1  **Season-specific carry-over of early-life associations in a monogamous bird**

2  **species**

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25

26 **Abstract**

27   Social relationships can have important fitness consequences. Although there is increasing

28   evidence that social relationships carry over across contexts, few studies have investigated

29   whether relationships formed early in life are carried over to adulthood. For example,

30   juveniles of monogamous species go through a major life-history stage transition—pair

31   formation—during which the pair bond becomes a central unit of the social organization. At

32   present, it remains unclear if pair members retain their early-life relationships after pair

33   formation. We investigated whether same-sex associations formed early in life carry over into

34   adulthood and whether carry-over was dependent on season, in a monogamous species.

35   Moreover, we investigated the role of familiarity, genetic relatedness and aggression on the

36   perseverance of social associations. We studied the social structure before and after pair

37   formation in captive barnacle geese (*Branta leucopsis*), a highly social, long-lived,

38   monogamous species. We constructed association networks of groups of geese before pair

39   formation, during the subsequent breeding season, and in the following wintering season.

40   Next, we studied how these associations carried over during seasonal changes. We found that

41   early-life associations in females were lost during the breeding season, but resurfaced during

42   the subsequent wintering season. In males, the early-life associations persisted across both

43   seasons. Association persistence was not mediated by genetic relatedness or familiarity. The

44   high level of aggressiveness of males, but not females, in the breeding season suggests that

45   males may have played a key role in shaping both their own social environment and that of

46   their partners. We show that early-life social relationships can be maintained well into later

47   life. Such relationships can be sustained even if they are temporarily disrupted, for example

48   due to reproductive behaviour. Our findings therefore highlight that the early-life social

49   environment can have life-long consequences on individuals' social environment.

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51    **Key-words**: aggression, early life, familiarity, genetic relatedness, monogamous, pair

52    formation, social relationships, social associations

53

## Introduction

The adaptive nature of sociality is a long-standing topic in ecology and evolution (Alexander, 1974; Krause & Ruxton, 2002), particularly the potential costs and benefits of maintaining stable social relationships. Repeated social interactions between the same individuals have, for example, been linked to faster predator-evasion responses, increased foraging success (Carter et al., 2009; Griffiths et al., 2004), and can, ultimately, affect fitness (Beletsky & Orians, 1989; Cameron et al., 2009; Kohn, 2017; Silk, 2007; Silk et al., 2009, 2010).

There is increasing evidence showing that social relationships carry over across time, place, and context. Shizuka et al. (2014) showed that golden-crowned sparrows (*Zonotrichia atricapilla*) that flocked together in one winter flocked together in the subsequent winter more often than expected based on the degree of home range overlap. Roosting associations in Bechstein's bats (*Myotis bechsteinii*) and Natterer's bats (*Myotis nattereri*) were found to remain stable across several years despite high fission-fusion dynamics (Kerth et al., 2011; Zeus et al., 2018). Stanley et al. (2018) revealed that, despite seasonal fluctuations in gregariousness and overall weak social associations, semi-feral ponies (*Equus caballus*) maintained stable association preferences over three years. Finally, Firth and Sheldon (2016) showed that great tits' (*Parus major*) winter social associations carried over into their subsequent breeding season, as individuals bred nearer to those they were most associated with during winter. Despite evidence that social associations between individuals can persist across time and context, it is still largely unknown when these relationships are formed in the first place.

Experiences in early life are known to regularly carry over to adulthood, influencing survival and reproductive performance (Lindström, 1999). Early-life social conditions are generally known to have long-lasting effects (Langenhof & Komdeur, 2018; Leris & Reader, 2016; Stanton & Mann, 2012; Szipl et al., 2019). Despite the likely significance of the early-

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79    life period for the formation of social relationships, only a few studies have tracked the social

80    associations of the same individuals from their early life into adulthood (e.g., Carter et al.,

81    2013; Linklater & Cameron, 2009; Mitani, 2009), and almost exclusively in mammals (but

82    see Frigerio et al., 2001 for long-term associations between female siblings in geese). As they

83    mature, individuals of many taxa go through major life-history transitions, such as dispersal

84    (Blumstein et al., 2009; Linklater & Cameron, 2009) and pair formation (Kurvers et al.,

85    2013). These transitions will strongly impact the structure of an individual's social

86    environment, but perturbations in the social environment do not necessarily impact the

87    stability of already-established relationships (e.g., Kerth et al., 2011). It remains an open

88    question if a life-history transition such as pair formation will cause preferred associations

89    formed in early life to disappear or whether these may persist into adulthood.

90          Here, we examined the social structure of barnacle geese, a highly social species,

91    before and after pair formation, in order to study the persistence (or disappearance) of early-

92    life same-sex associations after a major life-history transition: pair formation. Barnacle geese

93    are long-lived monogamous birds, which generally find a partner at 2–3 years of age

94    (Choudhury & Black, 1994). Barnacle geese are very selective in choosing a mate; they

95    sample one to six potential mates in so-called "trial liaisons" before settling with a permanent

96    partner (Choudhury & Black, 1993; van der Jeugd & Blaakmeer, 2001). The pair bond is

97    extremely strong and pair members generally stay in close proximity to each other and remain

98    together until one of them dies (Black, 2001; Owen et al., 1988). Pairs with a longer pair bond

99    show higher reproductive success than pairs with a shorter pair bond (Black, 2001). Pair

100    formation is thus a crucial step in the life history of geese. Here we took advantage of

101    controlled experiments to study how pair formation impacted same-sex foraging associations

102    formed early in life, allowing us to circumvent problems with missing individuals in

103    naturalistic data. We followed a captive population of barnacle geese over several years,

104    quantifying the dyadic association strength between individual geese before and after pair

105   formation. To study mediating factors underlying the potential persistence of these dyadic

106   associations, we furthermore quantified the degree of familiarity and genetic relatedness in

107   the population, as well as individuals' aggressive interactions. We focused on the persistence

108   of same-sex associations because, in comparison to inter-sex associations, these relationships

109   are less well studied in monogamous social species, but may have important adaptive

110   benefits, for example stress-reduction (Sachser et al., 1998), especially in competitive

111   contexts such as foraging.

112       In the wild, barnacle geese, like many migratory waterfowl, show a high site fidelity

113   to their breeding, wintering and staging areas (Percival, 1991; Robertson & Cooke, 1999),

114   creating opportunities for long-term maintenance of social relationships established early in

115   life. Both sexes show natal philopatry, though females have substantially higher levels of

116   natal philopatry than males (van der Jeugd, 2001; van der Jeugd et al., 2002). The extent to

117   which individuals maintain non-sexual relationships across seasons is not well understood,

118   partly because of the challenges of following individuals across space and time. van der Jeugd

119   et al. (2002) showed that during breeding, female, but not male, barnacle geese nested closer

120   to siblings than expected by chance. This occurred not only when the female siblings bred in

121   the same island as their parents, but also when they nested on a different island. Moreover,

122   this relationship was only observed for siblings hatched in the same year. Similar sex-specific

123   patterns have been observed in terms of resting proximity in semi-feral greylag geese, *Anser*

124   *anser,* in winter (Frigerio et al., 2001). Given these observations and females being the more

125   philopatric sex, we predicted that females would show a higher likelihood of maintaining their

126   early-life relationships than males after mating.

127       We constructed association matrices from foraging observations collected during the

128   breeding and wintering seasons. Geese are generally more gregarious during the wintering

129   season (Black et al., 2014; Szipl et al., 2019), while being more aggressive and territorial

130   during the breeding season (Owen & Wells, 1979). We, therefore, predicted that associations

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131  with early-life companions after pair formation would be stronger in the wintering than the

132  breeding season. Finally, based on the expected direct and indirect adaptive benefits of

133  associating with kin, for example by providing and receiving social support (Black & Owen,

134  1989; Raveling et al., 2000; Scheiber et al., 2009; Scheiber et al., 2005), we predicted that

135  genetic relatedness would positively impact the strength of the associations. Similarly, based

136  on the expected benefits of reduced aggression between familiar individuals (i.e. "dear enemy

137  effect"; van der Jeugd, 2001; Ydenberg et al., 1988), we predicted that long-term familiarity

138  would positively influence dyadic foraging association strength.

