1 SOCIAL NETWORKS DYNAMICS PRECEDE A MASS EVICTION IN GROUP-LIVING
2 RHESUS MACAQUES

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15 **Short Title**: Dynamic Social Networks Precede Mass Eviction

16

17 **ABSTRACT**

18 Network dynamics have the ability to reveal information about the adaptive function of

19 social behaviour and the extent to which social relationships can flexibly respond to

20 extrinsic pressures. Changes in social networks occur following changes to the social and

21 physical environment. By contrast, we have limited understanding of whether changes in

22 social networks precede major group events. Permanent evictions can be important

23 determinants of gene flow and population structure and are a clear example of an event

24 that might be preceded by social network dynamics. Here we examine the social networks

25 of a group of rhesus macaques (*Macaca mulatta*) in the two years leading up to the eviction

26 of 22% of adult females, who are the philopatric sex. We found that females engaged in the

27 same amount of aggression and grooming in the two years leading up to the eviction but

28 that there were clear changes in their choice of social partners. Females that would

29 eventually be evicted received more aggression from lower ranking females as the eviction

30 approached. Evicted females also became more discriminant in their grooming

31 relationships in the year nearer the split, showing a greater preference for one another and

32 becoming more cliquish. Put simply, the females that would later be evicted continued to

33 associate with the rest of the group as the eviction approached but were less likely to

34 interact with them in an affiliative manner. These results have potential implications for

35 understanding group cohesion and the balance between cooperation and competition that

36 mediates social groups.

37

INTRODUCTION

Animals that live in groups are faced with the challenge of balancing the benefits of group living with the costs of conflicting interests between group mates (Krause & Ruxton, 2002; Silk, 2007). Balancing these costs and benefits may be especially difficult for individuals that live in groups composed of both kin and non-kin (Seyfarth & Cheney, 2012). Much theoretical and empirical research has focused on how individuals may use aggression, social status, cooperation, and social bonds to cope with intra-group conflict. Yet a great deal about the origins and maintenance of group-living remains unclear (Brent, Chang Gariépy, & Platt, 2014; Krause & Ruxton, 2002; Nowak, Tarnita, & Wilson, 2010; Shultz, Opie, & Atkinson, 2011). Network dynamics within groups can reveal the processes that underpin the structuring of animal societies and can uncover information about the adaptive functions of social behaviours and relationships (Berger-Wolf & Saia, 2006; Bode, Wood, & Franks, 2011; Pinter-Wollman et al., 2014). Describing dynamic shifts in social networks and determining when and why these shifts occur is therefore an important route to understanding the maintenance of social groups, and hence the evolution of sociality.

A growing number of studies have documented network dynamics within groups that have followed changes to the physical environment. For example, association networks become more tightly connected when resources are scarce in killer whales (*Orcinus orca*: Foster et al., 2012). This finding is in accordance with the hypothesis that prosocial relationships are more valuable during times of hardship because they help individuals to cope with intra-group competition (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; van Schaik, 1989). In contrast, a negative relationship between network connectedness and the level of resource competition, as measured by group size, suggests competition rather than cooperation shapes sociality in wild chimpanzees (*Pan troglodytes*: Lehmann & Boesch, 2009). In sleepy lizards (*Tiliqua rugosa*), the number and strength of network connections does not change in response to changes in climate, although the nature of social connections differs with fewer inter-sexual associations in drier years (Godfrey, Sih, & Bull, 2013). In contrast, the social networks of some populations do not appear to respond at all to changes in the physical environment; Although guppies (*Poecilia reticulata*) from areas with low levels of predation show more social mixing than their high-predation

68 counterparts, no changes to social networks occur within populations following

69 experimental manipulation of habitat complexity or predation risk (Edenbrow et al., 2011).

70   In addition to changes in the physical environment, network dynamics following

71 changes in social factors, such as reproductive seasonality (Brent, Maclarnon, Platt, &

72 Semple, 2013; Hamede, Bashford, McCallum, & Jones, 2009) and group composition, have

73 revealed important information about social processes. For instance, network dynamics

74 following the simulated, experimental, or natural loss of individuals from groups suggests

75 that some individuals are more important to group cohesion than others (Kanngiesser,

76 Sueur, Riedl, Grossmann, & Call, 2010; Lehmann, Andrews, & Dunbar, 2010; Manno, 2008)

77 and can occupy specific social roles (Flack, Girvan, de Waal, & Krakauer, 2006). Following

78 experimental manipulation of the sex ratio of guppy groups, a breakdown in female-female

79 associations in populations with a greater number of males, and hence a greater level of

80 sexual harassment, suggests that repeated social interactions are needed to establish

81 individual recognition between group mates (Darden, James, Ramnarine, & Croft, 2009).

82 Wild chacma baboon (*Papio ursinus*) females compensate for the death of close relative by

83 broadening and strengthening their grooming networks (Engh et al., 2006), particularly by

84 extending their social relationships to unrelated group mates. This apparent compensatory

85 behaviour suggests that social relationships are valuable to female baboons, and also

86 provides preliminary evidence regarding the differential value of social relationships with

87 kin compared to non-kin. Finally, changes to social networks have been observed in

88 response to changes in the social hierarchy. The grooming networks of female chacma

89 baboons were less diverse in the weeks following a period of instability in the alpha male

90 position in their group (Wittig et al., 2008). Females who contracted their grooming

91 networks the most showed a less dramatic rise in faecal glucocorticoid metabolite levels

92 and returned to baseline levels more quickly (Wittig et al., 2008). Taken together, these

93 findings suggest that affiliative bonds with a small number of preferred partners help these

94 animals to cope with social instability.

95   Network dynamics can occur not only in response to changes to the environment

96 but can also precede or even provoke such changes. Understanding the links between

97 network dynamics that occur in advance of shifts in the physical or social environment can

98 therefore also have important implications for our understanding of social processes and

99   relationships, and may even allow scientists to predict the occurrence of major events.

100   Instances where we might expect network dynamics to occur in advance of social or

101   physical perturbations include: seasonally predictable changes in climate or resource

102   abundance; the joining/splitting of subgroups in species with high levels of fission-fusion

103   sociality (Sueur & Maire, 2014); large outbreaks of intra-group aggression; and the

104   dispersal, death (i.e. in cases where death is preceded by a gradual decline in condition) or

105   permanent eviction of group mates. However, few studies have documented network

106   dynamics prior to major events because the occurrence of these events can be difficult to

107   anticipate and studies of this nature often must rely on coincidental collection of

108   behavioural data.

