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Non-random associations in group housed rats (*Rattus norvegicus*)

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14   **ABSTRACT**

15   Ecological factors, such as predation, have traditionally been used to explain sociability. However, it is increasingly

16   recognised that individuals within a group do not associate randomly, and that these non-random associations can

17   generate fitness advantages. The majority of the empirical evidence on differentiated associations in group-living

18   mammals, however, comes from a limited number of taxa and we still know very little about their occurrence and

19   characteristics in some highly social species, such as rats (*Rattus spp*.). Here, using network analysis, we quantified

20   association patterns in four groups of male fancy rats. We found that the associations between rats were not

21   randomly distributed and that most individuals had significantly more preferred/avoided associates than expected

22   by random. We also found that these preferences can be stable over time, and that they were not influenced by

23   individuals' rank position in the dominance hierarchy. Our findings are consistent with work in other mammals, but

24   contrast with the limited evidence available for other rat strains. While further studies in groups with different

25   demographic composition are warranted to confirm our findings, the occurrence of differentiated associations in

26   all male groups of rats have important implications for the management and welfare of captive rat populations.

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28   **Key words:** domesticated rat, dominance, network analysis, *Rattus norvegicus,* non-random associations social

29   preference, social relationship

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INTRODUCTION

Sociability has traditionally been explained in terms of ecological factors, such as predation and resource distribution [1,2]. While these factors may explain the occurrence and diversity of social systems, it is increasingly recognised that individuals within a group do not associate randomly, and that the formation of these non-random associations can generate strong fitness advantages in terms of survival and reproductive performance [3]. The impact of differentiated associations on individuals' fitness extends beyond the benefits derived from associations within the reproductive context [4]. For example, forming strong well differentiated associations among same-sex individuals in baboons (*Papio hamadryas ursinus*) [5], horses (*Equus caballus*) [6], and house mice (*Mus musculus*) [7] affects individuals' long-term reproductive success and longevity, with individuals forming the strongest and most stable associations reproducing more successfully and living longer than other animals. More recent research suggests that the benefits of sociality may be more complex than previously described, with fitness related benefits associated with the number of associations (strong or otherwise) individuals have in their social group [8,9].

Following Hinde's conceptual framework [10], social relationships are considered to be the outcome of a series of social interactions between individuals and can be characterised by their content (e.g., sexual, parenting, affiliation or conflict), quality (e.g., intensity of affiliation or aggression), and temporal patterning (e.g., frequency) [10]. According to this framework, social relationships might vary among dyads since an individual can interact with different individuals in different ways. Differentiated social relationships occur when this variation of interaction patterns show consistency over time. When individuals are more likely to interact or associate with one another than with other potential partners, individuals can be said to have preferred social partners (e.g., [11,12]).

Animals can develop social preferences for particular group mates depending on a number of factors. Close associations between individuals are often strongly correlated with their genetic relatedness (e.g., primates [13]; ring-tailed coatis (*Nausa nasua*) [14], giraffe (*Giraffa camelopardalis*) [11]), but preferred associations are not limited to kin (e.g., equids [6]; greater ani (*Crotophaga major*) [15]). In many mammalian species sex also influences affiliation patterns among individuals in a group, with females affiliating with each other at high rates in, for instance, many cercopithecine species [16]. Social preferences might also emerge as a by-product of an

58   attraction to high-ranking individuals who might provide benefits to lower-ranking animals such as tolerance at

59   feeding sites or support in alliances [13]. Other variables such as similarity in age (mouflons (*Ovis gmelini*) [17];

60   coatis [14]) or personality traits (brown capuchin monkeys (*Sapajus spp.*) [18]) have also been identified as factors

61   predicting partner choice.

62   Despite the apparent ubiquitous occurrence of differentiated associations in group-living mammals and their

63   potential impact on individuals' fitness, the vast majority of empirical evidence comes from a limited number of

64   taxa (mainly primate species) and we still know very little about their occurrence and characteristics in some highly

65   social species, such as rats (*Rattus spp.*). In the wild, rats form complex societies of up to several hundred

66   individuals, often consisting of sub-groups of females and males with overlapping home ranges [19]. In domestic

67   and laboratory settings, however, they are rarely housed in groups larger than pairs, offering little opportunity to

68   fully express the range of social strategies that are part of their natural repertoire. Thus, despite 150 years of

69   captive breeding and estimates suggesting there are over twenty million rats in laboratories across the world [20],

70   we still know surprisingly little about their natural social behaviour or organisation. Most of the data on rats' social

71   behaviour were collected several decades ago when the research emphasis was on aggression and competition

72   [21,22]. More recent research has greatly contributed to our understanding of play behaviour [23], pro-social

73   tendencies [24], and cooperation [25], although the typical housing conditions of rats in laboratories and the social

74   manipulations used to induce these behaviours, such as isolating individuals from their groups or applying food

75   colorant to their fur [26,27], limit the generalization of the knowledge gained through these studies to other social

76   contexts.

