

1 **Ageing in a collective: The impact of ageing individuals on social network structure**

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3 Erin R. Siracusa<sup>a\*</sup>, André S. Pereira<sup>a,b</sup>, Josefine Bohr Brask<sup>c</sup>, Josué E. Negron-Del Valle<sup>d</sup>, Daniel  
4 Phillips<sup>d</sup>, Cayo Biobank Research Unit, Michael L. Platt<sup>e,f,g</sup>, James P. Higham<sup>h</sup>, Noah Snyder-  
5 Mackler<sup>d,i,j</sup>, Lauren J. N. Brent<sup>a</sup>

6

7 Affiliations:

8 <sup>a</sup>School of Psychology, Centre for Research in Animal Behaviour, University of Exeter, Exeter,  
9 UK

10 <sup>b</sup>Research Centre for Anthropology and Health, Department of Life Sciences, University of  
11 Coimbra, Portugal

12 <sup>c</sup>Department of Applied Mathematics and Computer Science, Technical University of Denmark,  
13 Kongens Lyngby, Denmark

14 <sup>d</sup>Center for Evolution and Medicine, Arizona State University, Arizona, USA

15 <sup>e</sup>Department of Neuroscience, University of Pennsylvania, PA, USA

16 <sup>f</sup>Department of Psychology, University of Pennsylvania, PA, USA

17 <sup>g</sup>Department of Marketing, University of Pennsylvania, PA, USA

18 <sup>h</sup>Department of Anthropology, New York University, New York, USA

19 <sup>i</sup>School of Life Sciences, Arizona State University, Arizona, USA

20 <sup>j</sup>School for Human Evolution and Social Change, Arizona State University, Arizona, USA

21

22 \*corresponding author; email: [erinsiracusa@gmail.com](mailto:erinsiracusa@gmail.com)

23

24 **Abstract**

25

26 Ageing affects many phenotypic traits, but its consequences for social behaviour have

27 only recently become apparent. Social networks emerge from associations between individuals.

28 The changes in sociality that occur as individuals get older are thus likely to impact network

29 structure, yet this remains unstudied. Here we use empirical data from free-ranging rhesus

30 macaques and an agent-based model to test how age-based changes in social behaviour feed up

31 to influence: (1) an individual's level of indirect connectedness in their network; and (2) overall

32 patterns of network structure. Our empirical analyses revealed that female macaques became less

33 indirectly connected as they aged for some, but not all network measures examined, suggesting

34 that indirect connectivity is affected by ageing, and that ageing animals can remain well

35 integrated in some social contexts. Surprisingly, we did not find evidence for a relationship  
36 between age distribution and the structure of female macaque networks. We used an agent-based  
37 model to gain further understanding of the link between age-based differences in sociality and  
38 global network structure, and under which circumstances global effects may be detectable.  
39 Overall, our results suggest a potentially important and underappreciated role of age in the  
40 structure and function of animal collectives, which warrants further investigation.

## 41 42 **Introduction**

43  
44 The costs and benefits of an animal's behaviour toward members of their collectives can  
45 shape lifespans, life history evolution, and the pace of senescence. For example, the support that  
46 cooperative breeding species receive from non-breeding helpers may lead to longer lifespans than  
47 those of related solitary species [1]. The transfer of enhanced ecological knowledge to close  
48 relatives during collective foraging may have contributed to the evolution of reproductive  
49 senescence and prolonged post-reproductive lifespan (i.e., menopause) in female killer whales [2–  
50 4]. The formation of strong relationships between group mates has also been linked to enhanced  
51 longevity in a range of group-living taxa [5]. It is therefore clear that living in collectives can alter  
52 the adult ageing process. However, an important question is whether ageing, in turn, influences  
53 the behaviour of adults in collectives, and ultimately the structure of collectives themselves.

54 Growing evidence suggests that older adults differ in their social behaviours and social  
55 relationships from young adults [6–11]. One pattern that seems to be emerging across taxa is that  
56 older adults interact with fewer individuals than do younger adults, concentrating social  
57 relationships on close associates and kin [6,12–15]. Given that social networks are an emergent  
58 feature of association rules between individuals [16], shifts in patterns of social behaviour with  
59 age might not only affect who ageing individuals associate with directly (i.e., their direct

60 connectedness), but could also affect higher-order network structure. Age-based changes in social  
61 behaviour could scale up to alter an individual's connections to the partners of their social partners  
62 (their indirect connectedness [17]) as well as the overall structure (“topology”) of the social  
63 network, both of which can have consequences for disease transmission [18–23], information  
64 transfer [24–26], the cohesive movement of groups [27,28], and many other eco-evolutionary  
65 dynamics [29,30]. Yet little attention has been given to understanding the impact of social ageing  
66 for the polyadic social world or the structure of the collective.