109   Here we evaluate network dynamics preceding the permanent mass eviction of

110   many females from a group of rhesus macaques (*Macaca mulatta*). Rhesus macaques, like

111   many primates, live in social groups composed of multiple adult males and females

112   (Thierry, 2007). Females are the philopatric sex and membership of females in rhesus

113   macaque groups is "closed" (i.e. females do not disperse in/out of groups, they must be

114   born into them). Nevertheless, rhesus macaque groups are characterised by a mixed

115   relatedness structure, containing both related and unrelated females (Brent, Maclarnon, et

116   al., 2013; Missakian, 1972). Affiliative relationships are often the strongest and most stable

117   between kin, but social bonds between unrelated females are also common (Beisner,

118   Jackson, Cameron, & McCowan, 2011; Cheney, 1992). In addition to high rates of affiliative

119   interactions, social life in female rhesus macaques is characterized by high rates of

120   aggression that is unidirectional (i.e. aggression is typically directed from high to low

121   ranking animals) and that occurs within strict, linear, and relatively stable dominance

122   hierarchies (Datta, 1988). Females inherit the rank immediately beneath their mother and

123   thus closely related females tend to be of similar dominance rank (Brent, Heilbronner, et

124   al., 2013; Missakian, 1972). Permanent evictions of females have been documented in this

125   species but are rare (Chepko-Sade & Sade, 1979; Ehardt & Bernstein, 1986; Widdig et al.,

126   2006). Because of the relatively stable social structure that characterises female rhesus

127   macaque life, it is reasonable to assume that social markers of instability would be

128   detectable prior to a mass eviction but this has not yet been described.

129   The eviction that is the focus of this study occurred in a group of 55 adult females

130   from three separate ancestral lines and resulted in the removal of the 13 highest ranking

131   females. We examined the aggression and grooming networks of all adult females during

132   two periods preceding the eviction, the year immediately before the eviction (2011), and

133   the year before that (2010). We determined whether network dynamics occurred in

134   advance of the eviction by examining three aspects of social networks: i) the rate at which

135   individuals engaged in social interactions, ii) individuals' choice of social partners and the

136   nature of their interactions with those partners, and iii) the clustering of local subgroups.

137

138

139   **METHODS**

140   ***Study Population and Eviction Event***

141   Our subjects were rhesus macaques living in the semi-free-ranging colony on Cayo Santiago

142   Island, Puerto Rico (18°09 N, 65°44 W; Rawlings & Kessler, 1986). Monkeys are

143   provisioned daily at this site with commercial feed and with water supplied *ad libitum*.

144   There are no predators present. Population control takes the form of annual removal of

145   mostly juveniles. Beyond these measures, the monkeys are free to roam and to self-

146   organise into groups and there is no medical intervention or contraceptive use.

147   We studied animals in a single social group ('F'), which at the time of study was the

148   largest of the six groups on the island (n = 55 adult females). Group F was made up of three

149   separate female ancestral lines, or matrilines, where all females in a given matriline are

150   descendants of a single unique female, and where maternal relatedness between members

151   of different matrilines is typically zero (Figure 1). The three matrilines were named after

152   their founding females, 065, 004 and 073, who were first documented ranging together in

153   group F over 50 years ago (unpublished, CPRC database), and varied in size (Mat_{065}, n = 32;

154   Mat_{004}, n = 17; Mat_{073}, n = 6). Due to the linear nature of dominance hierarchies and the

155   maternal inheritance of dominance rank, rhesus macaque matrilines can also generally be

156   categorised according to rank: Mat_{065} contained the highest-ranking females, females from

157   Mat_{004} were the next highest in rank (apart from three members of Mat_{065} that were lower

158   in rank than some members of Mat_{004} - two of these females did not to have many close

159 relatives in the group and may have therefore lacked the social support needed to maintain

160 high rank), and Mat$_{073}$ contained the lowest ranking females (Figure 1).

161

162 [INSERT FIGURE 1 ABOUT HERE]

163

164 At the beginning of 2012, we observed a sudden outbreak of aggression which

165 resulted in the death of the alpha female and the permanent eviction of 12 of group F's

166 highest ranking females (22% of all adult females) (Figure 1). Although we could not collect

167 systematic behavioural data during the aggressive outbreak, we opportunistically recorded

168 cuts and wounds on the bodies of these members of Mat$_{065}$. The injuries sustained by the

169 alpha female were especially severe and she died two weeks later, presumably from sepsis.

170 The remaining 12 females began to range independently from the group along with their

171 offspring and a few males. First, they ranged separately in two daughter groups then,

172 approximately eight months later, as one consolidated group.

173

174 ***Data Collection***

175 As part of an unrelated study we collected behavioural data on the adult females in group F

176 for two years prior to the eviction during two temporally similar periods: May-December

177 2010 and April-December 2011. These two periods were divided by a halt in behavioural

178 data collection that takes place annually in the colony. All subjects were individually

179 recognized and habituated to observer presence. We collected a total of 843.70 hours of

180 continuous data using 10-min focal animal samples with means (SD) per individual of 4.07

181 (0.39) and 5.02 (0.11) hours in 2010 and 2011, respectively. We balanced observations of

182 individuals across time to control for within-daily as well as monthly temporal variation.

183 We recorded all instances of aggression, submissive gestures, and grooming. We used

184 agonistic win/loss interactions to construct dominance hierarchies for the females

185 independently in each year, although female ranks were stable across years. We limited our

186 analyses to females that were present for the entirety of the two years, which excluded a

187 small number of females that died (n = 2) as well as juvenile females that aged into our

188 sample (n = 9).

189

190 ***Social Network Analysis***

191 We used social network analysis to explore social dynamics. Social network analysis is

192 comprised of a suite of statistics that describe various levels of a network: individualized

193 scores that describe properties of a node (e.g. a node's centrality), metrics that describe

194 dyadic interactions (e.g. the probability of an edge between two individuals), and metrics

195 that describe global network properties (e.g. size, shape, connectedness), making it apt at

196 addressing the variation between individuals within a network and between networks at a

197 subgroup, group, population, or species level (Brent, 2015; Krause, James, Franks, & Croft,

198 2014; Wasserman & Faust, 1994).