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140


141  **Methods**

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143  **Study subjects**

144  In late 2007 we obtained two mixed-sex groups of barnacle geese (see Fig. 1 for study

145  timeline, and Kurvers et al., 2013 for more details). The two groups consisted of 21 (13

146  female, 8 male) and 23 individuals (8 female, 15 male) respectively. The groups were housed

147  in separate outdoor aviaries (12 x 15 m) at the Netherlands Institute of Ecology (NIOO) in

148  Heteren, the Netherlands. Groups were visually, but not acoustically, isolated from each

149  other. The aviaries consisted of bare soil with a large pond (6 x 1 m) with running water for

150  drinking and bathing. Birds received ad libitum food consisting of a mixture of grains and

151  pellets occasionally supplemented with grass. Most individuals (40 of 44) were hatched in

152  2007 and were thus approximately 5 months old upon arrival. All birds were captive-hatched,

153  wing-clipped and (upon arrival) fitted with uniquely coded white leg rings for identification.

154  Birds from the two groups had different origins, implying that birds within (but not between)

155  groups could have a high genetic relatedness (see below). Birds within a group will

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156    henceforth be referred to as "familiar" individuals, and birds between groups as "unfamiliar".

157    Geese lived for approximately 1.5 years in these familiarity groups before the start of the

158    social network observations (see below).

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160    **Genetic relatedness**

161    We determined the genetic relatedness between each pair of individuals using a high-

162    resolution 374 single nucleotide polymorphism (SNP) marker set, developed for the barnacle

163    goose (Jonker et al., 2012). We took a small blood sample (± 1 ml) from each individual from

164    the brachial vein and preserved it in ethanol. Entire genomic DNA was isolated using the

165    Gentra Systems Puregene DNA purification kit. Genotyping was conducted with Vera Code

166    assays on an Illumina BeadXpress (described in Kraus et al., 2011). We calculated the

167    pairwise genetic relatedness ($r$) using the program Coancestry (version 1, Wang, 2011). To

168    determine which relatedness estimator best fitted our data, we used the empirical SNP allele

169    frequencies of our population and simulated 500 dyads of geese of varying relatedness

170    coefficients. Meeting real conditions as closely as possible, we simulated mainly unrelated

171    dyads ($N = 430$) but also dyads of close familial relationships, namely 30 full sibs dyads ($r = $

172    0.5), 10 half sibs dyads ($r = 0.25$), and 30 first cousins dyads ($r = 0.125$). Based on this

173    simulation, we found that the maximum-likelihood estimator of Milligan (2003) performed

174    best and used it for the final estimation of $r$. This produced a strong correlation with expected

175    values of $r$ ($r^2 = 0.9$; analysis of the simulated data set carried out with default settings).

176    Subsequently, all pairwise relatedness values of the experimental geese were obtained from

177    Coancestry with standard settings (see Kurvers et al., 2013 for more details).

178

179    **Observations prior to pair formation: early life**

180    After living for approximately 1.5 years in their respective familiarity groups—and prior to

181    any pair formation—we separated all geese into two single-sex groups (June 2009; Fig. 1) to

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182  study the factors shaping intra-sexual social association preferences while avoiding additional

183  'noise' caused by inter-sexual trial-liaisons (van der Jeugd & Blaakmeer, 2001). Moreover, by

184  separating individuals in single-sex groups, we could control the timing of pair formation and

185  keep this comparable and tractable for all subjects. Geese were sexed by visual inspection of

186  sexual organs in the cloaca. The sex of one individual could not be reliably determined at this

187  time. This individual was not included in the early-life observations, but joined the flock after

188  these observations finished. This individual was excluded from all analyses. Association

189  observations were conducted in the home aviaries during foraging. These foraging

190  associations were studied on five grass patches (40 x 20 cm, 1.5m apart) which were replaced

191  twice a day to avoid depletion. Other food sources were removed during the observations.

192      Each single-sex group was observed (9 a.m.–1 p.m.) for 15 days (females: 22 June–12

193  July 2009; males: 13–30 July 2009). The presence of all individuals on the patches was

194  recorded every 4 minutes. This interval was longer than the mixing time among individuals

195  (i.e., the time individuals need to exchange who they are association with), in order to ensure

196  independence of observations (Croft et al., 2008). Associations at feeding patches was rarely

197  the same in consecutive records (females: 5.9%; males: 7.9%). Observations were

198  occasionally interrupted for 10 minutes in the event of an external disturbance. Since patch

199  size (40 x 20 cm) and group size (mean females = 1.9, range 1–5; mean males = 2.0, range 1–

200  5; Fig. A1a, b) were small, we assumed that animals grazing on the same patch during a

201  sampling period were associating (a.k.a. gambit of the group, Franks et al., 2010; Whitehead,

202  2008).

203      The results of the foraging associations before pair formation are reported in Kurvers

204  et al. (2013). In brief, in both sexes, familiarity and genetic relatedness predicted association

205  strength, whereas boldness and dominance did not. Therefore, we focus here on the role of

206  familiarity and genetic relatedness in governing the stability of long-term associations.

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**Observations after pair formation: breeding and wintering**

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209 Geese remained in the single-sex groups for six months and were then placed together in one

210 group (January 2010; Fig. 1). By then, most geese were 2.5 years of age, approximating the

211 average age of final pair formation in barnacle geese (Choudhury & Black, 1994; van der

212 Jeugd & Blaakmeer, 2001). Pair formation started rapidly, and most geese quickly formed a

213 stable pair bond. Before starting the first post-pair formation association observations, 37 (of

214 44) geese had formed stable pair bonds. In total, geese formed 12 pairs (11 male-female pairs,

215 and one male-male pair), four triplets (three geese continuously moving together as one unit

216 without any aggression; two triplets consisted of two females and one male, and two triplets

217 of one female and two males) and seven geese (3 males, 4 females) remained unpaired. The

218 occurrence of triplets has also been observed in the wild, with a third party joining a pair

219 between 10 months and 4 years, however incidence in the field was lower (Black et al., 1996).

220 As reported in Kurvers et al. (2013) genetic relatedness did not play a role in mate choice,

221 whereas geese actively selected against familiarity in selecting a mate. After the geese formed

222 pair relationships, and during their first breeding season, we again conducted observations of

223 foraging associations. We placed 10 grass patches (40 x 40 cm) in the aviary. Observations

224 were conducted for five weeks (31 May–2 July 2010, 25 observation days) in two 2-hour

225 blocks per day (8 a.m.–1 p.m.) following the same observation protocol described above.

226 During the breeding season, many of the paired individuals started building nests and laying

227 eggs. We regularly checked all nests and removed any eggs to avoid the hatching of goslings.

228 To study the stability of associations across seasons, we repeated the observations of

229 foraging associations six months later, during the wintering season, following the same

230 protocol (17 December 2010–4 February 2011, 13 observation days). Comparing the pair

231 status of all geese between the breeding and wintering seasons, we observed that all pair

232 relationships but one remained the same—the one pair relationship that changed was the

233 male-male pair. This reflects the strong and long lasting pair bonds in barnacle geese, which

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234 generally stay together until one of the pair members dies (Black, 2001). One individual died

235 in between the breeding and wintering observations. To facilitate comparison across seasons,

236 we removed this individual from all analyses. The final sample size was thus 42 individuals

237 (20 females, 22 males).

238

239 **Agonistic interactions**

240 During all three observation periods (early life, breeding, wintering), we collected data on

241 agonistic interactions to study the role of aggression on the stability of early-life associations.

242 In between scoring the presence of individuals on the patches, we scored the winner and loser

243 of agonistic interactions, defined as a direct confrontation between two geese and ranging

244 from threats with lowered head and neck to active chases with flapping wings. In the early-

245 life observations, we identified a total of 1,429 interactions in the female group and 2,619

246 interactions in the male group. We then identified 3,411 and 786 interactions during the

247 subsequent breeding and wintering periods, respectively.

248

249 **Statistical analyses**

250

251 *Stability of early-life connections*

252 We used social network analysis to investigate carry-over effects of dyadic associations

253 between seasons. Within the networks, nodes represent individuals and are connected by

254 edges that represent associations. The edge weight varied with dyadic association strength.