67         Understanding how ageing shapes an individual's indirect connectedness may be  
68 particularly relevant as such connections are tightly linked to processes that can directly  
69 influence fitness, including those described above. Declines in indirect connectedness with age  
70 may help limit exposure to disease [20–22] which might be beneficial in aged animals  
71 experiencing immunosenescence, but simultaneously could inhibit the transfer of important  
72 socio-ecological information [26,31] which could exacerbate pre-existing fitness declines in old  
73 age. In some cases, indirect connectivity may be an even more important predictor of fitness than  
74 direct connections dyadic associations [17,32]. Therefore, changes in indirect connections may  
75 be a particularly important component of the social ageing phenotype to investigate. Recent work  
76 has offered some glimpses into how measures of indirect connectedness can differ between  
77 young and old adults. In marmots and Barbary macaques, older adults have measures of indirect  
78 connectedness that suggest they have partners who are themselves not well connected [9,33],  
79 (but this is not the case in rhesus macaques, see [34,35]). Older marmots and rhesus macaques  
80 are less effective at reaching disparate nodes in the network compared to younger adults [34–36].  
81 In contrast, older adults are more strongly embedded in cliques or clusters in their networks  
82 compared to younger adults in marmots [9], but not in either Barbary or rhesus macaques

83 [33,35]. However, most research to date has compared differences in measures of indirect  
84 connectedness among adults of different age classes (e.g., old versus young), but has lacked the  
85 longitudinal data required to quantify how the social positioning of individuals changes across  
86 their lifetimes (c.f., [9]). Such longitudinal analyses have the potential to reveal important  
87 patterns that might otherwise be masked by differences between individuals or cohorts [37].  
88 Tracking within-individual changes in measures of indirect connectedness is essential for more  
89 firmly placing changes in sociality across the lifespan within the larger ageing phenotype and  
90 therefore understanding the causes and consequences of these patterns of social ageing [38].

91 Populations composed of a greater proportion of older (or younger) adults may also be  
92 structured in meaningfully different ways, and this could affect important processes such as  
93 communication and cooperation. For example, the loss of old individuals through age-related  
94 disease or trophy hunting can disrupt intergenerational flow of accumulated social and ecological  
95 knowledge, impeding collective movement and the ability to locate critical resources [4,39–42].  
96 The age structure of a group can also regulate the behaviour of younger individuals [43,44],  
97 influencing aggression rates and social cohesion [45]. The impact of diminished cohorts of  
98 younger individuals on overall network structure is less well understood, but likely to have  
99 repercussions for network connectivity and cohesiveness given that younger adults are more  
100 socially active in many populations [8,10,12–14]. For example, the simulated removal of  
101 juvenile killer whales led to networks that were more fragmented than when random individuals  
102 were removed, suggesting an important role of young individuals in maintaining network  
103 cohesion [46]. Despite the established ecological and evolutionary importance of network  
104 structure [29,30] the underlying drivers of variation in network structure remain understudied  
105 [47–50]. Ageing, as an important process underlying patterns of individual-level variation in

106 sociality, might therefore provide a window into how simple processes can generate complex  
107 network structures [51,52].

108       Using both empirical data and a theoretical model, we explore how social ageing of  
109 individuals relates to measures of indirect connectedness and overall network structure in a  
110 group-living primate, the rhesus macaque (*Macaca mulatta*), which is an emerging model in  
111 social ageing research [38,53]. As female rhesus macaques grow older, they show clear changes  
112 in their patterns of direct connectedness: they reduce the size of their social networks and focus  
113 their social effort on a few important partners including close kin [6]. Despite this, females do  
114 not reduce the rate at which they engage in social interactions as they age, indicating that  
115 although their networks get smaller, older females continue to invest the same amount of time  
116 into fewer relationships [6].

117       Given these previously established changes in direct connections, here, we set out to test  
118 if age-based changes in social behaviour relate to measures of an individual's level of indirect  
119 connectedness [17,54], and if they scale up to influence network structure as a whole. Individual-  
120 level social network metrics, including measures of direct and indirect connectedness, relate to  
121 underlying, putatively simple, social differences or processes, such as individual-level variation  
122 in general sociability or reassociation tendency [51]. For example, an individual's general  
123 tendency to be sociable can be intuitively quantified using a direct network metric (e.g., strength,  
124 or the sum of the weights of an individual's ties to their partners), or using an indirect metric  
125 (e.g., weighted eigenvector centrality, which measures how well-connected an individual is to its  
126 partners and how well connected those partners are to others [51]). Drawing on this idea that  
127 underlying processes can predict an individual's position in the network, and on the age-based  
128 changes in direct connections we have previously documented in rhesus macaque females [6],

