may also increase social tolerance and reduce contest competition during foraging [2,6], leading  
461 to fewer antagonistic interactions and potentially more efficient resource acquisition and chick  
462 provisioning. During the pre-breeding period, particularly in winter, sociality may further  
463 influence energetic state through communal roosting. In sociable weavers, roosting together  
464 reduces thermoregulatory costs, especially during cold nights [23]. Individuals maintaining more  
465 strong bonds may therefore experience improved energetic condition prior to reproduction,  
466 either because they gain more consistent access to communal roosting chambers or because  
467 they roost in larger groups, with potential carry-over effects on subsequent reproductive  
468 allocation and performance.

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

478 We found no evidence that individual sociality influenced breeding timing within the season. In  
479 arid and semi-arid environments, breeding is often opportunistic, closely tied to fluctuating

480 resource availability [61] and highly variable in timing and length [62], which may limit the extent  
481 to which broader patterns of sociality influence seasonal reproductive timing. Instead, in this  
482 species, aligning reproduction with favourable breeding conditions may be more important. This  
483 may depend more strongly on breeder experience, which could explain why breeding timing  
484 was more closely associated with age, with older individuals initiating reproduction earlier, and  
485 with helper number. Advances in laying date with age are well documented in birds and are  
486 often attributed to increased breeding experience or improvements in individual performance,  
487 in line with maturation and learning hypotheses [63,64]. In sociable weavers specifically, longer  
488 pair-bond duration is also associated with earlier breeding [39], suggesting that the age effect  
489 detected here may partly reflect accumulated pair experience and partner familiarity.

490 We also detected a tendency for medium- and high-sociality males to show higher breeding  
491 probabilities, although this pattern did not reach significance in permutation tests and should  
492 therefore be interpreted with caution. Nonetheless, sociality may capture additional aspects of  
493 a male's social position within the colony that influence access to reproductive opportunities. A  
494 relatively greater number of strong bonds may increase exposure to reproductive cues from  
495 conspecifics and facilitate breeding activation when conditions are favourable [65,66]. It may  
496 also be associated with greater social tolerance and reduced conflict, potentially improving  
497 access to resources prior to the breeding season and helping meet the energetic demands  
498 associated with initiating reproduction [67]. At the same time, age remained a strong predictor  
499 of breeding probability: older individuals were significantly more likely to attempt reproduction,  
500 a pattern consistent with delayed entry into breeding roles typical of cooperative systems  
501 [68,69].

502 Finally, we found that age at first reproduction varied with sociality in males but not in females,  
503 with high-sociality males initiating reproduction approximately six months later than their low-  
504 sociality counterparts (roughly 26 vs 32 months). Although maximum recorded longevity in this

505 species exceeds 15 years [70], average adult survival is approximately 0.66 [71], corresponding  
506 to an expected adult lifespan of roughly three years under constant survival. A six-month delay  
507 therefore represents a substantial fraction of expected adult life and likely constitutes a  
508 biologically meaningful shift in reproductive timing. This male-specific pattern is also consistent  
509 with the life-history structure of sociable weavers, where males are predominantly philopatric  
510 and typically remain in their natal colony as helpers before breeding [72]. In this species, as in  
511 other cooperative breeders, breeding reflects a trade-off between current reproductive benefits  
512 and the advantages of remaining in a non-breeding role, a balance that is sensitive to ecological  
513 conditions [67,73]. Within this framework, higher sociality may shift this balance—either by  
514 increasing the relative benefits of delayed breeding and helping close relatives, or by reinforcing  
515 socially mediated constraints on access to reproduction—thereby delaying reproductive onset.  
516 If strong bonds are predominantly formed among philopatric males, higher sociality may also  
517 increase exposure to intra-sexual competition and socially mediated constraints on breeding  
518 positions on the one hand (e.g. [74]), but offer increased possibilities of helping close kin or close  
519 social partners on the other, which would lead to increased inclusive fitness [75] or possibilities  
520 of being reciprocated in the future [76].

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

531 [77,78]. In a densely connected colonial system such as that of sociable weavers, however, social  
532 positioning may not only reflect intrinsic traits but also influence access to information,  
533 tolerance during foraging, and energetic condition prior to reproduction. Under such conditions,  
534 social bonds could shape fitness trajectories through both direct and indirect pathways.  
535 Disentangling these alternatives will require experimental approaches. Manipulating social  
536 opportunities—for example by structuring feeding associations using automated feeders  
537 [79,80]—would provide stronger inference about whether social connectivity itself affects  
538 reproductive performance or instead covaries with underlying individual traits.