255 From the observation data, we thus generated undirected weighted networks (i.e., networks

256 based on associations without initiators or receivers) for each of the three periods (early life,

257 breeding season, and wintering season). Edge weights in the networks were calculated using

258 the simple ratio index (SRI) as an association measure using the 'asnipe' package (Farine,

259 2013) in R (v. 3.4.4). The SRI indicates the probability of observing two individuals in

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260    association with each other given that one was observed. Values range from 0 (two

261    individuals were never observed together) to 1 (two individuals were always observed

262    together). The SRI is considered an effective measure of dyadic association strength provided

263    there are no large sampling biases (Farine & Whitehead, 2015; Ginsberg & Young, 1992;

264    Hoppitt & Farine, 2018). Since all observations were performed within aviaries in which all

265    individuals feeding on all patches could be easily observed, we did not expect a strong

266    sampling bias.

267        We first analysed whether early-life associations (within the same sex) were

268    maintained after pair formation, i.e. during the subsequent breeding and wintering season.

269    Within each sex, we performed Mantel tests using the built-in node permutation test from the

270    'vegan' library Mantel test function—running 50,000 permutations and using the spearman

271    correlation (Oksanen et al., 2019)—to compare dyads' association strength between (i) early

272    life and breeding season, and (ii) early life and wintering season. We started with a separate

273    matrix for each sex for the early-life associations, one matrix (containing both sexes) for the

274    breeding season, and one matrix for the wintering season. To compare the matrix correlation

275    for females (/males), we therefore first subset all females (/males) from the breeding and

276    wintering matrix, constructing single-sex matrices. To confirm that our results were not

277    mainly driven by the associations of the unpaired individuals (as we were primarily interested

278    in the possible continuation of associations after pair formation), we repeated these analyses

279    after further excluding associations between the unpaired individuals. To investigate if our

280    results were driven by a few strong associations, we also repeated this analysis while

281    excluding all associations with an SRI value higher than 0.1.

282

283    ***Genetic relatedness and familiarity***

284    To investigate which factors might underlie a possible continuation of associations after pair

285    formation, we studied the effect of genetic relatedness and familiarity on dyadic association

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286    strength during the breeding and wintering season. We tested the effect of familiarity and

287    relatedness using multiple regression quadratic assignment procedures (MRQAP; Krackhardt,

288    1988) using the mrqap.dsp function in the R package asnipe (Farine, 2013). With this

289    procedure, the association matrix was first regressed against two matrices, one with data on

290    relatedness and one on familiarity.  We used a version of the function allowing us to combine

291    the mrqap.dsp model with pre-network permutations (Farine, 2017). Specifically, we

292    generated 1,000 random networks by re-organising the observations of individuals in the

293    original group-by-individual matrices following the method first described by Bejder et al.

294    (1998). We then compared the resulting distribution of coefficient values from these permuted

295    networks to the coefficient value generated from the original observation data to obtain *P*-

296    values. Further, because our random distributions were not centred on 0 (see Farine, 2017),

297    we rescaled measures to an effect size by taking the difference between the observed

298    coefficient values and the mean of the corresponding distribution of coefficient values based

299    on the permutated networks. We performed the MRQAP separately for each season and sex.

300

301    *Patch visits and aggression*

302    As we found sex differences in the continuation of early-life associations (see below), we

303    investigated the role of patch visitation rates and aggression as potential underlying

304    mechanisms. For each individual, for each period, we calculated the mean number of patch

305    visits per hour. We then used a Mann-Whitney U test to determine whether the sexes differed

306    in their patch visitation rates in each of the three seasons. Similarly, for each individual and

307    for each season, we determined the mean number of aggressive interactions initiated per hour,

308    and tested whether the sexes differed in their likelihood to display aggression in each of the

309    three seasons.

310

311    **Ethical permission**

312    The animal ethical committee of both the Royal Netherlands Academy of Arts and Sciences

313    (KNAW) and the Wageningen University approved all experiments [protocol numbers:

314    2010008.b (blood sampling)]. Geese were obtained from a waterfowl breeding farm (Kooy

315    and Sons, 't Zand, the Netherlands) and returned there after the experiments had finished.

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317

318    **Results**

319

320    **Sex- and season-dependent effects of persistence of early-life associations**

321    We quantified the foraging association networks for each of the three observation periods

322    (i.e., early life, breeding season, and wintering season, see Fig. 2), and compared the strength

323    of the dyadic associations that were formed early in life to those in subsequent seasons. We

324    found that a female's dyadic association strengths from early life (i.e. prior to pair formation)

325    were not significantly correlated with its dyadic association strengths to the same pool of

326    individuals (i.e. other females) in the subsequent breeding season ($r = 0.04$; $P = 0.32$; Fig.

327    3a). A female's early-life dyadic association strengths were, however, significantly correlated

328    with its dyadic association strengths in the subsequent wintering season ($r = 0.18$; $P = 0.019$;

329    Fig. 3b). A male's early-life dyadic association strengths were significantly correlated with its

330    dyadic association strengths to other males in both the subsequent breeding ($r = 0.26$; $P = $

331    0.002; Fig. 3c) and the following wintering season ($r = 0.31$; $P = 0.002$; Fig. 3d).

332        When excluding the associations among individuals that remained unpaired (7 of 42;

333    but maintaining the associations between paired and unpaired individuals), we obtained

334    similar results (females: early life vs. breeding: $r = 0.00$, $P = 0.49$; early life vs. wintering: $r$

335    $= 0.19$, $P = 0.018$; males: early life vs. breeding: $r = 0.26$, $P = 0.003$; early life vs. wintering:

336    $r = 0.31$, $P = 0.003$).

337       When excluding all dyadic associations with an SRI value above 0.1 (which excluded

338    38 associations for females (7% of all associations) and 26 for males (5%)), we, again,

339    obtained similar results (females: early life vs. breeding: $r = 0.00$, $P = 0.52$; early life vs.

340    wintering: $r = 0.18$, $P = 0.022$; males: early life vs. breeding: $r = 0.23$, $P = 0.004$; early life

341    vs. wintering: $r = 0.34$, $P = 0.002$).

342

343    **Genetic relatedness and familiarity do not drive associations in females or males**

344    In females, there was no effect of genetic relatedness or familiarity on dyadic association

345    strength in the breeding season (effect sizes: genetic relatedness: -0.00006; familiarity:

346    0.0001) or in the wintering season (genetic relatedness: 0.0016; familiarity: 0.0001).

347    Likewise, for males, we found no effect of genetic relatedness or familiarity on dyadic

348    association strength in the breeding season (genetic relatedness: -0.00035; familiarity: -

349    0.00006) or in the wintering season (genetic relatedness: 0.0002; familiarity: -0.00026).

350    Thus, although familiarity and genetic relatedness positively impacted single-sex associations

351    in females and males in early life (see Kurvers et al., 2013 and see Fig. A2 and Fig. A3), these

352    factors did not drive same-sex associations after pair formation (all $P > 0.1$).

353

354    **Elevated aggression in males and during the breeding season**

355    We investigated two mechanisms that might drive the disappearance of social associations in

356    females—but not males—during the breeding season. First, females may simply visit the food

357    patches less than males during the breeding season, which would lower their opportunities for

358    maintaining relationships. Though females visited patches less than males in the single-sex

359    groups before pair-formation ($W = 50$, $P < 0.001$; Fig. 4a), females visited the patches equally

360    often as males in the breeding and wintering season (both $P > 0.35$; Fig. 4b, c), ruling out this

361    explanation.

362     A second mechanism might be that males, being generally the more dominant member

363     of a pair, play a stronger role in determining the association members of a pair than do

364     females, especially in the breeding season. Before pair formation, males showed a higher

365     level of aggression than females in the single-sex groups ($W = 142$, $P = 0.049$; Fig. 4d).

366     Likewise, males showed a substantially higher level of aggression than females during the

367     breeding ($W = 8$, $P < 0.001$; Fig. 4e) and wintering seasons ($W = 39$, $P < 0.001$; Fig. 4f).