77   Thus, the nature and stability of differentiated associations in rats remains understudied. To our knowledge, only

78   one study has investigated the occurrence of differentiated relationships with group members in captive female

79   rats, concluding that although rats show considerable levels of cooperation, they associate randomly and lack

80   stable relationships [28]. However, this study included only a few observations of each group (i.e., a total of two

81   observation sessions of one hour each per group) while rats were in either altered (i.e., their home cage with all

82   hiding possibilities removed) or new environments (i.e., an unfamiliar big arena), which could have affected their

83   association patterns. More importantly, since social relationships are defined as the outcome of a series of social

84 interactions between individuals over time, and observation time affects the probability of observing individuals

85 interacting, social preferences are likely to be detected only by more comprehensive studies of behaviour.

86 Furthermore, this previous study focused on female rats and it is currently unknown whether male rats display

87 similar association patterns. Here we examine the occurrence of differentiated associations in group living male

88 rats by applying network analysis on social interactions recorded over a three-month observation period. Social

89 network analysis is a powerful and flexible tool for analysing association patterns in animals that takes into

90 account not only direct (dyadic) interaction (as methods quantifying variation in pairwise association indices do),

91 but also indirect connections between individuals [29, 30]. We then examine whether any observed patterns of

92 social preferences are consistent across time and whether dominance rank plays a role in determining association

93 patterns.

94

95 **RESULTS**

96 ***Distribution of Social Relationships***

97 Twenty-seven male Fancy rats (i.e., domesticated rats with a variety of fur patterns typically kept as companion

98 animals) living in four groups (G1=7, G2=7, G3=6, and G4=7) were the subjects of the study. When testing whether

99 the observed association patterns could have arisen by chance, given spatial proximities, we found that the overall

100 gregariousness (i.e. the average network strength) of all groups was significantly different from the average

101 network strength of random association (G1*:* mean strength = 3.359, mean random strength ± SD: 2.774 ± 0.155,

102 P_{rand} = 0.0001; G2*:* mean strength = 3.354, mean random strength ± SD: 2.752 ± 0.154, P_{rand} = 0.0001; G3*:* mean

103 strength = 3.057, mean random strength ± SD: 2.414 ± 0.149, P_{rand} = 0.0002, G4*:* mean strength = 2.479, mean

104 random strength ± SD: 1.965 ± 0.118, P_{rand} = 0.0005, Figure 1), suggesting that patterns of association between

105 individuals were not random (see Table S1 for results using only body contact data).

106 Furthermore, the analyses also show that the observed network coefficient of variation (CV) was significantly

107 different from the random networks CV in all groups but one (i.e. G1, G2, G3), suggesting that individuals in these

108 groups had significantly more preferred/avoided relationships than expected at random (permutation tests, G1: CV

109 = 0.462, mean random CV ± SD 0.439 ± 0.012, P_{rand} = 0.026; G2: CV = 0.498, mean random CV ± SD 0.461 ± 0.015,

110 P_{rand} = 0.008; G3: CV = 0.287, mean random CV ± SD 0.236 ± 0.016, P_{rand} = 0.001). However, in one of the groups

111 (G4), CV from the observed and random networks were not significantly different, indicating that for this group the

112 inter-individual association patterns did not differ from random (permutation test, CV = 0.277, mean random CV ±