199   To determine whether changes to networks occurred as the eviction approached,

200 we compared the females' grooming and aggression networks from 2010 to those in 2011.

201 We created one grooming and one aggression network for each year, resulting in four

202 networks in total (Figure 2). Edges in these networks represented all observed grooming

203 and aggressive interactions recorded within a given dyad. We treated networks as directed

204 (i.e. the donor and recipients of an interaction are defined) and weighted (i.e. the rate at

205 which a dyad interacted is represented rather than the simple presence/absence of an

206 interaction). For grooming networks, edges were weighted by the seconds per hour of

207 grooming that took place within each dyad; for aggression networks, edges were weighted

208 by the frequency of aggressive interactions per hour per dyad. Within years, our grooming

209 and aggression networks were not significantly related to one another (2010: correlation

210 coefficient = -0.025, p = 0.052; 2011: correlation coefficient = 0.026, p = 0.086) and thus we

211 treat them separately in analyses.

212

213 ***Changes in rates of social interaction.*** We first determined whether the general tendency

214 for all females to engage in social interactions changed as the eviction event approached by

215 comparing grooming network and aggression network densities across years. We

216 performed this analysis using the paired nodes density function in UCINET v6.588

217 (Borgatti, Everett, & Freeman, 2002). Assessing changes to network density is an important

218 first step before analysing differences in network structure because apparent structural

219 changes can be brought about by changes to density alone (Brent, Maclarnon, et al., 2013)

220 and so the impact of density on structural changes must be taken into account.

221

Changes in the identity of social partners and the nature of social relationships. We

next explored whether the identity of social partners and/or the nature of social

relationships changed in the year nearer to the eviction. Due to the maternal relatedness

structure that underpins aggressive and affiliative interactions in this species (Brent,

Heilbronner, et al., 2013; Missakian, 1972), we divided females according to their three

ancestral matrilines in order to explore changes in social partnerships that occurred within

and between related partitions of females. We further divided matriline 065 into two

partitions, 'Evicted' and 'Resident' to reflect the fact that the eviction was localised within

this matriline and to allow us to examine any social changes that occurred

between/amongst these females.

We evaluated the extent to which social interactions were directed within and

between partitions in each study period using a joint-count analysis. This procedure starts

by calculating the ratio of the observed edge weights that occurred within or between a

particular partition(s) and the expected edge weights, which are generated from networks

of similar size, density, and for which the edge weights are the median of the observed

values. The ratio of observed to expected edge weights therefore describes the extent to

which observed edge weights differ from those that would be observed if individuals

interacted at random (that is, a model in which our chosen partitions were not meaningful).

We then simulated 5000 random graphs in which the edges were reshuffled randomly

between nodes (Erdős–Rényi networks). For each permuted network we calculated the

observed to expected edge weight ratio. We evaluated the statistical significance of our

observed edge weights by determining the proportion of permuted values that met or

exceeded the observed value, a technique that is akin to traditional p-values (Croft,

Madden, Franks, & James, 2011). We also compared the ratio of observed to expected edge

weights across study periods in order to assess how partner choice changed as the eviction

approached.

We predicted that the nature of aggressive interactions would change the year

nearer to the eviction in a manner that would indicate instability in the dominance

hierarchy. We therefore determined if there was greater tendency for females from lower

ranking partitions to direct aggression at higher ranking partitions in the year closer to the

252   eviction. We additionally explored changes to aggression within partitions, as instability

253   could also be localised to more closely related females. For affiliative interactions, we

254   predicted that grooming would be more focused onto related partners (i.e. within

255   partitions) in the year nearer the eviction, as an additional indicator of social instability

256   (Beisner et al., 2011) and in accordance with previous findings in Old World monkeys that

257   suggest that kin-based relationships are more valuable during times of hardship (e.g. Engh

258   et al., 2006).

259

260   ***Changes to clustering of local networks.*** Finally, we determined whether there were

261   changes to the nature of local grooming networks across years. To do this, we compared

262   the mean clustering coefficient for each partition in each study period. Clustering

263   coefficient measures the degree to which an individual's social partners are connected to

264   each other (Newman, 2003). The mean of this measure is therefore an indicator of the

265   degree to which a partition is structured into tightly-knit cliques or clusters. We explored

266   clustering coefficients of the grooming networks only due to the linear, non-triadic, nature

267   of aggressive interactions in this species (Datta, 1988). We calculated a weighted version of

268   clustering coefficient of using the tnet package in R (Opsahl, 2009), which first necessitated

269   converting our directed networks to undirected. We evaluated the statistical significance of

270   observed clustering coefficients in two ways. First, we compared the clustering coefficient

271   of a given partition within each study period to the clustering coefficient derived from a

272   model of random association. To create random models, we generated 5000 (Erdős–Rényi

273   graphs of similar size and density to the observed networks and calculated the mean

274   weighted clustering coefficient in each partition for each permutation. We determined the

275   proportion of these permuted values that met or exceeded observed values as a measure of

276   statistical significance. In order to compare clustering coefficients across partitions, we

277   performed a two-sample bootstrapping test. Here, we took the difference in mean

278   clustering coefficients of the two partitions being compared (either the same partition

279   across years, or different partitions within the same year). Then, we pooled together the

280   clustering coefficients for each female in each partition. We resampled from this pool with

281   replacement sets of equal size 5000 times, and calculated the difference in the clustering

282   coefficients that were generated to create a null distribution. We calculated p-values as the

283   proportion of differences in clustering coefficients between bootstrapped partitions that

284   were more extreme than observed differences. To visualize differences in clustering across

285   years, we generated 5000 random graphs in which the edge weights from a given partition

286   were permuted but the positions of the edges held constant and created violin plots of the

287   resulting values.

288   *Ethical note.* This research complied with protocols approved by the Institutional Animal

289   Care and Use Committee of the University of Puerto Rico (protocol #A6850108) and by the

290   University of Exeter School of Psychology's Ethics Committee.

291

292

293   **RESULTS**

294   **Rates of social interactions were static across years.** We found no evidence for changes

295   between 2010 and 2011 in the overall rate of aggression (2010: 0.02, 2011: 0.02;

296   tstat=0.49; p =0.31) or grooming (2010: 1.20; 2011: 1.17; t-stat=0.13; p = 0.43), as

297   indicated by network densities. Any other structural differences in the observed networks

298   (e.g. differences in clustering) cannot therefore be owed to differences in network density.