368     Males displayed equal levels of aggression towards males and females in the breeding season

369     (Wilcoxon signed-rank test: $V = 76$, $P = 0.10$, Fig. 4e) but slightly higher levels of aggression

370     towards males than females in the wintering season ($V = 50$, $P = 0.02$; Fig. 4f). As expected,

371     male geese displayed higher levels of aggression in the breeding than in the wintering season

372     (Wilcoxon signed-rank test, males only: $V = 240$, $P < 0.001$; Fig. 4e, f). In accordance, the

373     mean group size at patches was higher during the wintering than during the breeding season

374     (mean group size wintering: 2.4; breeding: 2.0; Fig. A1c, d). Moreover, paired individuals

375     were more tolerant to the presence of other individuals (i.e., not belonging to the pair) at a

376     patch during wintering season. In the breeding season, in 80% of cases when pair members

377     were observed together on a patch, there were no other individuals present. In the wintering

378     season, this percentage dropped to 60% (mean number of non-pair individuals at a patch with

379     a pair during breeding: 0.26, during wintering: 0.76; Fig. A4c, d). This is also apparent in the

380     network graphs showing more edges during the wintering season (Fig. 2c, d).

381

382

383     **Discussion**

384     Maintaining stable social associations across time and contexts can have adaptive benefits

385     (Kohn, 2017). Yet the importance of the early-life period for the formation of such long-term

386     stable relationships has so far received little attention. Here we show that early-life same-sex

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387    foraging associations can persist after a major life-history transition—pair formation—in a

388    monogamous and long-lived bird species. However, which associations were maintained

389    depended on sex and season. Early-life associations in females were lost during the breeding

390    season, but resurfaced again during the subsequent wintering season. In males, the early-life

391    associations persisted across both seasons. We found no evidence of genetic relatedness or

392    familiarity on association persistence. Elevated male aggression likely influenced the limited

393    number of contacts outside of the pair bond during the breeding season—and thereby the

394    extent to which early-life associations could be maintained, especially by females during the

395    breeding season. Our findings extend the understanding of how social relationships develop

396    and are maintained over different life-history phases and how their importance to individuals

397    may vary with season.

398        Across taxa, females are well-known for maintaining long-term social relationships

399    (Cameron et al., 2009; Carter et al., 2013; Ilany et al., 2015; Silk et al., 2003), which is

400    commonly attributed to their reproductive strategies. In our study, males, not females,

401    maintained their associations throughout both the breeding and wintering season. Benefits of

402    social relationships in males have been observed in other species: male red-winged blackbirds

403    (*Agelaius phoeniceus*) that bred close to familiar neighbours fledged more offspring (Beletsky

404    & Orians, 1989) and male Assamese macaques (*Macaca assamensis*) with stronger social

405    associations sired more offspring (Schulke et al., 2010). Males can thus clearly form, and

406    benefit from, long-lasting social relationships.

407        Social relationships in males often take the form of coalitions or alliances (Connor et

408    al., 2017; Gilby et al., 2013; Schulke et al., 2010), benefiting individuals by providing

409    cooperation partners in agonistic interactions with conspecifics. But reduced aggression, for

410    instance, via dear-enemy effects (Temeles, 1994), can likewise be an important benefit of

411    maintaining long-term social relationships, especially in territorial animals (Chuang et al.,

412    2017; Jaeger, 1981; Siracusa et al., 2019). Additionally, repeated association with certain

413     individuals can influence vigilance behaviour, with individuals showing reduced vigilance in

414     the proximity of well-known conspecifics (Carter et al., 2009; Kutsukake, 2006). In a

415     monogamous prey species such as barnacle geese, in which the male spends much of its time

416     during the breeding season on vigilance at the expense of foraging (Forslund, 1993), such

417     benefits can be especially substantial. The expected benefits of maintaining long-term social

418     relationships vary with ecological and social conditions (Connor et al., 2017; Kappeler et al.,

419     2013; Maher & Burger, 2011), and studying the social structure of both sexes in taxa with

420     distinct space use (e.g., natal philopatry), life history (e.g., long life-span), social organization

421     (e.g., fission-fusion), and mating system (e.g., monogamy) characteristics, offers us greater

422     insight into the drivers and constraints of maintaining long-term stable associations in animal

423     societies.

424          The apparent lack of social association persistence for females in the breeding season

425     is surprising, but adds to our understanding of social flexibility by showing that the

426     persistence of social relationships not only varies between species and individuals (Kappeler

427     et al., 2013) but can also have sex-specific effects across seasons. Female chacma baboons

428     (*Papio hamadryas ursinus*) were similarly found to vary in their social preferences depending

429     on ecological context (Henzi et al., 2009): social preferences were more pronounced when

430     food resources were scarce, but females acted more "gregariously" (i.e., without social

431     preferences) when resources were plentiful. For geese, winter is a time when resources

432     become scarce; barnacle geese, however, are highly gregarious in winter (Black et al., 2014),

433     possibly to access social information on foraging opportunities (Drent & Swierstra, 1977;

434     Kurvers et al., 2009; Kurvers et al., 2010) (but see Kurvers et al., 2014). Alternatively, the

435     fluctuations in female social preferences may have been the result of the male partner

436     unselectively excluding his partner's—but not his own—early-life companions during the

437     breeding season. The high level of aggression displayed by the males during the breeding

438     season compared to the wintering season supports this hypothesis.

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439        The absence of continued association with early-life companions in females in the

440    breeding season appears to be in contrast to previous findings. An earlier study on wild

441    barnacle geese found that female, but not male, geese exhibited social preferences in terms of

442    nesting proximity, with females nesting closer to familiar females (van der Jeugd et al., 2002).

443    It is possible that nest choice offers female geese an alternative way to maintain early-life

444    social associations, circumventing the potentially controlling influence of their partner during

445    foraging. Possibly, breeding in proximity to familiar and/or related conspecifics provides

446    context-specific benefits that foraging together does not. Intraspecific brood parasitism and

447    adoption is common in waterfowl (Anderholm et al., 2009a; Andersson et al., 2019;

448    Choudhury et al., 1993; Forslund & Larsson, 1995) and breeding close to related individuals

449    may decrease the costs, through inclusive fitness benefits, of having to care for additional

450    offspring. Moreover, breeding in proximity could enable siblings to defend each other's nests

451    against unrelated brood parasites. Female siblings may also actively or passively support each

452    other in the acquisition of high-quality nest locations. Indeed, in geese, social support from

453    family members is known to give individuals an advantage in competitive interactions,

454    starting from an early age (Black & Owen, 1989; Raveling et al., 2000; Scheiber et al., 2009;

455    Scheiber et al., 2005). Lastly, neighbouring barnacle geese pairs are known to defend their

456    nests together (Black & Owen, 1995) and nesting closely to familiars may facilitate

457    cooperative nest defence (Grabowska-Zhang et al., 2012; Olendorf et al., 2004). Nest

458    predation is a major threat for geese (Drent & Prop, 2008) that exposes the females in

459    particular to considerable predation risk (Samelius & Alisauskas, 2006).

460        Our captive study design had several important limitations compared to natural

461    settings. First, the group size under study was relatively small compared to natural groups. In

462    natural groups, the number of genetically related and/or familiar individuals may be

463    substantially higher, allowing geese more opportunities to associate with these types of

464    individuals. Second, the space available to our subjects was reduced as compared to natural

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465    conditions. This may have led to higher levels of aggression, especially among males, and/or,

466    more and stronger associations as compared to more natural settings. Third, we removed the

467    eggs of breeding females to avoid the undesired hatching of more experimental animals. This

468    may have caused heightened aggression, and may have had repercussions for social

469    relationships. The pair bonds did, however, almost all remain intact till the next wintering

470    season, suggesting that egg removal did not cause major disruption of pair bonds.