113 SD 0.264 ± 0.015, P_{rand} = 0.216) (see Table S1 for results using only body contact data).

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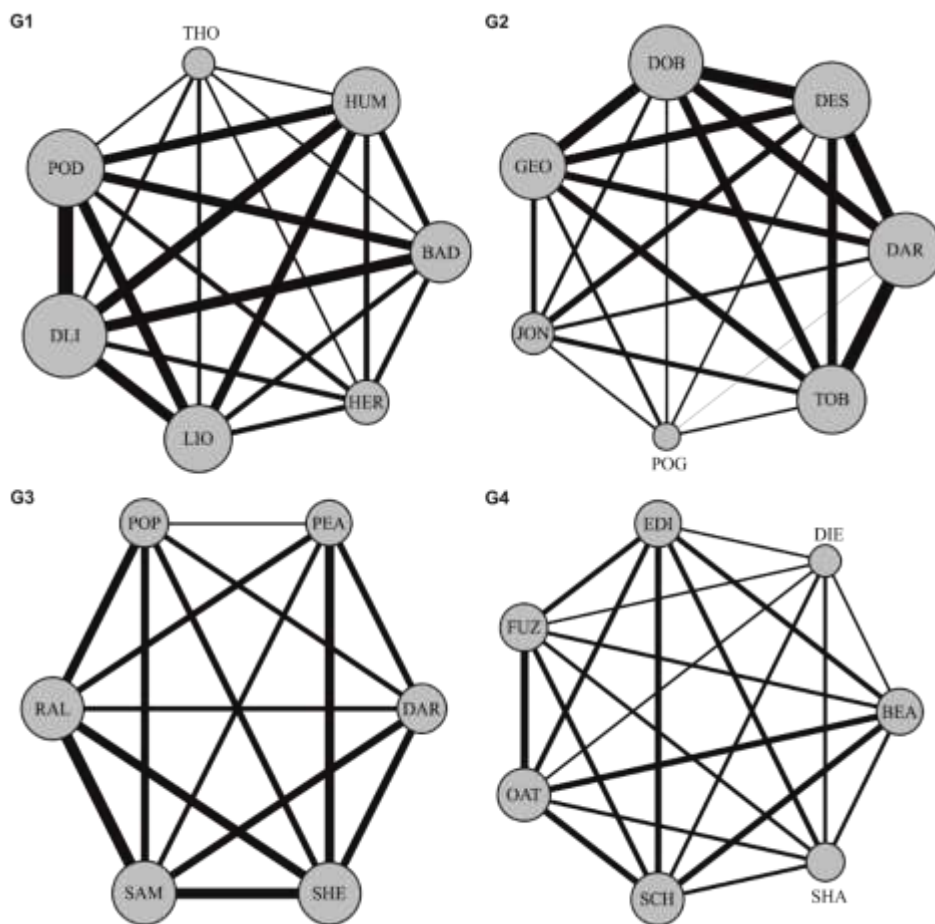
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116 **Figure 1. Social network diagrams for study groups (G1-G4).** Nodes represent individual rats and their

117 size is proportional to an individual's network strength. Edge thickness represents the association index

118 (SRI) between individuals. The three letter codes indicate individual rats' names.

119

Consistency of Association Patterns over Time

121   When analysing the consistency of the social preferences we found that for two of the study groups (G1, G2) there

122   was a significant positive correlation between the association network of the first and second observation periods

123   (Mantel test; G1: $z = 1.87$, $P = 0.040$; G2: $z = 1.96$, $P = 0.013$), whereas no relationship was found for the other two

124   groups (Mantel test; G3: $z = 1.45$, $P = 0.129$; G4: $z = 0.89$, $P = 0.928$).

Association Patterns and Dominance Relationships

126   Both observed Landau's corrected index (h') and the directional consistency index (DCI) values were non-

127   significant in all cases (Table 1), indicating that rats in this population do not form linear dominance hierarchies.

128   The h' index ranged between 0.31 and 0.68 and the DCI between 0.41 and 0.75. Furthermore, there was a very

129   high proportion of two-way interactions in all groups (Table 1). When testing the effect of dominance scores on

130   social associations we found that across groups, individual network strength was not significantly related to

131   individual dominance scores (coefficient ± SE: 0.016 ± 0.022, $t = 0.759$, $P_{rand} = 0.442$), suggesting that the observed

132   association patterns are not driven by the social status of individuals.

133

134   **Table 1**. Results from the Matman test for linearity of dominance hierarchies for the four study groups of rats.