539 Taken together, these results suggest that cooperative breeding systems should not be  
540 understood solely through helping effort or breeding-group composition. Instead, cooperative  
541 breeders are likely embedded within multi-layered social structures [28,81] in which individual-  
542 level social network attributes can shape breeding opportunities and reproductive outcomes  
543 [82]. Incorporating social network metrics alongside helper number may therefore provide a  
544 more complete framework for understanding reproductive dynamics in cooperative societies.  
545 These findings align with growing comparative evidence that sociality predicts survival and  
546 reproductive success across taxa (e.g. [83]). Moreover, the marked sex differences observed  
547 here further highlight the importance of considering dispersal strategies and social structure  
548 when examining fitness consequences of social behaviour [84].

549 Finally, our results combined with earlier evidence that high- and medium-sociality sociable  
550 weavers show higher survival [26], suggest that individual sociality in males, while overall  
551 beneficial, may also be linked to life-history trade-offs [85,86] rather than to uniformly positive  
552 or negative fitness effects [2]. High-sociality males have higher survival and later onset of  
553 reproduction, but performed better in terms of reproductive output. Conversely, less social  
554 males reproduced earlier, which may partly compensate for reduced performance and survival  
555 later in life [86]. This pattern is consistent with the idea that alternative life-history trajectories

556 may be shaped by social conditions, which may favour different patterns of allocation between  
557 reproduction and survival. Individual sociality in sociable weavers is moderately repeatable [26],  
558 and this temporal stability, together with the contrasting associations between sociality and  
559 different fitness components observed here, aligns with the social niche specialization  
560 hypothesis [87], whereby persistent individual differences can be maintained when alternative  
561 levels of sociality are linked to distinct life-history strategies. In this context, repeatability  
562 suggests that variation in sociality may be stable enough for different social trajectories to  
563 become associated with distinct life-history strategies. Further work encompassing lifetime  
564 reproductive success is required to further investigate this fascinating possibility.

565

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- 815



26 **SUMMARY**

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

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## 49 INTRODUCTION

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

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

75 Emerging evidence from cooperatively breeding species also suggests that reproductive  
76 performance may depend on a broader social context than helper number alone. In dwarf  
77 mongooses (*Helogale parvula*), social instability is associated with reduced reproductive success  
78 [18], and in greater anis (*Guira guira*), prior social associations between females synchronize  
79 reproduction and increase nest survival [10]. This raises the possibility that, in cooperative  
80 breeders, reproductive performance may depend not only on helper number but also on the  
81 broader social context in which helping occurs. However, the independent effects of breeder  
82 sociality and helper number remain largely unresolved. Evaluating both simultaneously is  
83 therefore essential to determine their relative contributions to reproductive performance.

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

97 Within this social and demographic context, sociable weavers exhibit consistent individual  
98 differences in sociality, measured as the relative number of strong social bonds each individual  
99 maintains within its colony [26]. Because sociable weavers forage in highly cohesive flocks that

100 often include most colony members [27], networks based on simple co-occurrence at RFID  
101 feeders can reflect general gregariousness rather than preferential social relationships [22]. In  
102 contrast, focusing on strong bonds (derived from time-overlapping foraging associations  
103 recorded at RFID feeders [22]) captures persistent, preferential associations among specific  
104 partners, with important implications for survival [26]. This distinction is critical, as recent  
105 theoretical work has highlighted that relationship quality (investment in specific partners) and  
106 relationship quantity (overall gregariousness) represent distinct dimensions of sociality that may  
107 have different adaptive consequences [2].

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

120

## 121 **METHODS**

### 122 **Site and study species**

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

125 1993. Since 2008, the population has been regularly monitored through annual captures, and  
126 since 2010, breeding activity has been consistently monitored (see below).

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

133

#### 134 **RFID data collection and social network metrics**

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

149 sociable weavers more accurately than simple co-occurrence approaches, as individuals often  
150 forage in cohesive flocks that include most colony members.

151 To identify strong social bonds (e.g. [28,29]), we followed [26] and ranked all pairwise  
152 association weights within each colony-year, classifying edges with values equal to or above the  
153 80th percentile as strong bonds. In the same study system, the main downstream results were  
154 qualitatively robust to alternative strong-bond thresholds (70th and 90th percentiles [26]). This  
155 approach allows us to distinguish relatively high-quality bonds from more general gregarious  
156 associations [2] within each colony-year, while accounting for variation in colony size and overall  
157 network density. After identifying strong social bonds within each colony, we calculated how  
158 many each individual had. Finally, individuals were classified into three sociality categories  
159 (“Low”, “Medium”, “High”) by dividing the distribution of strong bond counts within each  
160 colony-year into terciles (33rd and 66th percentiles [26]). This relative classification captures  
161 variation in social bond number within each colony-year and was used as the predictor of  
162 sociality in subsequent analyses (see Table S1 for colony-year–specific ranges).