471         Taken together, our findings suggest that different types of social associations may be

472    beneficial in different contexts and that the early-life period can be a crucial time for the

473    formation of these associations. The next step is to disentangle whether individuals actively

474    choose to (re)associate with earlier companions depending on season- and context-dependent

475    benefits, or whether the observed fluctuations in social association persistence are an

476    emergent property following relatively simple season-dependent social processes, such as

477    heightened aggression. The first scenario may have important implications for our

478    understanding of the cognitive abilities of animals. Notably, Scheiber et al. (2011) found that

479    six-week-old juvenile greylag geese can already discriminate between two of their siblings,

480    showing that individual-level recognition is already present from an early age. Our findings

481    here suggest that geese may be able to keep track of multiple types of relationships in a large

482    fission–fusion society, despite extended breaks, supporting similar observations in wild

483    barnacle geese (Black & Owen, 1995), and that they can re-evaluate the benefits of these

484    relationships depending on context. Given the strong evidence for birthplace-independent

485    long-term kin discrimination in both migrating and captive barnacle geese (Anderholm et al.,

486    2009b; Kurvers et al., 2013; van der Jeugd et al., 2002), this level of cognitive ability is

487    certainly feasible and makes the long-lived barnacle goose an interesting study system to

488    further examine such mechanisms. Complex social patterns can be driven by cognitive ability,

489    but also emerge from relatively simple processes (Kappeler, 2019), such as site fidelity

490    combined with season- and sex-dependent aggression. Unravelling how these mechanisms

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491     underlie social complexity in a diversity of social systems will be central to our understanding

492     of the evolution of animal societies.

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495     **Acknowledgements**

508

509     **Data Availability Statement**

510     The raw social association observations, the matrices containing the SRI values per sex per

511     season, the matrices containing the familiarity and genetic relatedness data per sex, and the

512     raw aggression data are uploaded on the Open Science Framework for referee inspection

513     (link). These files will be made public in case of acceptance.

514

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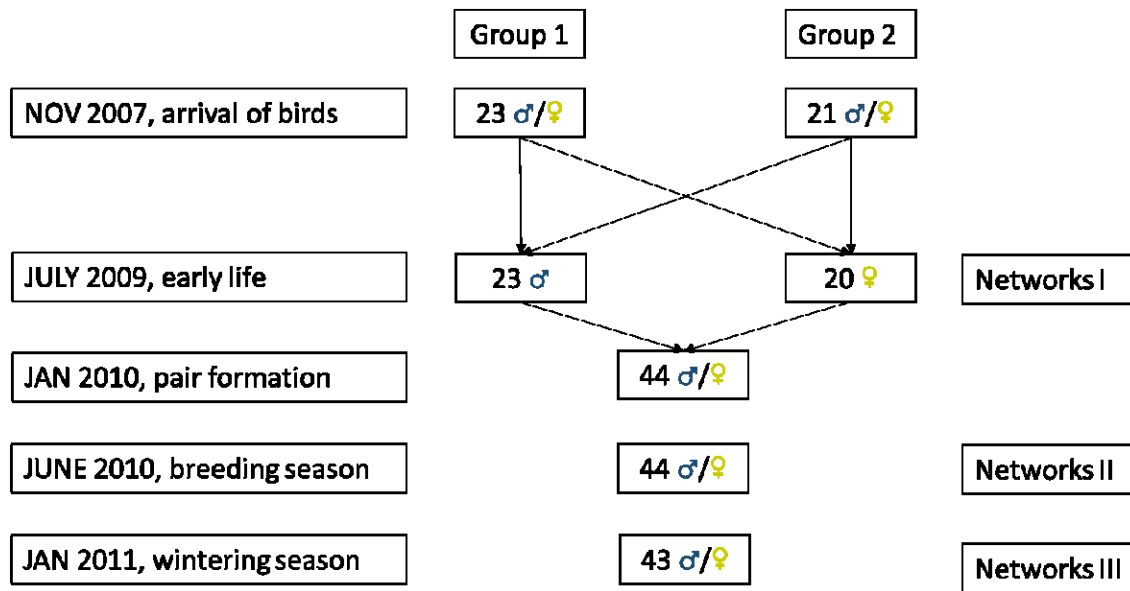
**Figure 1.** Schematic overview of the experimental procedures. Geese were procured in November 2007—at which point almost all were juveniles (hatched in 2007)—and placed in one of two familiarity groups. In July 2009, males and females of both groups were placed together and we quantified the social network structure of both groups (to examine the role of familiarity and genetic relatedness on social structure, Kurvers et al., 2013). In January 2010, all geese were placed together in one group and individuals rapidly started to form pairs. In the subsequent breeding season (June 2010) and wintering season (January 2011), we quantified the social network structure of the entire group. Note that the sex of one individual could not be reliably determined at the time of the first network observation and hence was not included in the early-life observations. Another individual died in between the breeding and wintering season. Both individuals were excluded from all analyses, resulting in a final sample size of 42 (20 females, 22 males).
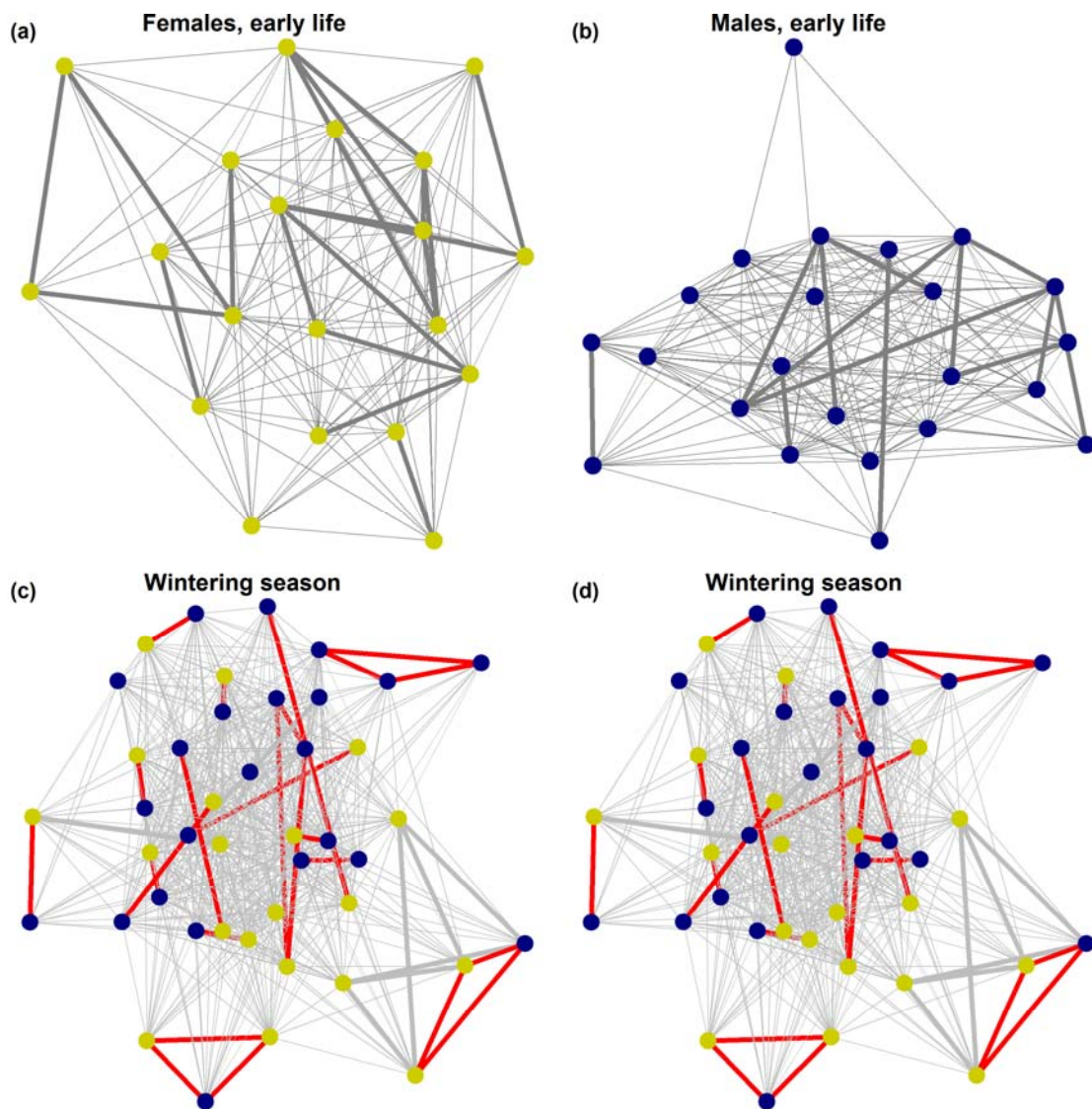
**Figure 2.** The (a) female and (b) male network in single-sex groups prior to pair formation and the network of all individuals after pair formation during the (c) breeding, and (d) wintering season. Yellow/blue circles represent females/males respectively. For visualization, we removed associations below SRI values of 0.005. Thin/thick lines represent SRI values below/above 0.1. Coloured lines indicate a pair bond. Networks were created with the ggnet2 function in R using the Fruchterman-Reingold algorithm for node placement.
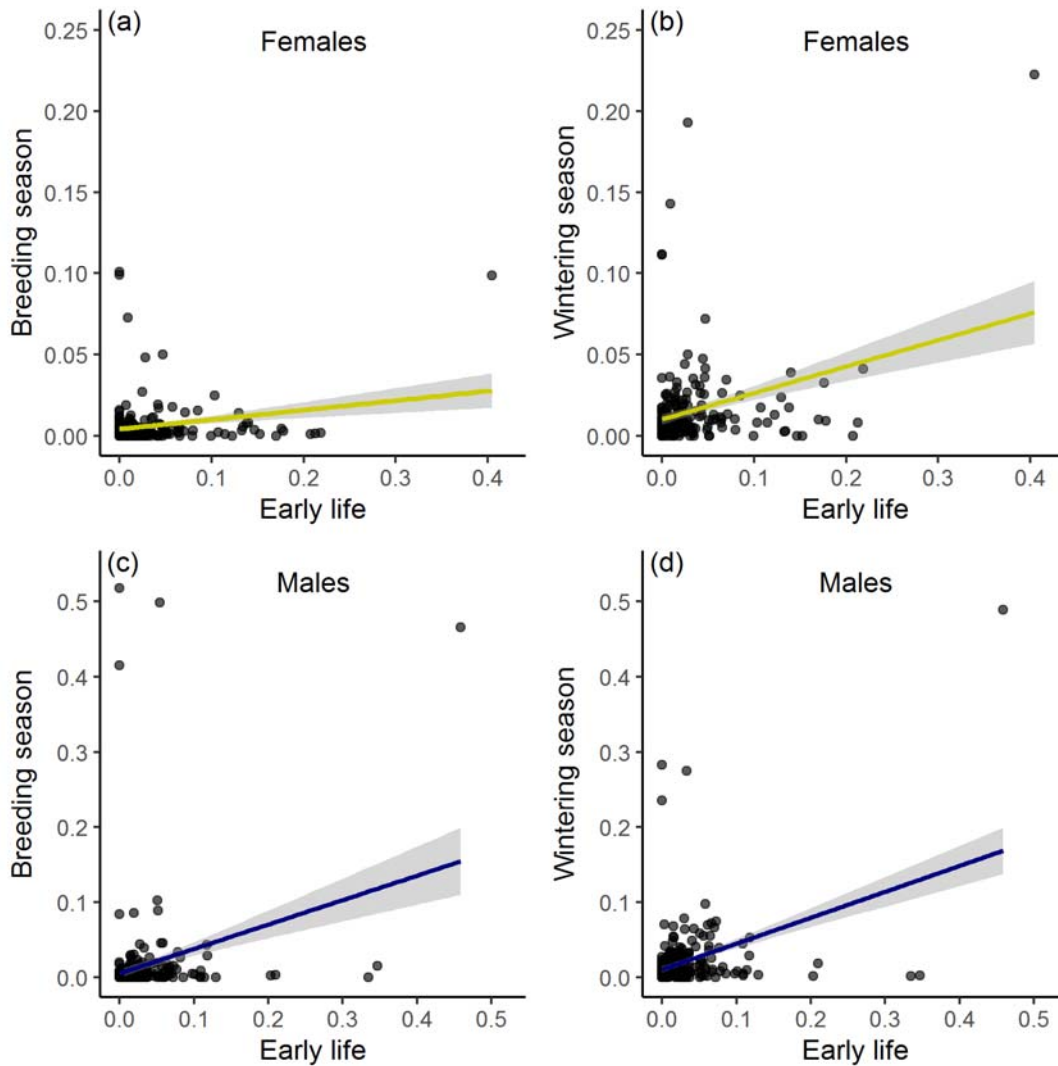
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780 **Figure 3.** The relationship between the association strength of female dyads comparing (a)