299   **Aggression directed up the hierarchy was more likely in the year nearer the eviction.**

300   Aggressive interactions generally reflected the dominance hierarchy, with the majority of

301   aggression emanating from higher ranking females and being directed at lower ranking

302   females in both years (Table 1). However, changes from 2010 to 2011 in the extent to

303   which aggression was directed up the hierarchy occurred and may suggest that there was

304   instability in the dominance hierarchy that was largely localised to the 065 matriline. In

305   particular, females from low-ranking matrilines 004 and 073 were more likely to give

306   aggression to the Evicted females in 2011 compared to in 2010. Females from Mat_{004} were

307   also more likely to give aggression to the Resident females in 2011 compared to 2010

308   (Table 1). Although these increases represent only a small absolute number of aggressive

309   interactions, reflecting the smaller number of females that belonged to the lower ranking

310   matrilines (Figure 2), they are notable due to the typically unidirectional nature of

311   aggression in rhesus macaques. The probability of aggressive interactions also increased

312   amongst Evicted females from 2010 to 2011. However, there were decreases in the

313   probability of aggression being directed from the Evicted females to the Resident females,

314   and from the Resident females to the Evicted females.

315
316   [INSERT FIGURE 2 ABOUT HERE]
317
318   **Females changed grooming partners as the eviction approached.** We found that, as

319   expected, females were more likely to engage in grooming with members of their own

320   partition. The Evicted, Resident, and Mat_{004} females were more likely to groom members of

321   their own partition compared to members of other partitions in both 2010 and 2011 (Table

322   1). This pattern was not significant for females from the small 073 matriline Females also

323   tended to groom females outside their own partition at rates either expected by chance or

324   significantly lower than chance in both years. Yet there were notable differences in the

325   identities of grooming partners both within and between partitions across years (Figure 2).

326   For example, the tendency for females to groom members of their own partition increased

327   from 2010 to 2011 for Evicted, Resident, and Mat_{004} females, with the Evicted females

328   showing the largest increase in within-partition grooming (2010: 5.02 Obs/Exp, p < 0.01;

329   2011: 6.45, p < 0.01). In addition, the amount of grooming that occurred between Evicted

330   and Resident females did not differ from chance levels in 2010 but was smaller than

331   expected in 2011 (2010: 0.96, p = 0.25; 2011: 0.34, p = 0.01). In other words, in the year

332   nearer to the eviction, Evicted females were more likely to groom one another and less

333   likely to groom the Resident members of their matriline.

334   **Evicted females formed tighter grooming clusters in the year before their eviction.**

335   The mean clustering coefficient of the grooming network of Evicted females was

336   significantly greater than expected in 2011 but not in 2010 (Table 2). The mean clustering

337   coefficient of no other partition differed from expected values in either year. In other

338   words, the grooming relationships of Evicted females were more cliquish than expected

339   based on random association in the year directly before their eviction, whereas no such

340   differences were observed in the other partitions, including the Resident members of this

341   matriline. The grooming relationships of the Evicted females were also significantly more

342   clustered in 2011 than in 2010, and were significantly more clustered in 2011 than any

                                                                                               12

343   other partition examined (Figure 3). Although there were small increases in clustering

344   from 2010 to 2011 for the Resident and Mat_{004} females, this was only significant for the

345   latter (Table 2). The clustering coefficient for Mat_{073} was zero because there were no closed

346   triads within the network and thus no amount of edge-weight reshuffling could produce a

347   result other than zero. We found relative similarities between our random graphs across

348   years (Figure 3). Because changes in network densities were the central drivers of

349   differences between the random graphs, which further suggests that differences across

350   time in our observed clustering coefficients were not driven by differences in density alone.

351   [INSERT FIGURE 3 ABOUT HERE]

352
353
354   **DISCUSSION**

355   The study of dynamic social networks is an area of rapidly growing research interest (Bode,

356   Wood, & Franks, 2011; Ilany, Booms, & Holekamp, 2015; Pinter-Wollman et al., 2014).

357   Although social networks appear to be able to flexibly respond to changes in the social and

358   physical environment, whether changes to social networks also precede major events is

359   less clear. Here we report network dynamics in advance of the mass eviction of members of

360   the philopatric sex. Prior to the eviction, researchers present in the group reported no

361   conspicuous signs of social instability. Therefore the changes to the networks of these

362   animals occurred in advance of a major event but were subtle and revealed only through

363   subsequent analysis. Permanent evictions can have serious consequences for individuals;

364   intragroup aggression prior to evictions can result in fatal injuries (Ehardt & Bernstein,

365   1986; Gygax, Harley, & Kummer, 1997; Samuels & Henrickson, 1983), decreased

366   reproduction, (Dettmer, Woodward, & Suomi, 2015) and smaller post-eviction daughter

367   groups can be subjected to higher risks of predation and reduced foraging efficiency

368   (Krause & Ruxton, 2002). There is some evidence that reproductive competition is the

369   trigger for evictions in cooperative breeding species (Thompson et al., 2016) but it is

370   unclear whether similar factors would be at play in a primate such as the rhesus macaque

371   that has highly polygynous mating and only moderate levels of reproductive skew (Dubuc,

372   Ruiz-Lambides, & Widdig, 2014). Although we do not know whether there are causal links

                                                                                            13

373 between changes to the social networks in this study and the eviction, a consistent

374 patterning of network dynamics prior to evictions would nevertheless allow evictions to be

375 predicted in future, which could have implications for the management of captive groups

376 (Beisner et al., 2011) and the design of naturalistic experimental studies.

377 A number of theories have been put forward regarding the maintenance of group

378 cohesion and the balance of competition and cooperation between unrelated group mates.

379 For instance, group cohesion may be limited by the amount of time individuals have

380 available to spend engaged in social interactions. This 'time-constraints' model predicts

381 that groups break apart once individuals can no longer maintain or keep track of

382 relationships with all other groups members (Dunbar, 1991, 1992). Prior to the mass

383 eviction in this study, we did not detect any changes in the amount of time individuals

384 dedicated to grooming or aggressive interactions. Although these animals are provisioned

385 and may not easily suffer from restrictions in their daily time budgets, our results

386 nonetheless suggest that the break down in group cohesion did not follow from reductions

387 in social effort.