Group	G1	G2	G3	G4
Matrix total	75	106	85	215
Landau's corrected index (h')	0.678	0.446	0.343	0.643
Directional consistency index	0.466	0.755	0.412	0.6
% of unknown relationships	19.05	0	6.67	0
% of one-way relationships	42.86	57.14	26.67	28.57
% of two-way relationships	38.10	42.86	66.67	71.43
% tied relationships	4.76	4.76	13.33	0

Improved linearity test (R-tailed probability)	0.103	0.284	0.641	0.110

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DISCUSSION

138 Using a network approach, we quantified association patterns in groups of male rats over a three-month period.

139 Our findings revealed that associations between rats were not randomly distributed and that most individuals have

140 significantly more preferred/avoided associates than expected by chance, indicating that when kept in all-male

141 groups, male rats can form differentiated social relationships. Evidence from a range of species shows that animals

142 living in groups do not associate randomly with their group mates, which has been linked to individuals' survival

143 and reproductive performance [e.g. 3]. Multiple mechanisms can guide partner selection, with factors such as sex

144 or kinship greatly influencing the distribution of social associations in many species [4]. For instance, in female

145 philopatric species, females tend to associate preferentially with their maternal kin [5]. Since rats are able to

146 recognise kin [31], it is possible that rats' association patterns may depend on the kinship relationship between

147 group mates. Kinship information was not available for the study groups and therefore we were not able to

148 explore this possibility. Future studies examining kinships and other possible mechanisms underlying social

149 preferences in rats are therefore warranted.

150 The occurrence of non-random association patterns in rats is consistent with work in other species that has used

151 quantitative measures of individuals' behaviour. For instance, birds [15], fish [32], bats [12], or primates [5] are

152 known to have preferred associates within their groups. Social preferences outside reproductive contexts are also

153 found in some rodent species, such as house mice [7] or striped mice (*Rhabdomys pumilio*) [33]. To our knowledge,

154 our study is the first showing that male rats can also form non-random associations when living in all-male groups.

155 However, we do not know whether these differentiated associations were driven mainly by preference towards

156 certain individuals, which would suggest the occurrence of close social bonds in rats, or primarily by avoidance,

157   primarily by avoidance of certain individuals, leading to others moving into proximity. Therefore, further work is

158   needed to determine the underlying drivers of these observed social differentiations.

159   Our findings, however, contrast with results from a previous study examining in-group social preferences in female

160   wild-type Norway rats, which did not detect preferential associations in all-female groups [28]. There is extensive

161   literature reporting sex differences in sociability and social behaviour in many mammal species, and how these sex

162   differences are influenced not only by hormones, but also by developmental processes and prior social experiences

163   [34]. Thus, it is possible that male rats, but not female rats, establish non-random associations with group mates.

164   However, female rodents are in general more social and less resilient to isolation than males [35], and females

165   from other rodent species do exhibit differentiated social relationships, which significantly impact their fitness [7].

166   Thus, given the occurrence of differentiated associations in group-living rodents, including male rats, and their

167   relevant fitness consequences, it is possible that female rats may have the potential for forming preferential

168   associations when given the choice between several social partners. However, these associations might be of a

169   looser nature than those found in female-bonded species (e.g., some primates) and therefore difficult to readily

170   detect without sufficient sampling effort and the application of powerful analytical tools, such as the ones used in

171   this study. A further possibility is that the tendency of forming differentiated social relationships in rats depends

172   on their strain. Although the overall affiliative, agonistic and sexual repertoire among different strains is similar,

173   there is much variation in the frequency, degree of asymmetry and complexity of their behaviours, with wild-type

174   strains typically showing lower levels of social tolerance and higher levels of agonistic behaviours [36-38]. Thus, it

175   is possible that social preferences are formed in some strains (e.g., fancy rats, this study), but not in others (e.g.,

176   wild-type rats [28]). It would be important that future research explore this possibility by investigating the

177   occurrence of preferred associations in different rat strains bred and housed under similar conditions.

178   In addition to showing the presence of differentiated associations in groups of male rats, our results also suggest

179   that these associations can be stable over time. In half of our study groups, there was a significant positive

180   correlation between the association network of the first and second observation periods, indicating consistency of

181   their social preferences, for a period of a few months at least. However, in the other two groups, we did not find

182   any correlation between the association networks of the two observation periods, suggesting that although the

183   number of their preferred/avoided associations might be similar between study periods, associations in these

184   groups may be of a more opportunistic nature. Evidence accumulated over the last 15 years shows that in some

185   group living species individuals are able to maintain stable social preferences over extended periods of time [39-

186   40]. However, stability is not an essential or indispensable characteristic for social relationships to occur, nor to