781 early life and breeding season, and (b) early life and wintering season, and the relationship

782 between the association strength of male dyads comparing (c) early life and breeding season,

783 and (d) early life and wintering season. Lines are linear regression lines, including 95%

784 confidence bands.

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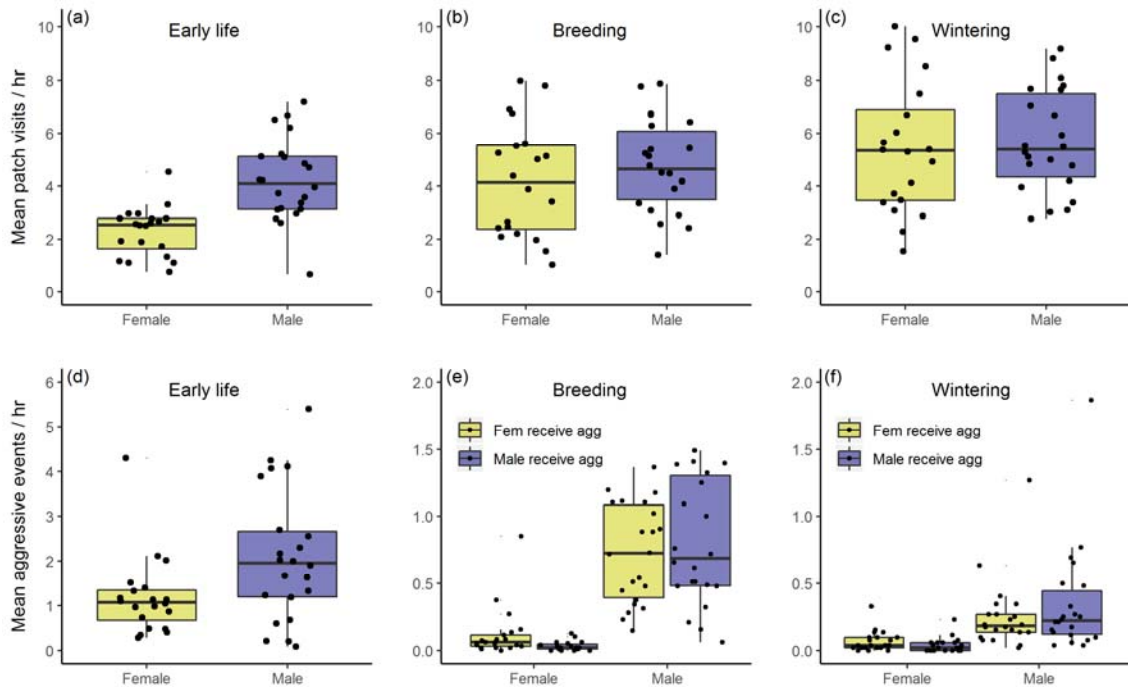
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787    **Figure 4.** The mean number of patches visited per hour for (a) females and males in the

788    single-sex groups prior to pair formation, and for both sexes during the (b) breeding and (c)

789    wintering seasons after pair formation. The mean number of aggressive events initiated per

790    hour for (d) females and males in the single-sex groups prior to pair formation, and for both

791    sexes during the (e) breeding and (f) wintering season after pair formation. (e, f) Colours

792    indicate the sex of the individual receiving the aggression. Dots represent individuals.

793    Boxplots show median, interquartile ranges and whiskers show the lowest/highest values

794    within the 1.5 interquartile range.