388 Group cohesion may depend not only on the amount of time individuals engage in

389 social interactions but also on with whom they interact. For example, pay-to-stay

390 mechanisms, whereby individuals 'pay' their group mates with affiliative interactions, have

391 been proposed as a means to maintain groups of cooperative breeders with highly skewed

392 reproductive success (Bergmüller & Taborsky, 2005; Gaston, 1978; Johnstone & Cant,

393 1999), as well as groups of unrelated animals faced with intense between-group

394 competition (Radford, 2008; van Schaik, 1989; Wrangham, 1980). In the latter instance,

395 dominant animals are proposed to use social interactions, e.g. grooming, to establish

396 alliances with their lower-ranking group mates in order to ensure they will help in contests

397 with other groups (Cheney, 1992; van Schaik, 1989). A meta-analysis of data from

398 cercopithecine primates suggests the link between grooming relationships, intra-group

399 contest, and the maintenance of group cohesion is weak if non-existent (Cheney, 1992)

400 (although see: Majolo, de Bortoli Vizioli, & Lehmann, 2016). In the present study, an

401 increase in cliquishness in the local grooming networks of evicted females suggests that

402 grooming relationships amongst kin and non-kin of divergent social status may indeed play

403 a role in the cohesion of rhesus macaque groups. However, cause and consequence cannot

404   be disentangled here and just as the reduced diversity of grooming relationships may have

405   caused the eviction, the pending eviction may have resulted in the reduction of diversity in

406   grooming relationships.

407   Changes to affiliative relationships leading up to a mass eviction also reveal more

408   direct information about the patterns and processes that underpin social relationships in

409   these animals. Biologists' understanding of the evolution of social bonds in animals has

410   grown rapidly in recent years (Archie, Tung, Clark, Altmann, & Alberts, 2014; Brent,

411   Heilbronner, et al., 2013; Chang et al., 2013; Seyfarth & Cheney, 2012; Silk et al., 2009).

412   Affiliative tendencies have been shown to be heritable (Brent, Heilbronner, et al., 2013;

413   Brent, Semple, et al., 2014; Lea, Blumstein, Wey, & Martin, 2010), and a positive association

414   between affiliative relationships and proxies of fitness have been found in a small range of

415   species, including baboons (Archie et al., 2014; Silk et al., 2009; Cheney et al. 2016) and

416   rhesus macaques (Brent, Heilbronner, et al., 2013; Brent et al. 2017). Yet despite these

417   advances, the adaptive functions of social bonds remains unclear (Brent, Chang, et al.,

418   2014). A growing number of studies that have shown that affiliative social relationships

419   between members of the philopatric sex are more flexible in nonhuman primates than

420   traditionally believed (e.g. (Barrett, Gaynor, & Henzi, 2002; Barrett & Henzi, 2002; Engh et

421   al., 2006; Wittig et al., 2008). In accordance with this work, we found evidence for dynamic

422   shifts in affiliative relationships in this study. Together, these findings may reflect the use of

423   social relationships to cope with the vicissitudes of life such as death, disease, and shifts in

424   social status, as well as other short-term social, environmental, and demographic events.

425   Our results may also hint that some social bonds are more valuable than others.

426   Previous work has shown that instability in primate groups can be followed by shifts in

427   social partners. Following the death of the alpha male in wild chimpanzees, individuals

428   became more socially discriminant of grooming partners that failed to reciprocate (Kaburu

429   & Newton-Fisher, 2013). In cercopithecines, social relationships are most common

430   amongst related females (Cheney, 1992). Relatedness may be a useful shorthand for

431   reliable cooperative partners because of the ability to gain inclusive fitness benefits via

432   these relationships. Female baboons focused their grooming networks onto close kin

433   following instability in the male hierarchy (Wittig et al., 2008). In the current study,

434   grooming relationships largely collapsed along kin-lines prior to the mass eviction, with the

15

435   females that would be evicted focusing their relationships onto their closest kin; in times of

436   social instability, affiliative relationships with non-relatives may become too risky for

437   rhesus macaque females.

438   The adaptive role of social relationships in variable contexts begs an understanding

439   of how individuals of variable phenotypes integrate to form particular group dynamics.

440   Here, we focused on rates of interactions and the formation of clusters as indicators of

441   changes in network structure and partner choice. Other network metrics with alternative

442   properties might differently elucidate social dynamics (Brent 2015). For example,

443   eigenvector centrality, which uses direct and indirect connections to parse socially

444   integrated from marginal individuals, was found to positively correlate with proxies of

445   fitness in wild baboons (Cheney et al. 2016) and in the Cayo Santiago rhesus macaques

446   (Brent et al. 2013). As our current analyses indicated the emergence of distinct

447   subgroupings over time without any changes in the overall rates of interactions, we felt

448   eigenvector centrality would be of limited analytical power (although will nevertheless

449   continue to be important to consider in future studies focused on revealing information

450   about differences in social connectedness between individuals) and we instead performed

451   a joint count analysis to explore not just how involved the different subgroups were in

452   social life, but with whom.

453   The stability of a group is not attributable to the phenotype of any one particular

454   individual but it is nevertheless likely to impact upon individual fitness. Research in group-

455   living species suggests that the interplay between group stability and individual fitness is

456   complex (Muir, 2005; Saltz, 2013; Wolf, Brodie, & Cheverud, 1998). A more thorough

457   understanding of how the metagenome (i.e. the influence of one individual's genotype and

458   phenotype on another's) influences network dynamics will also be useful for behavioural

459   ecologists approaching these questions.