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

169

## 170 **Reproduction monitoring**

171 To monitor reproduction, during our study period (2018–2023), all nest chambers within each  
172 colony were checked every three days throughout the breeding season to detect new clutches  
173 [4,31]. This frequency allowed us to accurately estimate laying dates, as clutches typically consist

174 of 3-4 eggs laid on consecutive days. Nestlings were ringed and blood-sampled at 9 days of age  
175 for individual identification and parentage analysis. Body mass was recorded at 17 days, close  
176 to fledging (typically from 20 days onwards [32]; unpublished data).

## 177 **Breeder identification**

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

191

## 192 **Statistical analysis**

### 193 General procedures

194 All statistical analyses were conducted in R (v4.0.5) using generalized linear mixed models  
195 (GLMMs) implemented in the glmmTMB package (v1.1.7). The aim of our analyses was to  
196 examine how individual sociality (Low, Medium, High) related to several reproductive metrics,  
197 using model structures appropriate for the distribution and nature of each response variable

198 (see below). To explicitly disentangle the effects of breeder sociality from those of helper  
199 number, the number of helpers at the nest was included as a covariate in all models where  
200 applicable. The only exception was the analysis of breeding probability. Because this response  
201 included both breeders and non-breeders, helper number at the nest could only be defined for  
202 individuals that actually initiated a breeding attempt, and therefore could not be included as a  
203 predictor in that model.

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

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

222 helpers and age were mean-centred and scaled before analysis to aid interpretation and model  
223 convergence.

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

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

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

244

245

246 Relationship between individual sociality and helper number

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

255 Fledgling survival

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

263 Fledgling mass

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

271 Timing of reproduction within the season

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

282 Probability of reproduction attempt

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

295

## 296 Age at first reproduction attempt

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

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

307

## 308 **RESULTS**

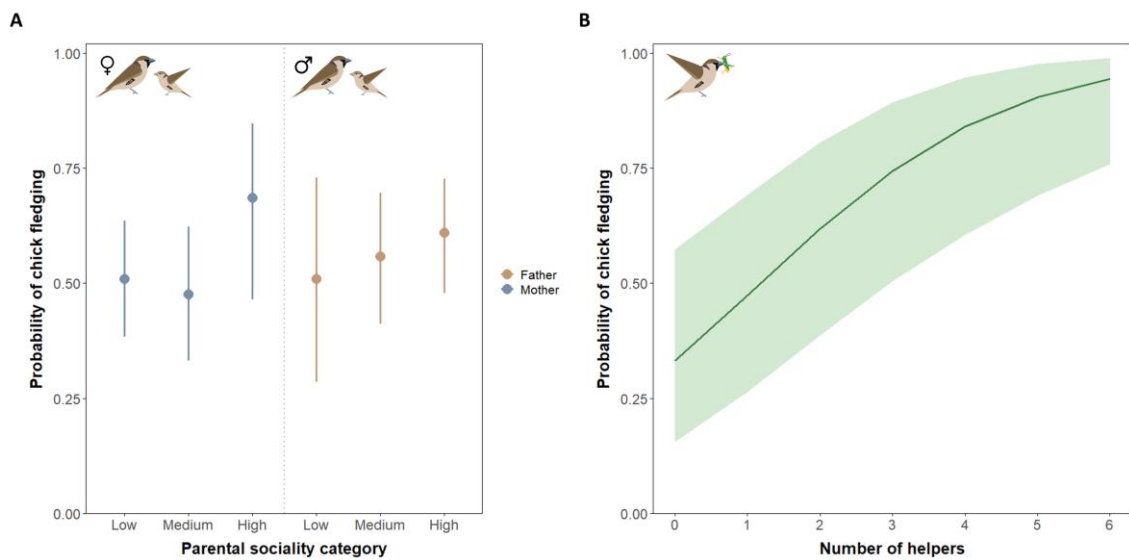
### 309 Relationship between individual sociality and helper number

310 The raw number of strong social bonds was not correlated with the number of helpers present  
311 at the nest, either in males ( $n = 498$ ; Spearman's  $\rho = -0.02$ ,  $p = 0.63$ ) or in females ( $n = 298$ ;  $\rho =$   
312  $-0.04$ ,  $p = 0.45$ ).