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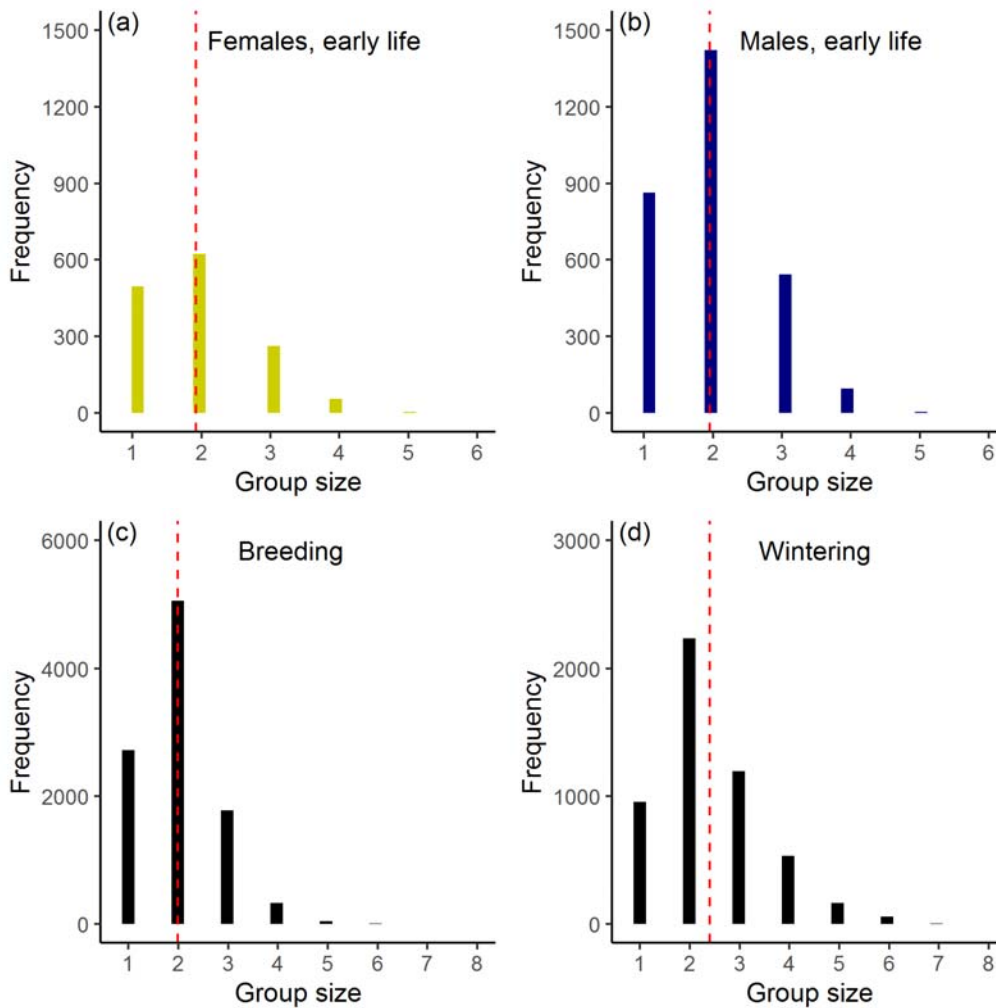
**Figure A1.** (a, b) The frequency of observed group sizes during the early-life social network observations for (a) females and (b) males. Red dashed lines represent mean group size (mean group size females: 1.92; males: 1.96). Males frequented patches at a higher rate (see also Fig. 4a). (c, d) The frequency of observed group sizes during the (c) breeding and (d) wintering season. Red dashed lines represent mean group size (mean group size breeding: 2.0; wintering: 2.4). Note that the overall higher frequency of group sizes in the breeding season is due to more observation days during breeding ($N = 25$ days) than during wintering season ($N = 13$ days). The mean patch visit rate was in fact slightly higher in wintering than in breeding season (see Fig. 4b, c).
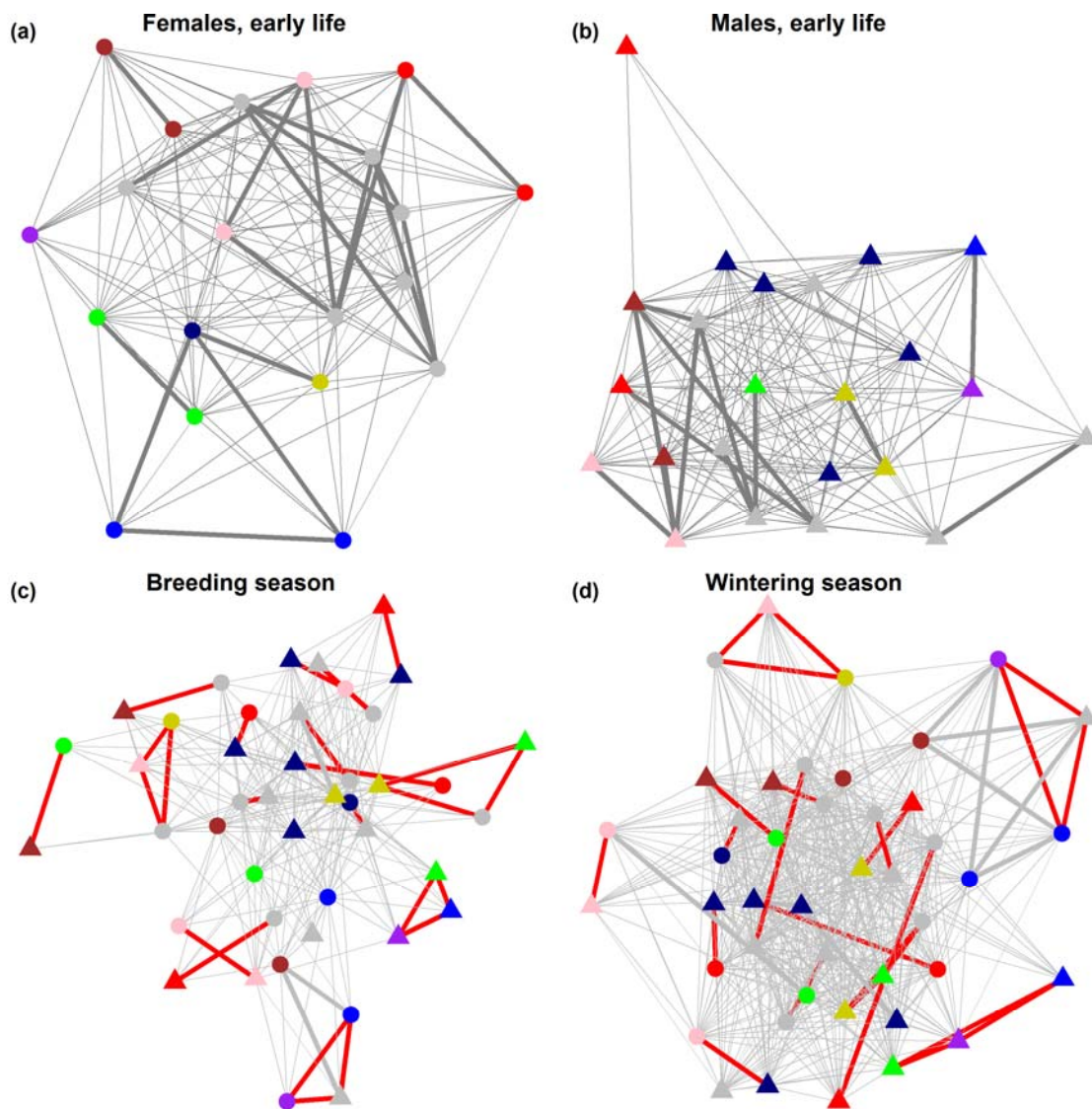
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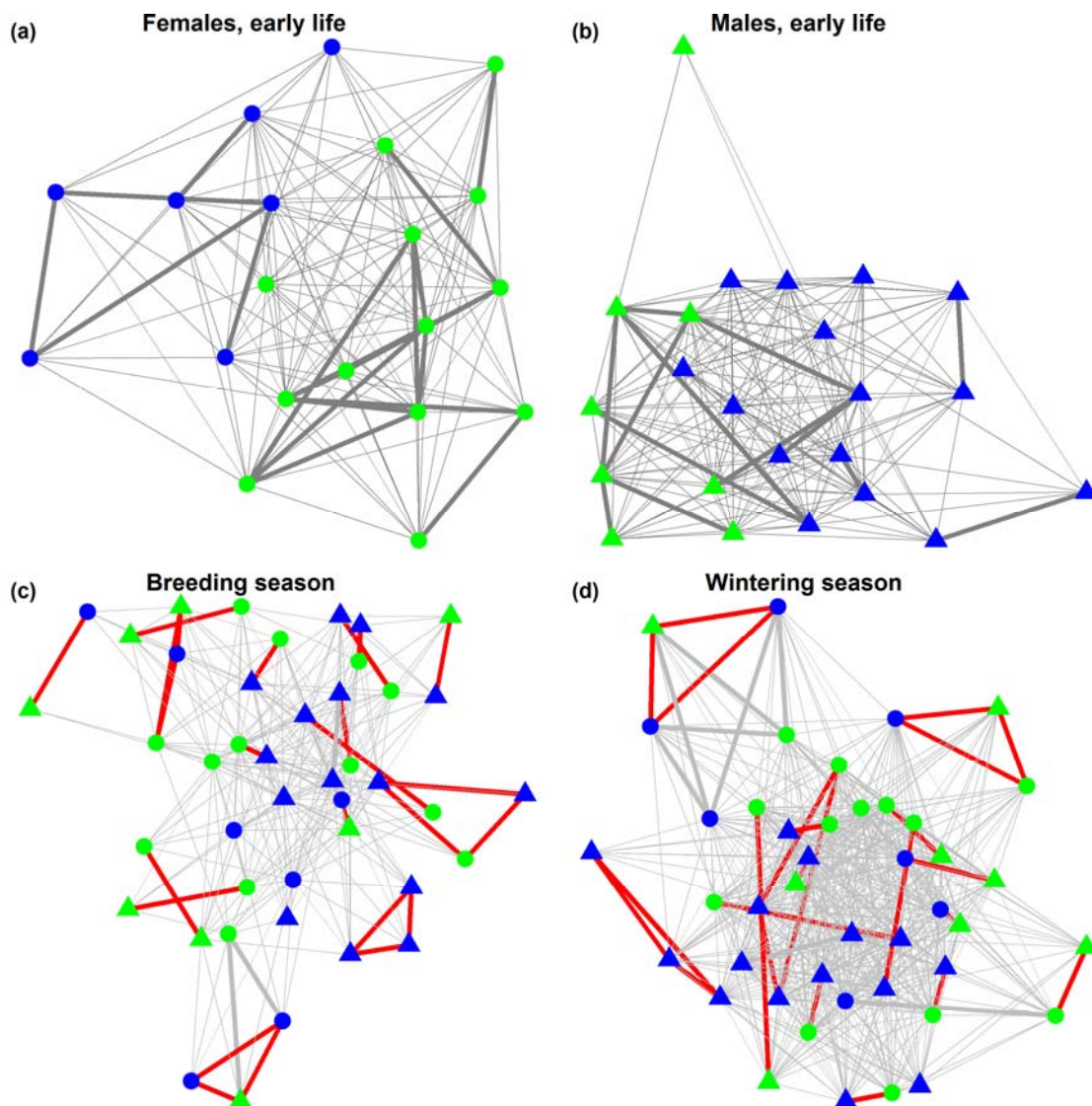
**Figure A2.** Nodes with the same colour indicate individuals coming from the same familiarity group. In the single-sex groups prior to pair formation, geese associated more with individuals from their own familiarity group as shown by the strong segregation of colours (and as reported in Kurvers et al., 2013). This pattern is, however, not present anymore in the breeding and wintering season. Circles represent females, and triangles males.