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469 Care and Use Committee of the University of Puerto Rico (protocol: A6850108).
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472 **REFERENCES**

473 Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: both same-sex and
474   opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B:*
475   *Biological Sciences, 281*, 20141261.
476 Barrett, L., Gaynor, D., & Henzi, S. P. (2002). A dynamic interaction between aggression and grooming reciprocity
477   among female chacma baboons. *Animal Behaviour, 63*, 1047-1053.
478 Barrett, L., & Henzi, S. P. (2002). Constraints on relationship formation among female primates. *Behaviour, 139*,
479   263-289.
480 Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market Forces Predict Grooming Reciprocity in
481   Female Baboons. *Proceedings of the Royal Society B: Biological Sciences, 266*, 665-670.
482 Beisner, B. A., Jackson, M. E., Cameron, A. N., & McCowan, B. (2011). Detecting Instability in Animal Social
483   Networks: Genetic Fragmentation Is Associated with Social Instability in Rhesus Macaques. *PLoS ONE, 6*,
484   e16365.
485 Berger-Wolf, T. Y., & Saia, J. (2006). *A framework for analysis of dynamic social networks*. Paper presented at the
486   Proceedings of the 12th ACM SIGKDD international conference on Knowledge discovery and data mining,
487   Philadelphia, PA, USA.
488 Bergmüller, R., & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers 'pay
489   to stay' by pre-emptive appeasement. *Animal Behaviour, 69*, 19-28.
490 Bode, N. W., Wood, A. J., & Franks, D. W. (2011). Social networks and models for collective motion in animals.
491   *Behavioral Ecology and Sociobiology, 65*, 117-130.
492 Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011). The impact of social networks on animal collective motion.
493   *Animal Behaviour, 82*, 29-38.
494 Borgatti, S.P., Everett M.G., & Freeman, L.C. (2002). *Ucinet for Windows: Software for Network Analysis*. Harvard,
495   MA: Analytic Technologies.
496 Brent, L. J. N. (2015). Friends of friends: are indirect connections in social networks important to animal behaviour?
497   *Animal Behaviour, 103*, 211-222.
498 Brent, L. J. N., Chang, S. W. C., Gariépy, J.-F., & Platt, M. L. (2014). The neuroethology of friendship. *Annals of the*
499   *New York Academy of Sciences, 1316*, 1-17.
500 Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., . . . Platt,
501   M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports, 3*, 1042-1042.
502 Brent, L. J. N., Maclarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque
503   social networks. *Behavioral ecology and sociobiology, 67*(3), 349-359.
504 Brent, L.J.N., Ruiz-Lambides, A., Platt, M.L. (2017). Family network size and survival across the lifespan of female
505   macaques. *Proceedings of the Royal Society B: Biological Sciences¸284*, 20170515.
506 Brent, L. J. N., Semple, S., Maclarnon, A., Ruiz-Lambides, A., Gonzalez-Martinez, J., & Platt, M. L. (2014). Personality
507   traits in rhesus macaques (Macaca mulatta) are heritable but do not predict reproductive output.
508   *International Journal of Primatology, 35*(1), 188-209.
509 Cheney, D. L. (1992). Intragroup cohesion and intergroup hostility: the relation between grooming distributions
510   and intergroup competition among female primates. *Behavioral Ecology, 3*, 334-345.
511 Cheney, D.L., Silk, J.B., & Seyfarth, R.M. (2016). Network connections, dyadic bonds, and fitness in wild female
512   baboons. *Royal Society Open Science, 3(7)*, 160255.
513 Chepko-Sade, B. D., & Sade, D. S. (1979). Patterns of group splitting within matrilineal kinship groups. *Behavioral*
514   *Ecology and Sociobiology, 5*, 67-86.
515 Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in*
516   *Ecology & Evolution, 26*, 502-507.

517   Darden, S. K., James, R., Ramnarine, I. W., & Croft, D. P. (2009). Social implications of the battle of the sexes: Sexual
518   harassment disrupts female sociality and social recognition. *Proceedings of the Royal Society B-Biological*
519   *Sciences, 276*, 2651-2656.
520   Datta, S. (1988). The acquisition of dominance among free-ranging rhesus monkey siblings. *Animal Behaviour, 36*,
521   754-772.
522   Dettmer, A. M., Woodward, R. A., & Suomi, S. J. (2015). Reproductive consequences of a matrilineal overthrow in
523   rhesus monkeys. *American Journal of Primatology, 77*, 346-352.
524   Dubuc, C., Ruiz-Lambides, A., & Widdig, A. (2014). Variance in male lifetime reproductive success and estimation of
525   the degree of polygyny in a primate. *Behavioral Ecology*, aru052.
526   Dunbar, R. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatologica*, *57*, 121–
527   131. Dunbar, R. (1992). Time: a hidden constraint on the behavioural ecology of baboons.
528   *Behavioral Ecology and Sociobiology*, *31*, 35–49.
529   Edenbrow, M., Darden, S. K., Ramnarine, I. W., Evans, J. P., James, R., & Croft, D. P. (2011). Environmental effects
530   on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*. *Animal*
531   *Behaviour, 81*, 551-558.
532   Ehardt, C. L., & Bernstein, I. S. (1986). Matrilineal overthrows in rhesus monkey groups. *International Journal of*
533   *Primatology, 7*, 157-181.
534   Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., & Cheney, D. L. (2006).
535   Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*).
536   *Proceedings of the Royal Society, Series B, 273*, 707-712.
537   Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in
538   primates. *Nature, 439*, 426-429.
539   Foster, E. A., Franks, D. W., Morrell, L. J., Balcomb, K. C., Parsons, K. M., van Ginneken, A., & Croft, D. P. (2012).
540   Social network correlates of food availability in an endangered population of killer whales, Orcinus orca.
541   *Animal Behaviour, 83*, 731-736.
542   Gaston, A. J. (1978). The Evolution of Group Territorial Behavior and Cooperative Breeding. *The American*
543   *Naturalist, 112*, 1091-1100.
544   Godfrey, S. S., Sih, A., & Bull, C. M. (2013). The response of a sleepy lizard social network to altered ecological
545   conditions. *Animal Behaviour, 86*, 763-772.
546   Gygax, L., Harley, N., & Kummer, H. (1997). A matrilineal overthrow with destructive aggression in *Macaca*
547   *fascicularis*. *Primates, 38*, 149-158.
548   Hamede, R. K., Bashford, J., McCallum, H., & Jones, M. (2009). Contact networks in a wild Tasmanian devil
549   (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social
550   behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters, 12*, 1147-
551   1157.
552   Ilany, A., Booms, A. S., & Holekamp, K. E. (2015). Topological effects of network structure on long-term social
553   network dynamics in a wild mammal. *Ecology letters, 18*, 687-695.
554   Johnstone, R. A., & Cant, M. A. (1999). Reproductive skew and the threat of eviction: A new perspective.
555   *Proceedings of the Royal Society B: Biological Sciences, 266*, 275-279.
556   Kaburu, S.S.K., & Newton-Fisher, N.E. (2013). Social instability raises the stakes during social grooming among wild
557   male chimpanzees. *Animal Behaviour*, *86(3)*, 519-527.
558   Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2010). Grooming network cohesion and the role of
559   individuals in a captive chimpanzee group. *American Journal of Primatology*, doi: 10.1002/ajp.20914
560   Krause, J., James, R., Franks, D. W., & Croft, D. P. (2014). *Animal social networks*. Oxford University Press, USA.
561   Krause, J., & Ruxton, G. D. (2002). *Living in Groups* (Vol. I). Oxford University Press, USA.
562   Lea, A. J., Blumstein, D. T., Wey, T. W., & Martin, J. G. A. (2010). Heritable victimization and the benefits of
563   agonistic relationships. *Proceedings of the National Academy of Sciences, 107*, 21587-21592.
564   Lehmann, J., Andrews, K., & Dunbar, R. I. M. (2010). Social networks and social complexity in female-bonded
565   primates. In R. I. M. Dunbar, C. Gamble & J. A. Gowlett (Eds.), *Social brain, distributed mind*. Oxford:
566   Oxford University Press.