### 313 Probability of chick fledging

314 We analysed fledging success in 145 broods. We found a tendency for chicks of high-sociality  
315 mothers to show higher fledging probabilities (0.69) than those of low- (0.51) or medium-  
316 sociality mothers (0.48), corresponding to absolute differences of 0.18 (High vs Low) and 0.21  
317 (High vs Medium) (Table S2; Fig. 1). However, these differences did not reach statistical  
318 significance in the permutation tests (Low vs High:  $p_{\text{perm}} = 0.104$ ; Medium vs High:  $p_{\text{perm}} = 0.066$ ;  
319 Table S3). For paternal sociality, all contrasts were non-significant (all  $p_{\text{perm}} \geq 0.442$ ). The number

320 of helpers at the nest was positively associated with fledging probability. Because the reduced  
 321 model excluding helper number failed to converge, likelihood-ratio tests could not be computed  
 322 for this term. Nonetheless, the full model indicated a strong positive effect of helper number ( $z$   
 323 = 3.83,  $p < 0.001$ ; Table S4; Fig. 1). Finally, age of the breeding parents did not influence the  
 324 probability of fledging young (mother: LRT = 0.16,  $p = 0.688$ ; father: LRT = 2.48,  $p = 0.117$ ; Table  
 325 S4).



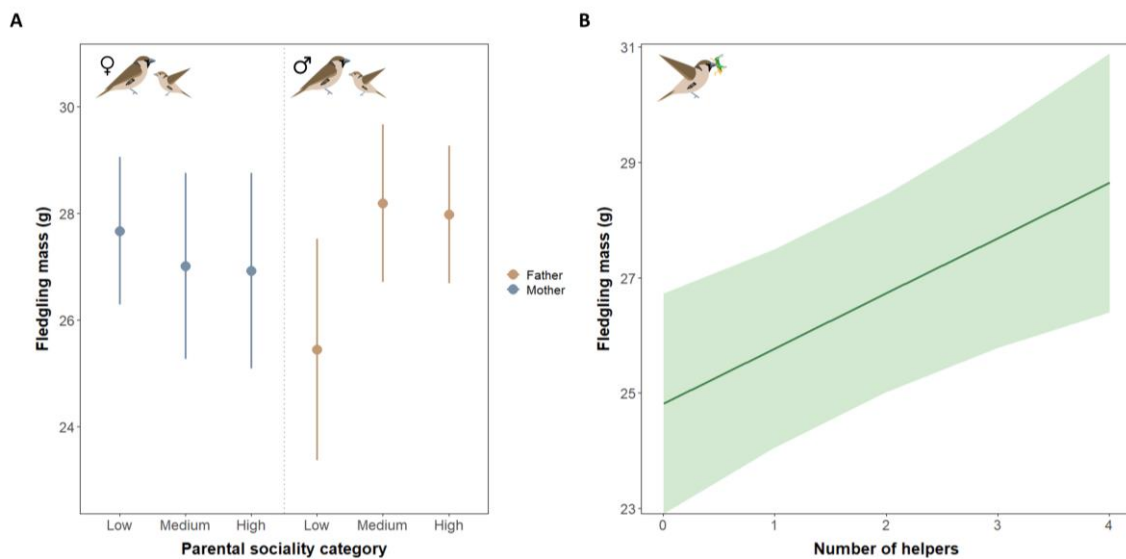
326

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

### 334 Fledgling mass

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

338 S6). No significant difference was detected between medium- and high-sociality fathers ( $p_{perm} =$   
 339 0.787). Maternal sociality showed no detectable association with fledgling mass (all  $p_{perm} \geq$   
 340 0.420). The number of helpers showed a positive association with fledgling mass (LRT = 8.41,  $p$   
 341 = 0.008; ; Table S7; Fig. 2). Finally, age of the breeding parents was not associated chick mass  
 342 (mother: LRT = 0.58,  $p = 0.46$ ; father: LRT = 1.70,  $p = 0.19$ ; Table S7).