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**Figure A3.** Nodes with the same colour indicate individuals with high genetic relatedness. Each cluster of colours has a mean genetic relatedness above 0.3. Grey-coloured nodes represent individuals not sharing a high genetic relatedness with any individual in the population. In the single-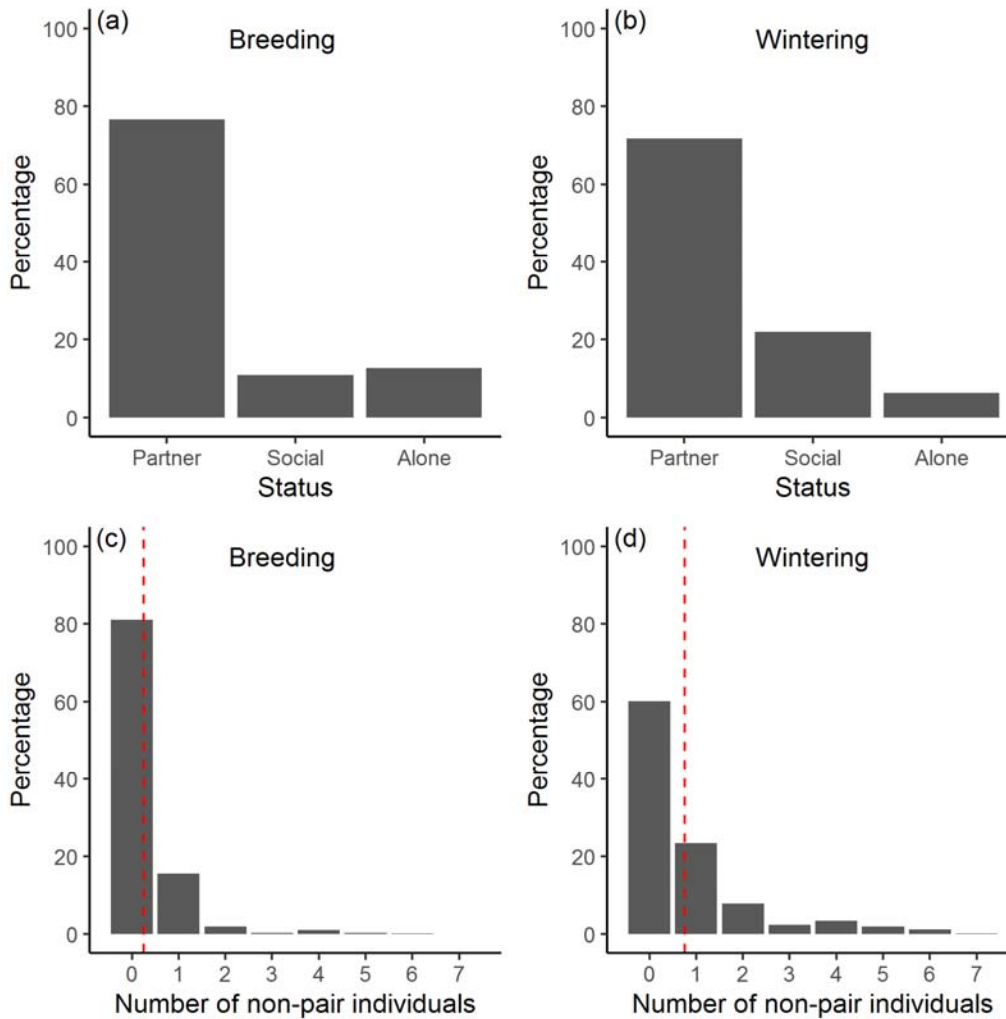sex groups before pair formation, geese associated more with genetically related individuals colours (as reported in Kurvers et al., 2013). This pattern is, however, not present anymore in the breeding and wintering season. Circles represent females, and triangles males.

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**Figure A4.** (a, b) The observed likelihood that when a paired individual was present on a patch that its partner was also present ('partner'), that it was together with another individual but not its partner ('social'), or that it was alone ('alone'), for the (a) breeding, and (b) wintering season. (c, d) The observed likelihood of the number of individuals not belonging to the pair, which were present at a patch in the presence of a pair during the (c) breeding, and (d) wintering season. To illustrate, in the breeding season, in 80% of cases when pair members were observed together on a patch, there would be no other individuals (i.e., not belonging to that pair) present. In the wintering season, this percentage was around 60%. Red dashed lines represent the average number of non-paired geese present with a pair (mean during breeding: 0.26, during wintering: 0.76).