129 we made predictions for four common measures of indirect connectedness: eigenvector  
130 centrality, betweenness, closeness, and clustering coefficient (Table 1). Adult female rhesus  
131 macaques maintain their strength of grooming ties to others as they age, despite reducing their  
132 number of partners [6]. We therefore predicted that weighted eigenvector centrality (a measure  
133 of overall connectedness in the network) would also remain stable with age, as by retaining  
134 strong connections to some of their partners, females therefore (indirectly) retain connections to  
135 the partners of their partners. We also previously found that as female rhesus macaques age, they  
136 increase their likelihood of interacting with certain partners, especially their kin [6]. That is,  
137 ageing females increase both their tendency to reassociate with others, and their tendency to  
138 interact with someone from their own (kin-based) sub-group. Individuals with higher within-  
139 group association tendencies mix less widely in their networks and those with greater  
140 reassociation tendency are less likely to associate with new individuals and connect disparate  
141 parts of the network [51]. Therefore, we predicted that as females aged, they would have lower  
142 measures of betweenness (capacity for linking discrete clusters in a network) and closeness  
143 (capacity to reach others or be reached), but a higher clustering coefficient (cliquishness).

144 To determine if age-based changes at the individual level can result in changes in overall  
145 network structure we used empirical data from 19 networks of female rhesus macaques to test  
146 how variable proportions of old individuals in a network was related to three common measures  
147 of global network structure: mean degree, network diameter and transitivity (Table 1). We  
148 predicted that networks with a greater proportion of old individuals would be more sparsely  
149 connected due to older animals having fewer social partners (i.e., have lower mean degree and  
150 network diameter). Given greater kin clustering with age, we expected networks with more old  
151 individuals would be more clustered (i.e., have higher transitivity). Finally, to help inform our

152 empirical findings and better understand the link between age distribution and global structure,  
153 we built an agent-based model (parameterized using information from our empirical data) to  
154 simulate how different proportions of old individuals would be expected to affect network  
155 structure under simplified conditions where everything else is equal. Our results provide a first  
156 step to understanding how and when individual changes in social tendencies with age might scale  
157 up to detectable effects on global network structure, offering important insight into the  
158 consequences of demography for the structure and function of collectives.

## 159 **Methods**

160

### 161 **Study population and data**

162

163 Data used in this study were collected on a well-studied population of rhesus macaques  
164 on the island of Cayo Santiago, off the southeastern coast of Puerto Rico. The current population  
165 is maintained by the Caribbean Primate Research Center (CPRC) and is descended from 409  
166 macaques that were introduced to the island from India in 1938. The animals are food  
167 supplemented and provided with *ad libitum* access to water. There is no medical intervention,  
168 and so the major causes of death at this predator-free site are illness and injury [55,56]. The  
169 CPRC staff collect demographic data five days per week and thus track dates of birth and death  
170 of all individuals with a high degree of accuracy.

171 Rhesus macaques are highly social cercopithecine primates that live in matrilineal kin-  
172 groups and exhibit clearly differentiated social relationships with kin-biased affiliation  
173 [55,57,58]. At six years old, females are deemed adults [59] and previous research on the  
174 macaque population of Cayo Santiago has shown that, for females that survive to reproductive  
175 age, the median lifespan is 18 years with a maximum lifespan of about 30 years [53,60]. Female  
176 rhesus macaques have a strict dominance hierarchy with maternal rank inheritance and youngest

177 ascendancy [61]. Patterns of social interactions and social attention vary between young and old  
178 adults [6,34,62]. Female macaques show clear evidence of within-individual declines in the  
179 number of grooming partners with age, although the amount of time spent giving and receiving  
180 grooming remains constant across adulthood [38].

181         For this study, subjects were mature adult females 6 years and older [59] from 6 naturally  
182 formed mixed-sex social groups. We used data collected between 2010-2017, a time period for  
183 which we had detailed behavioural data from which to estimate social networks. We collected  
184 behavioural data between 07:30 and 14:00, which are the working hours of the field station,  
185 using 10-min focal animal samples and recording all behaviours continuously [63]. We balanced  
186 data collection to ensure equal sampling of individuals throughout the day and over the course of  
187 the year, resulting in approximately the same number of focal samples per individual per year.  
188 For these analyses we used grooming interactions to build our networks, given the clear age-  
189 based changes in grooming associations previously demonstrated in this system [6]. Grooming  
190 behaviour was collected by recording the duration of a grooming bout along with the identities of  
191 the interactants and the direction of grooming. We focused only on interactions between adult  
192 females ( $\geq 6$  years old) and did not include interactions with infants ( $<1$  year old), juveniles (2-3  
193 years old), or sub-adult females (4-5 years old). We also did not include interactions with males  
194 as we wanted to avoid capturing changes in socio-sexual behaviour with age. We established  
195 dominance ranks for all females in a given year using observed win-loss interactions (as per  
196 [64,65]). Rank was assigned as “high” ( $\geq 80\%$  of other females dominated), “medium” (50%-  
197 79% of other females dominated) or “low” ( $\leq 49\%$  of other females dominated).