343

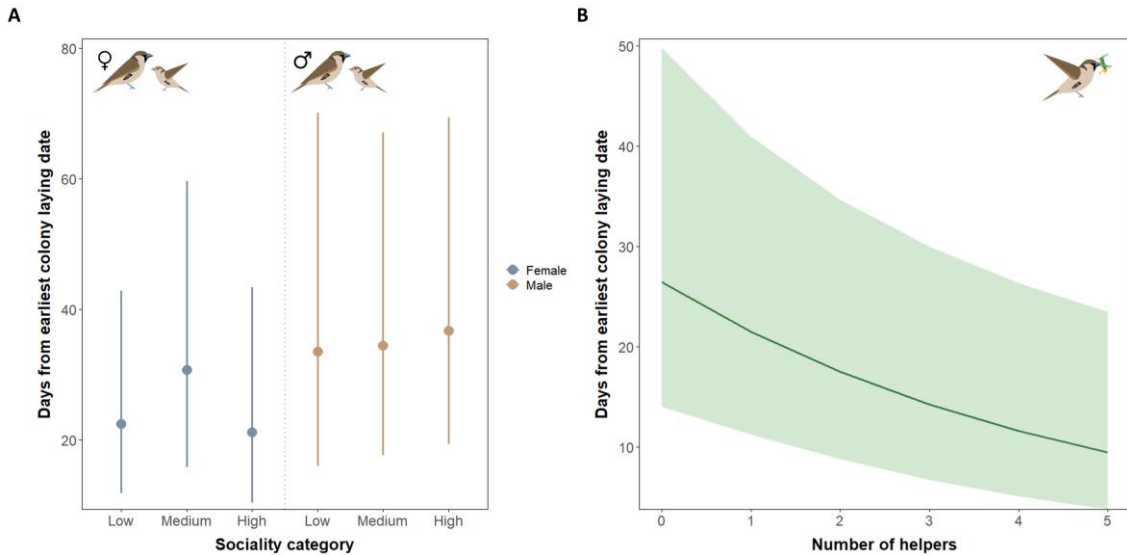
344 **Figure 2. Fledgling mass in relation to parental sociality and number of helpers.** A) Model  
 345 predictions from the Gaussian LMM for fledgling mass at day 17 across maternal (blue) and  
 346 paternal (brown) sociality categories. Points represent estimated means and vertical bars 95%  
 347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

350

### 351 Timing of reproduction within the season

352 We analysed breeding timing in 288 breeding attempts. We found no evidence that individual  
 353 sociality influenced breeding timing in either sex (Table S8; Fig. 3). All pairwise contrasts  
 354 between sociality categories were non-significant for females (all  $p_{perm} \geq 0.146$ ; Table S9) and for

355 males (all  $p_{perm} \geq 0.747$ ; Table S9). In contrast, older individuals bred earlier (LRT = 10.02,  $p =$   
 356 0.0016), and birds with more helpers also initiated reproduction earlier (LRT = 8.97,  $p = 0.0027$ ;  
 357 Table S10; Fig. 3). The effect of sociality on reproductive timing did not differ between males  
 358 and females (interaction: LRT = 1.58,  $p = 0.454$ ; ; Table S10).



359

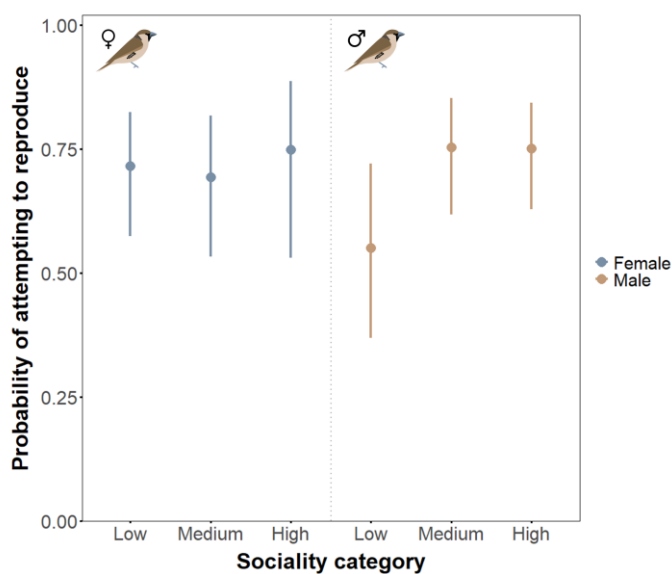
360 **Figure 3. Timing of first breeding attempt within the season in relation to individual sociality**  
 361 **and number of helpers.** A) Model predictions from the negative binomial GLMM for the number  
 362 of days between an individual's first laying date and the earliest laying date recorded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

368

369 Probability of attempting to reproduce

370 We analysed breeding probability in 443 individual–season observations. We found a tendency  
 371 for low-sociality males to show lower breeding probabilities (0.55) than medium- and high-