187   bring fitness benefits [41]. According to Hinde's framework [10], social relationships are not static entities, they are

188   dynamic and can change over time due to both predictable (e.g., development) and unpredictable events (e.g.,

189   migration of individuals between groups). Some of the most common variables that modulate social preferences,

190   such as significant changes in group composition or resource availability (e.g., food, hiding resting places),

191   remained stable during our study period, but we did not measure other potential variables that could have

192   affected relationship between group members (e.g., hierarchical changes [42]). Further studies exploring variables

193   affecting relationships formation and maintenance over a longer period of time and on a larger sample size of

194   male, female and mixed-sex groups of rats will further our understanding of the nature of differentiated

195   associations and social dynamics in rats.

196   We also found that rats in this population did not form linear dominance hierarchies. In many social species,

197   including rats, the dominance status of individuals is mainly determined by their fighting ability (e.g. red deer,

198   *Cervus elaphus*, [43]; rats, [21]) and outcomes of dyadic interactions can be used to construct their dominance

199   hierarchies. Although previous descriptions of dominance relations in male rats suggest clear and stable rank

200   orders [44], systematic analyses of the linearity of their dominance hierarchies are typically not reported and thus

201   it is difficult to compare previous work with our findings. However, it should be noted that a lack of linearity in a

202   dominance hierarchy does not imply lack of dominance relations between individuals. All dyads in a group can

203   have clear dominance relations, and yet the overall hierarchy could be non-linear if it contains intransitive triads.

204   Analyses of dominance rank revealed that male rats' associations were not influenced by individuals' rank position,

205   suggesting that dominance rank is not responsible for the observed pattern of social preferences. Social

206   associations can be affected by dominance rank if, for instance, individuals prefer to associate with high-ranking

207   partners who can potentially provide greater benefits than low-ranking individuals (e.g., access to monopolised

208   resources). Association biases in favour of dominant individuals have been reported for a variety of species. For

209   instance, hyenas associate more often with dominant individuals than with subordinate ones [45], and primates

210   from many species of cercopithecine monkeys tend to affiliate more often with high-ranking than low-ranking

211   group mates [13]. Similarly, when mixed-sex groups of wild-type rats are kept in semi-naturalistic environments,

212   adult males form clear dominance relationships with high-ranking males being frequently contacted by lower-

213   ranking ones [21]. However, clear dominance relationships are not always observed in domesticated rat strains

214   [46] and males in our colony showed a high proportion of two-way interactions resulting in a lack of linearity in

215   their dominance hierarchies. Therefore, it is possible that this lack of linearity in their dominance hierarchies

216   reduced the attractiveness of higher-ranking individuals.

217   While our study focused only on all-male groups of rats, thus limiting the generalisation of our findings, our results

218   show that rats have the potential of forming non-random associations with group mates. Our results can also have

219   important implications for the management and welfare of captive rat populations, and in particular for those

220   colonies where rats are housed in large same-sex groups, as is often the case with pet rats. Accumulated evidence

221   (including this study) shows that group living animals often form non-random associations with fellow group

222   members, which can generate strong benefits to individuals, from tolerance around limited resources [47] to social

223   thermoregulation [48]. More importantly for captive environments, social partners have also been shown to

224   positively affect psychological, physiological, and behavioural functions, as well as to attenuate physiological stress

225   [49-51]. Thus, providing individuals with appropriate social environments that enable them to exercise partner

226   choice (i.e., more than one single partner) could positively affect their welfare. On the other hand, the disruption

227   of preferred associations can also have negative consequences on individuals. In both humans and non-human

228   animals, disruption of social relationships can lead to an increase of physiological and behavioural stress responses

229   [52,53]. While the effect of the removal of individual rats from their social groups is known to affect social stability

230   [54], the welfare implications of the disruption of rats preferred social associations remains to be studied. A better

231   understanding of rats' sociality is increasingly necessary in lab animal husbandry, as more animals are housed in

232   groups rather than individually. We suggest that our findings on differentiated relationships in rats are

233   incorporated in future work addressing the welfare of captive rat populations.

234   Finally, the fact that male rats can have preferred/avoided partners in their groups has also important implications

235   for research examining physiological, neurological or behavioural processes. For instance, familiar individuals (i.e.,

236   individuals co-habiting an enclosure for a period of time) have been found to mitigate conspecific's stress

237   responses more effectively than unfamiliar ones [55,56], but this effect has not always been found [57,58].