567   Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female
568   chimpanzees, *Pan troglodytes*. *Animal Behaviour, 77*, 377-387.
569   Majolo, B., de Bortoli Vizioli, A., & Lehmann, J. (2016). The effect of intergroup competition on intragroup
570   affiliation in primates. *Animal Behaviour, 114*, 13-19.
571   Manno, T. G. (2008). Social networking in the Columbian ground squirrel, *Spermophilus columbianus*. *Animal
572   Behaviour, 75*, 1221-1228.
573   Missakian, E. A. (1972). Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus
574   monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates, 13*, 169-180.
575   Muir, W. (2005). Incorporation of competitive effects in forest tree or animal breeding programs. *Genetics, 170*,
576   1247-1259.
577   Newman, M. E. J. (2003). The structure and function of complex networks. *Siam Review, 45*, 167-256.
578   Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature, 466*(7310), 1057-1062.
579   Opsahl, T. (2009). *Structure and Evolution of Weighted Networks.* PhD Thesis, Queen Mary University, London.
580   Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., . . . Wittemyer, G. (2014). The
581   dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology,
582   25*, 242-255.
583   Radford, A. N. (2008). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour.
584   *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 2787-2791.
585   Rawlings, R., & Kessler, M. (1986). *The Cayo Santiago Macaques: History, Behavior & Biology.* New York: State
586   University of New York Press.
587   Saltz, J. B. (2013). Genetic composition of social groups influences male aggressive behaviour and fitness in natural
588   genotypes of Drosophila melanogaster. *Proceedings of the Royal Society B: Biological Sciences, 280*,
589   20131926.
590   Samuels, A., & Henrickson, R. V. (1983). Brief report: outbreak of severe aggression in captive *Macaca mulatta*.
591   *American Journal of Primatology, 5*, 277-281.
592   Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual review of psychology, 63*,
593   153-177.
594   Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature, 479*,
595   219222.
596   Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal
597   Society B: Biological Sciences Biological sciences, 362*, 539-559.
598   Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2009). The
599   benefits of social capital: close social bonds among female baboons enhance offspring survival.
600   *Proceedings of the Royal Society B: Biological Sciences, 276*, 3099-3104.
601   Sueur, C., & Maire, A. (2014). Modelling Animal Group Fission Using Social Network Dynamics. *PloS one, 9*,
602   e97813e97813.
603   Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and
604   Reviews*. *16*, 224-238.
605   Thompson, F. J., Marshall, H. H., Sanderson, J. L., Vitikainen, E. I. K., Nichols, H. J., Gilchrist, J. S., . . . Cant, M. A.
606   (2016). Reproductive competition triggers mass eviction in cooperative banded mongooses. *Proceedings
607   of the Royal Society of London B: Biological Sciences, 283*, 20152607.
608   van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen and R.A. Foley
609   (eds): *Comparative socioecology: The behavioural ecology of humans and other mammals*. Wiley
610   Blackwell.
611   Wasserman, S., & Faust, K. (1994). *Social Network Analysis: Methods and Applications* (Vol. 8). Cambridge
612   University Press.
613   Wittig, A., Nürnberg, P., Bercovitch, F.B., Trefilov, A., Berard, J.B., Kessler, M.J.,…Krawczak, M. (2006).
614   Consequences of group fission for the patterns of relatedness among rhesus macaques. *Molecular
615   Ecology*, *15*, 3825-3832

616 Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming
617   networks and stress alleviation in wild female baboons. *Hormones and Behavior, 54*, 170-177.
618 Wolf, J. B., Brodie Iii, E. D., & Cheverud, J. M. (1998). Evolutionary consequences of indirect genetic effects. *Trends*
619   *in Ecology & Evolution, 13*, 64-69.
620 Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*, 262-300.

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624 **FIGURE LEGENDS**

625

626 **Figure 1. Maternal relatedness structure for the adult females in group F.** Female names are
627 listed along the top and right-hand edge and are coloured by matriline membership. Matriline 065
628 has been partitioned into females that were evicted and those that remained in the parent group
629 ('resident') Females are ordered by descending dominance rank. Cells represent the maternal
630 relatedness coefficient for each pair of individuals.

631

632
633 **Figure 2. Grooming and Aggression Networks.** The grooming (A,B) and aggression (C, D)
634 networks for 2010 (A,C) and 2011 (B,D). Node colour represents partition membership where
635 Evicted females are red, Resident females purple, Mat_{004} females green and Mat_{073} females blue.
636 Colour intensity of the edge arrows indicates the relative weight of the interaction, with darker
637 edges indicating greater intensity. Each network is force-directed using the Fruchterman-Reingold
638 algorithm. Inset chord diagrams: width of chords represents that summation of interactions
639 emanating from a given partition to other partitions. Chords take the colour of the partition from
640 which interactions emanate.