372 sociality males (both 0.75; Table S11; Fig. 4), although these differences were not supported by  
 373 permutation tests (Low vs Medium  $p_{\text{perm}} = 0.125$ ; Low vs High:  $p_{\text{perm}} = 0.116$ ; Table S12). In  
 374 females, all pairwise contrasts between sociality categories were non-significant (all  $p_{\text{perm}} \geq$   
 375 0.619; Table S12). There was no statistical support for a difference in the effect of sociality  
 376 between males and females (interaction: LRT = 2.55,  $p = 0.279$ ; Table S13). In contrast, age  
 377 showed a strong positive association with breeding probability, with older individuals being  
 378 more likely to attempt reproduction (LRT = 82.13,  $p < 0.001$ ; Table S13).



379

380 **Figure 4. Probability of attempting to reproduce in relation to individual sociality.**

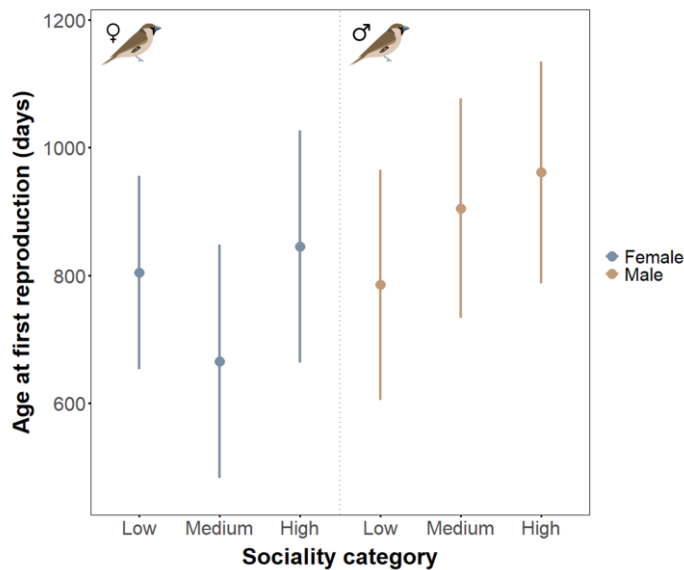
381 Model predictions (binomial GLMM) for the probability of attempting reproduction for females  
 382 (blue) and males (brown) across sociality categories. Points represent estimated means and  
 383 vertical bars their 95% confidence intervals.

384

#### 385 Age at first reproduction attempt

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

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



394

395 **Figure 5. Age at first reproduction in relation to individual sociality.** Model predictions  
 396 (Gaussian GLMM) for age at first reproduction (days since hatching) for females (blue) and males  
 397 (brown) across sociality categories. Points represent estimated means and vertical bars their  
 398 95% confidence intervals.

399

#### 400 **DISCUSSION**

401 Our results suggest that individual sociality, beyond the number of helpers at the nest, is  
 402 associated with multiple components of reproductive success in sociable weavers, although  
 403 support varied across traits and between the sexes. At the offspring level, chicks raised by high-  
 404 sociality breeding females tended to show higher fledging success than those raised by medium-  
 405 and low-sociality females, although support for this pattern was only marginal. For breeding

406 males, fledglings raised by medium- and high-sociality fathers were heavier than those raised by  
407 low-sociality fathers, and males with higher sociality also tended to show a higher probability of  
408 attempting reproduction, although this latter pattern did not reach statistical significance. In  
409 contrast, high-sociality males initiated reproduction later in life than low-sociality males.  
410 Together, these patterns reveal sex-specific effects and a potential male-specific life-history  
411 trade-off, whereby high-sociality males delay reproductive onset while producing heavier  
412 fledglings and tending to show higher breeding probability.

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

429 We also found that helper number was consistently associated with reproductive performance  
430 and breeding timing, in line with previous work in sociable weavers [4,21,50] and other

431 cooperative breeders (e.g., [51]). A higher number of helpers increased fledging probability and  
432 was positively associated with fledging mass, which is consistent with evidence that helpers can  
433 increase provisioning and reduce parental workload during chick rearing [21,52]. In addition,  
434 individuals breeding in groups with more helpers initiated reproduction earlier in the season, a  
435 pattern also reported in other cooperative species [53,54] and potentially explained by reduced  
436 costs of breeding initiation [5].