238   Similarly, familiarity seems to influence how animals use social information in diverse species, including rats, with

239   animals prioritizing information from familiar individuals in some studies [59,60] but not in others [61,62]. It might

240   be possible that variation in social preferences for familiar individuals could in part explain these contradictory

241   results. We suggest that research addressing the role of familiarity on physiological, neurological or behavioural

242   processes in rats consider including a finer measure of individual's social preferences.

243

244   **METHODS**

245   *Ethical Note*

246   This study adheres to all legal requirements and guidelines of the U.K. government and to the ASAB/ABS guidelines

247   for the Treatment of Animals in Behavioural Research and Teaching, and was carried out in compliance with the

248   ARRIVE guidelines. The delegated authority of the University of Lincoln Research Ethics Committee approved this

249   research (CoSREC374).

250   *Subjects and Housing*

251   Twenty-seven male Fancy rats (i.e., domesticated rats with a variety of fur patterns typically kept as companion

252   animals) living in four groups (G1=7, G2=7, G3=6, and G4=7) were the subjects of the study. On arrival at the

253   Animal Unit of the University at circa 6-8 weeks of age, rats were housed in groups (6-7 individuals) based on

254   combining individuals with differing markings to aid identification and remained in their groups for their natural

255   lifespan or until rehomed as companion animals. At the start of the study, rats were approximately 8 months old,

256   ensuring that the social groups were well established. Each group was housed in Mid-West Critter Nation Animal

257   Habitat cages (double units: 61 x 91 x 124 cm) with platforms at different heights, and several shelters, nesting

258   material (i.e., shredded paper), and enrichment (e.g., a variety of toys, chewing material, ropes, climbing tubes).

259   Room temperature was 21.0 ± 2.0 °C and natural light was provided from dimmed windows. Supplementary

260   artificial light was used during husbandry activities (e.g., cleaning and feeding) if needed. Rats were scatter fed

261   (Supreme Science Selective, supplemented with fresh vegetables at least once a week) and water was available *ad*

262   *libitum*. Individuals were recognisable through distinguishing characteristics (i.e., size, and natural colour patterns),

263   except in the case of five individuals who were marked using red-food dye applied to their backs (individuals THO,

264   DLI (Group 1), DAR, JON (Group 2), SAM (Group 3), Figure 1). In order to avoid any possible effect of dye

265   application on rats' behaviour, behavioural recording started at least 15 min after dye was applied. Red dye was

266   chosen because rats do not see those wavelengths [63].

267   ***Behavioural Measures***

268   Behavioural data were collected from video recordings (SONY HDR-CX675 & HikVision DS-7600) between January

269   and March 2018, with a total of 120 recording sessions of 30 minutes each; that is, 30 recordings per group, each

270   recording taking place on a different day, thus totalling 30 recording days, which is estimated to be enough to

271   detect the occurrence of non-random associations for moderately to highly socially differentiated networks [64].

272   Video recordings were taken while the rats were in their enclosures during day time (between 12:00 and 16:00)

273   and outside feeding periods. Although rats have been described as being primarily nocturnal [65], they can also be

274   active during the day [37], and the rats in this study were regularly handled and participated in behavioural and

275   cognitive tests during the light period, including on days when behavioural observations were conducted. All rats

276   participated in the same behavioural and cognitive tests, were tested individually, and none of the tests involved

277   any social tasks. During recording sessions, the animals were left undisturbed for the entire session. Recordings

278   were later used to conduct scan samples every 2 minutes of the state behaviours body contact (i.e., any body part

279   of two individuals (except their tails) were in physical contact), and proximity (i.e., individuals were within one

280   body length (circa 20cm)). Body contact and proximity were only recorded if individuals were in the same level of

281   their enclosure with no physical obstacles between them and were not exchanging any agonistic behaviour. All

282   videos were coded by CAT. A subset (5%) of the videos was coded by an independent observer who was naïve to

283   the aims of the study. Scores for social proximity (i.e., individuals in contact or in proximity) were highly correlated

284   between the two coders (r = 0.89).