641

642 **Figure 3. Mean Clustering Coefficients by Partition.** Violin Plots showing estimates of the
643 mean clustering coefficient for each partition in each study period. Grey plots show
644 estimates for the given partition and year based on Erdős–Rényi random graphs.
645 Coloured densities represent mean clustering coefficients from 5000 permuted graphs
646 in which we shuffled weights across edges while holding the positions of edges
647 constant.
648

Table 1. Observed and expected rates of grooming and aggression within and between females

		Grooming Networks					
		2010			2011		
Donor	Recipient	Exp	Obs	Obs / Exp (Pval)	Exp	Obs	Obs / Exp (Pval)
Evicted	themselves	142	712	**5.02 (0.001)**	140	904	**6.45 (<0.001)**
	Resident	207	201	0.96 (0.25)	205	69	**0.34 (0.01)**
	Mat_{004}	185	3	**0.02 (<0.001)**	183	19	**0.10 (0.001)**
	Mat_{073}	65	0	**0.00 (0.05)**	65	0	**0.00 (0.03)**
Resident	Evicted	207	290	1.40 (0.48)	205	176	0.86 (0.17)
	themselves	303	825	**2.73 (0.01)**	299	983	**3.29 (0.001)**
	Mat_{004}	271	147	**0.54 (0.03)**	268	168	**0.63 (0.04)**
	Mat_{073}	96	0	**0.00 (0.02)**	95	25	**0.27 (0.05)**
Mat_{004}	Evicted	185	48	**0.26 (0.01)**	183	177	0.97 (0.24)
	Resident	271	244	0.90 (0.17)	268	245	0.91 (0.15)
	themselves	242	890	**3.67 (<0.001)**	240	666	**2.78 (0.01)**
	Mat_{073}	86	72	0.84 (0.32)	85	14	**0.17 (0.04)**
Mat_{073}	Evicted	65	32	0.49 (0.22)	65	5	**0.08 (0.04)**
	Resident	96	0	**0.00 (0.01)**	95	21	**0.22 (0.04)**
	Mat_{004}	86	68	0.79 (0.29)	85	7	**0.08 (0.02)**
	themselves	30	45	1.49 (0.30)	30	104	3.49 (0.08)

		Aggression Networks					
Donor	Recipient	Exp	Obs	Obs / Exp (Pval)	Exp	Obs	Obs / Exp (Pval)
Evicted	themselves	2.43	8.00	**3.30 (<0.001)**	2.18	8.37	**3.84 (<0.001)**
	Resident	3.56	11.73	**3.29 (<0.001)**	3.18	8.98	**2.82 (<0.001)**
	Mat_{004}	3.18	7.94	**2.50 (<0.001)**	2.85	9.56	**3.35 (<0.001)**
	Mat_{073}	1.12	2.50	**2.23 (0.04)**	1.01	2.93	**2.92 (0.004)**
Resident	Evicted	3.56	0.59	**0.17 (<0.001)**	3.18	0.40	**0.13 (<0.001)**
	themselves	5.20	6.21	1.19 (0.38)	4.65	5.26	1.13 (0.19)
	Mat_{004}	4.65	7.77	1.67 (0.08)	4.16	5.76	1.38 (0.48)
	Mat_{073}	1.64	2.56	1.56 (0.27)	1.47	1.48	1.01 (0.15)
Mat_{004}	Evicted	3.18	0.25	**0.08 (<0.001)**	2.85	0.49	**0.17 (<0.001)**
	Resident	4.65	1.13	**0.24 (<0.001)**	4.16	1.20	**0.29 (<0.001)**
	themselves	4.16	4.35	1.05 (0.19)	3.72	5.16	1.38 (0.37)
	Mat_{073}	1.47	2.80	1.92 (0.09)	1.32	2.75	2.09 (0.08)
Mat_{073}	Evicted	1.12	0.00	**0.00 (<0.001)**	1.01	0.10	**0.10 (<0.001)**
	Resident	1.64	0.12	**0.07 (<0.001)**	1.47	0.10	**0.07 (<0.001)**
	Mat_{004}	1.47	0.12	**0.08 (<0.001)**	1.32	0.10	**0.07 (<0.001)**
	themselves	0.51	0.95	1.82 (0.14)	0.46	1.17	**2.52 (0.04)**

The observed (Obs) and expected rates (Exp) of interaction, and the ratio of observed to expected for each network within and between the 4 partitions (Evicted, Resident, Mat_{004}, and Mat_{073}). Interactions emanate from "donors" and are received by "recipients." Pval is calculated as the proportion of simulated networks in which the Obs/Exp value exceeded or met the observed Obs/Exp value. Values in bold differed significantly from chance.

Table 2. Clustering of grooming relationships: Observed compared to randomised networks, comparisons between partitions of females, and comparisons within partitions of females across years.

	Year	Observed Clustering Coefficient	Randomised Networks	Evicted 2010	Evicted 2011	Resident 2010	Resident 2011	Mat_{004} 2010	Mat_{004} 2011	Mat_{073} 2010	Mat_{073} 2011
Evicted	2010	0.04	0.01 (0.49)		**0.23 (<0.01)**	-0.01 (0.31)	-0.02 (0.23)	0.03 (0.08)	**0.05 (0.05)**	0.05 (0.09)	0.05 (0.09)
	2011	0.28	**0.21 (<0.01)**			**0.24 (<0.01)**	**0.21 (<0.01)**	**0.26 (<0.01)**	**0.18 (<0.01)**	**0.28 (<0.01)**	**0.28 (<0.01)**
Resident	2010	0.02	0.02 (0.35)				0.03 (0.13)	0.02 (0.15)	**0.06 (0.03)**	0.04 (0.17)	0.04 (0.17)
	2011	0.07	0.001 (0.43)					**0.04 (0.01)**	0.03 (0.15)	**0.06 (0.02)**	**0.06 (0.02)**
Mat_{004}	2010	0.02	0.03 (0.22)						**0.08 (<0.01)**	0.02 (0.14)	0.02 (0.14)
	2011	0.08	0.02 (0.24)							**0.09 (0.01)**	**0.09 (0.01)**
Mat_{073}	2010	0.00	0.04 (0.69)								0.00 (1.00)
	2011	0.00	0.06 (0.29)								

P-values for the difference in observed and random networks are calculated as the proportion of random networks that produced values as extreme the observed value. P-values for the difference of observed values across partitions and study periods are based on a bootstrap two-sample permutation tests. Values in bold differ significantly from chance.