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

450 While future work on the formation and maintenance of strong bonds will be needed to test  
451 these sex differences explicitly, several non-exclusive mechanisms could help explain the  
452 positive association between sociality and reproductive performance observed here. First,  
453 individuals with a higher number of strong bonds may benefit from enhanced information  
454 sharing within the colony [2]. Sociable weavers forage predominantly on the ground, typically in  
455 cohesive colony groups [20,27] and, during breeding, also in smaller groups foraging closer to

456 the colony (Covas & Doutrelant, pers. obs.). Under these conditions, a higher number of strong  
457 bonds may facilitate information sharing within the colony [2], potentially improving access to  
458 socially acquired information about novel food patches, such as termite emergences, an  
459 important food source in this species [55]. Similar links between social associations and the  
460 discovery of novel food patches have been shown in other wild songbirds [56]. Higher sociality  
461 may also increase social tolerance and reduce contest competition during foraging [2,6], leading  
462 to fewer antagonistic interactions and potentially more efficient resource acquisition and chick  
463 provisioning. During the pre-breeding period, particularly in winter, sociality may further  
464 influence energetic state through communal roosting. In sociable weavers, roosting together  
465 reduces thermoregulatory costs, especially during cold nights [23]. Individuals maintaining more  
466 strong bonds may therefore experience improved energetic condition prior to reproduction,  
467 either because they gain more consistent access to communal roosting chambers or because  
468 they roost in larger groups, with potential carry-over effects on subsequent reproductive  
469 allocation and performance.

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

479 We found no evidence that individual sociality influenced breeding timing within the season. In  
480 arid and semi-arid environments, breeding is often opportunistic, closely tied to fluctuating

481 resource availability [61] and highly variable in timing and length [62], which may limit the extent  
482 to which broader patterns of sociality influence seasonal reproductive timing. Instead, in this  
483 species, aligning reproduction with favourable breeding conditions may be more important. This  
484 may depend more strongly on breeder experience, which could explain why breeding timing  
485 was more closely associated with age, with older individuals initiating reproduction earlier, and  
486 with helper number. Advances in laying date with age are well documented in birds and are  
487 often attributed to increased breeding experience or improvements in individual performance,  
488 in line with maturation and learning hypotheses [63,64]. In sociable weavers specifically, longer  
489 pair-bond duration is also associated with earlier breeding [39], suggesting that the age effect  
490 detected here may partly reflect accumulated pair experience and partner familiarity.

491 We also detected a tendency for medium- and high-sociality males to show higher breeding  
492 probabilities, although this pattern did not reach significance in permutation tests and should  
493 therefore be interpreted with caution. Nonetheless, sociality may capture additional aspects of  
494 a male's social position within the colony that influence access to reproductive opportunities. A  
495 relatively greater number of strong bonds may increase exposure to reproductive cues from  
496 conspecifics and facilitate breeding activation when conditions are favourable [65,66]. It may  
497 also be associated with greater social tolerance and reduced conflict, potentially improving  
498 access to resources prior to the breeding season and helping meet the energetic demands  
499 associated with initiating reproduction [67]. At the same time, age remained a strong predictor  
500 of breeding probability: older individuals were significantly more likely to attempt reproduction,  
501 a pattern consistent with delayed entry into breeding roles typical of cooperative systems  
502 [68,69].

503 Finally, we found that age at first reproduction varied with sociality in males but not in females,  
504 with high-sociality males initiating reproduction approximately six months later than their low-  
505 sociality counterparts (roughly 26 vs 32 months). Although maximum recorded longevity in this

506 species exceeds 15 years [70], average adult survival is approximately 0.66 [71], corresponding  
507 to an expected adult lifespan of roughly three years under constant survival. A six-month delay  
508 therefore represents a substantial fraction of expected adult life and likely constitutes a  
509 biologically meaningful shift in reproductive timing. This male-specific pattern is also consistent  
510 with the life-history structure of sociable weavers, where males are predominantly philopatric  
511 and typically remain in their natal colony as helpers before breeding [72]. In this species, as in  
512 other cooperative breeders, breeding reflects a trade-off between current reproductive benefits  
513 and the advantages of remaining in a non-breeding role, a balance that is sensitive to ecological  
514 conditions [67,73]. Within this framework, higher sociality may shift this balance—either by  
515 increasing the relative benefits of delayed breeding and helping close relatives, or by reinforcing  
516 socially mediated constraints on access to reproduction—thereby delaying reproductive onset.  
517 If strong bonds are predominantly formed among philopatric males, higher sociality may also  
518 increase exposure to intra-sexual competition and socially mediated constraints on breeding  
519 positions on the one hand (e.g. [74]), but offer increased possibilities of helping close kin or close  
520 social partners on the other, which would lead to increased inclusive fitness [75] or possibilities  
521 of being reciprocated in the future [76].