285   *Dominance*

286   In order to assess dominance relationships between individuals, 5 min controlled observations were conducted in

287   which a small amount of food (<10% of their daily food intake) was given to each group prior to the evening

288   feeding time. During the observations, the occurrence and direction of any agonistic interaction (including biting,

289   wrestling, boxing, aggressive posturing, chasing, pinning, and fleeing, see [21] for definitions), along with supplants

290   (i.e., individual approaches another one and gains access over space or food without showing any aggressive

291   behaviour and the other retreats without showing any submissive behaviour) were recorded using an all-

292   occurrence sampling technique [66]. A total of 30 dominance observations per group were conducted (i.e., 150

293   min per group) during the study period, and only dyadic interactions were used to determine social dominance.

294   For each interaction, the participant supplanting (i.e., gaining access to food or space), chasing, biting or pinning

295   down their opponent was designated the winner, and the other individual the loser. If both individuals exhibited

296   aggressive behaviours, then the conflict was considered undecided and no winner and loser designated.

297   Dominance matrices were constructed using the total number of wins and losses (see Table S2).

298   *Data Analysis*

299   *Distribution of social relationships*

300   Analyses were conducted in R v. 3.4.4 [67]. Social associations between individuals were calculated using social

301   proximity data (i.e., individuals were in contact or in proximity) recorded during scan sampling. Non-directed

302   weighted association networks for each group of rats were generated using the *asnipe* package [68] for the total

303   observation period. Associations between individuals were then calculated using the simple ratio index (SRI [69])

304   which estimates the probability of co-observing two individuals in social proximity versus being observed on their

305   own. This association index is commonly used in network analysis when observations between individuals are

306   rarely missed during data collection [64], as is the case in the present study. Social network diagrams were

307   produced to visualise interaction patterns between rats using the *igraph* package in R [70].

308   In order to investigate if overall gregariousness in groups differed from random, average network strength (i.e., the

309   average of the sum of the edge weights (SRI) of each node (individual) [64]) was calculated for all groups using the

310   *igraph* package [70] and compared to the average network strength of random association networks generated

311   from 10,000 data-stream permutations, which sequentially swap associations between pairs of individuals

312   observed at the same time point [29,68]. Additionally, to test if rats have more preferred/avoided relationships

313   than expected at random (i.e., differentiated associations), the coefficient of variation (CV) of the SRIs between

314   individuals of the observed association networks for each group was compared to the CV of the SRIs measured for

315   random association networks generated as described before [29]. Significance for both measures was estimated by

316   comparing the observed metric for each group (i.e., average network strength and CV) to the distribution of the

317   same metric generated using the permutations [29].

318   ***Consistency of association patterns over time***

319   To examine the consistency of the association patterns over time, we built association networks for the first and

320   second half of the observation period for each group (i.e., 240 sample points on each period) using the

321   *get_network* function in the *asnipe* package (version 1.1.11 [68]). We then ran Mantel tests using 10,000

322   permutations (*ape* package [71]) to test for an association between the networks of the first and second

323   observation period for each group.

324   ***Association patterns and dominance relationships***

325   In order to evaluate dominance relationships (cf. [72]) we carried out hierarchical rank order analysis [73].

326   Dominance networks of dyadic interactions were constructed using the total number of wins and losses and then

327   analysed by means of MatMan (Noldus, v1.1). Hierarchies were estimated using both the de Landau's index of

328   linearity (h') [73] and the directional consistency index (DCI), since de Landau's index provides inaccurately low

329   linearity index values when the number of individuals or interaction frequencies are low [74]. Additionally, we

330   calculated individual dominance scores using the David's score method (DS) [75], which is a type of cardinal rank

331   measure based upon dyadic dominance proportions (i.e., individual's proportions of wins and losses), taking into

332   account the relative strengths of opponents [76].

333   A linear mixed-effects model (using the *lmer* function of the *lme4* package [77]) was conducted to investigate if an

334   individual's network strength differed as a function of the individual dominance scores (DS). Group was included as

335   a random effect. Significance was measured by comparing the t- statistic extracted from the output of the linear

336   model fitted to the observed data with the t-statistic calculated from models fitted to randomly generated

337   network data using 10,000 data-stream permutations using the *asnipe* package in R [78,79].

338   **DATA AVAILABILITY**

339   The datasets analysed during the current study are available at https://doi.org/10.24385/45818

340

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499   **AUTHOR CONTRIBUTIONS**

500   TR and LP designed the study, CAT conducted data collection, TK and TR performed data analysis, TK prepared the

501   figures, TR wrote the manuscript, and all authors discussed the results and reviewed the final manuscript.

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503   **COMPETING INTERESTS**

504   The authors declare no competing interests.