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

532 [77,78]. In a densely connected colonial system such as that of sociable weavers, however, social  
533 positioning may not only reflect intrinsic traits but also influence access to information,  
534 tolerance during foraging, and energetic condition prior to reproduction. Under such conditions,  
535 social bonds could shape fitness trajectories through both direct and indirect pathways.  
536 Disentangling these alternatives will require experimental approaches. Manipulating social  
537 opportunities—for example by structuring feeding associations using automated feeders  
538 [79,80]—would provide stronger inference about whether social connectivity itself affects  
539 reproductive performance or instead covaries with underlying individual traits.

540 Taken together, these results suggest that cooperative breeding systems should not be  
541 understood solely through helping effort or breeding-group composition. Instead, cooperative  
542 breeders are likely embedded within multi-layered social structures [28,81] in which individual-  
543 level social network attributes can shape breeding opportunities and reproductive outcomes  
544 [82]. Incorporating social network metrics alongside helper number may therefore provide a  
545 more complete framework for understanding reproductive dynamics in cooperative societies.  
546 These findings align with growing comparative evidence that sociality predicts survival and  
547 reproductive success across taxa (e.g. [83]). Moreover, the marked sex differences observed  
548 here further highlight the importance of considering dispersal strategies and social structure  
549 when examining fitness consequences of social behaviour [84].

550 Finally, our results combined with earlier evidence that high- and medium-sociality sociable  
551 weavers show higher survival [26], suggest that individual sociality in males, while overall  
552 beneficial, may also be linked to life-history trade-offs [85,86] rather than to uniformly positive  
553 or negative fitness effects [2]. High-sociality males have higher survival and later onset of  
554 reproduction, but performed better in terms of reproductive output. Conversely, less social  
555 males reproduced earlier, which may partly compensate for reduced performance and survival  
556 later in life [86]. This pattern is consistent with the idea that alternative life-history trajectories

557 may be shaped by social conditions, which may favour different patterns of allocation between  
558 reproduction and survival. Individual sociality in sociable weavers is moderately repeatable [26],  
559 and this temporal stability, together with the contrasting associations between sociality and  
560 different fitness components observed here, aligns with the social niche specialization  
561 hypothesis [87], whereby persistent individual differences can be maintained when alternative  
562 levels of sociality are linked to distinct life-history strategies. In this context, repeatability  
563 suggests that variation in sociality may be stable enough for different social trajectories to  
564 become associated with distinct life-history strategies. Further work encompassing lifetime  
565 reproductive success is required to further investigate this fascinating possibility.

566

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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	
2022	11	Medium	7	8	28
		High	9	19	
		Low	0	1	
2022	11	Medium	2	5	28
		High	6	11	
		Low	0	1	

	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 ( $p_{perm}$ ) 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 =  $1.95 \times 10^{-9}$ ), paternal identity ( $1.91 \times 10^{-9}$ ), colony ( $2.25 \times 10^{-12}$ ), and season ( $3.03 \times 10^{-12}$ ). 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
<b>Mother</b>	Low	27.67	26.28-29.05
<b>Mother</b>	Medium	27.01	25.26-28.75
<b>Mother</b>	High	26.92	25.09-28.75
<b>Father</b>	Low	25.44	23.36-27.52
<b>Father</b>	Medium	28.18	26.70-29.66
<b>Father</b>	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 <sub>perm</sub>
<b>Mother</b>	Low vs Medium	0.66	0.78	0.388
<b>Mother</b>	Low vs High	0.75	0.71	0.451
<b>Mother</b>	Medium vs High	0.08	0.07	0.942
<b>Father</b>	Low vs Medium	-2.74	-2.30	0.014
<b>Father</b>	Low vs High	-2.53	-2.26	0.016
<b>Father</b>	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 ( $1.012 \times 10^{-9}$ ), 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
<b>Intercept</b>	25.997	0.868	29.942
<b>Father Medium</b>	2.742	1.039	2.639
<b>Father High</b>	2.535	0.932	2.720
<b>Mother Medium</b>	-0.660	0.729	-0.906
<b>Mother High</b>	-0.745	0.827	-0.901
<b>Father age (scaled)</b>	-0.360	0.350	-1.029
<b>Mother age (scaled)</b>	0.064	0.409	0.157
<b>Number of helpers (scaled)</b>	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 <sub>perm</sub>
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 <sub>perm</sub>
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 =  $1.42 \times 10^{-10}$ ), individual identity (0.956), and season ( $6.13 \times 10^{-10}$ ). 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 <sub>perm</sub>
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