## 198 **Social networks**

199         We built 19 grooming networks including all adult females ( $\geq 6$  years old) from the



200 following group-years (group F 2010-2017; group HH 2014; group KK 2015; group R 2015-  
201 2016; group S 2011; group V 2015-2016), with data availability based on the focus of projects  
202 over time given limited person power. We used weighted network metrics, as these are more  
203 robust and provide higher resolution than binary measures [66]. In these weighted networks,  
204 edges represented the undirected rate of grooming between a pair of individuals (seconds of  
205 grooming/total number of hours that both individuals were observed in focal animal samples).  
206 We note that using undirected grooming rates may fail to capture some finer nuances of age-  
207 based variation in social behaviour if, for instance, older individuals were likely to give less  
208 grooming than they received [61]. However, our most recent within-individual analyses suggest  
209 that while the number of grooming partners does decline as females age, both the amount of  
210 grooming given and received remains constant [6]. Therefore, the use of undirected grooming  
211 rates to build networks should provide a comprehensive picture of how individual connectedness  
212 to the wider network changes with age, without missing essential changes in the form that the  
213 connectedness takes. The average size of our networks was 50.7 ( $\pm$  SE = 3.9) adult females. All  
214 network metrics were calculated in R (version 4.2.0; [67]) using the igraph package (version  
215 1.3.1; [68]).

## 216 **Empirical analyses**

217 All empirical models were fitted in a Bayesian framework with different error structures  
218 and random effects dependent on the data analysed (see below). We conducted all analyses using  
219 R (version 4.2.0; [67]) and fitted all models in the Bayesian software STAN [69] using the brms  
220 package (version 2.17.0; [70]). All fixed effects were given weakly informative priors (see  
221 Supplementary Information for more details). We ran all models for 10,000 iterations across two  
222 chains with a warm-up period of 2,000 iterations. We assessed model convergence by examining

223 trace plots to assess sampling mixing and by ensuring  $R_{hat} = 1$ . We considered estimates of  
224 fixed effects to be significantly different from zero when the 95% credible intervals of the  
225 posterior distribution did not overlap zero.

226  
227 *Investigating the relationship between age and indirect connectedness*

228  
229 For these analyses we set out to test how individuals' level of indirect connectedness  
230 to their social network changed from prime adulthood into later life. In our dataset, the median  
231 age of adult females was 10-years and previous studies in this system have shown that  
232 individuals aged 10 and beyond show clear evidence of physical [71–74], immunological [75],  
233 reproductive [71], and social ageing [6]. To capture later-life changes in indirect connectedness  
234 we focused our analyses on individuals aged 10 and older, in line with previous ageing studies  
235 [6]. Females in this analysis therefore ranged between 10 and 28 years old, although, to be clear,  
236 all measures of indirect connectedness for these females were extracted from the networks  
237 including all adult females ( $\geq 6$  years old; see above). We had 563 macaque years of data over  
238 204 unique females, with an average of 2.8 years of data per individual (range: 1-8 years; Fig.  
239 S1). Because there was variation in the age-ranges over which individuals were sampled, we  
240 used a within-individual centering approach to capture changes in indirect connectedness across  
241 individuals' lifespans [76]. Briefly, following the methodology of van de Pol & Wright (2009)  
242 we split our age term into a between-individual effect (calculated as the mean age of an  
243 individual across all observations; hereafter called average age) and a within-individual effect  
244 (calculated as the deviation of an individual's age from their mean age; hereafter called within-  
245 individual age). This within-individual age term was our primary variable of interest and reflects  
246 how an individual's deviation from its age affects its indirect connectedness in the network (see  
247 [6] for a more detailed description of these methods).

248           We fitted four models with our four response variables of interest: eigenvector centrality,  
249 betweenness, closeness, and clustering coefficient. All statistical models included average age  
250 and within-individual age as continuous fixed effects. Given the strict dominance hierarchy  
251 exhibited by female rhesus macaques [61], we assessed whether social status affected the change  
252 in an individual's measures of indirect connectedness with age [6] by fitting an interaction  
253 between rank and within-individual age in all models. We removed the interaction when not  
254 significant. We included individual ID, group, and year, as random effects to account for  
255 repeated observations and to capture any variation in indirect connectedness measures that might  
256 be due to differences between individuals, groups, or years. We also fitted within-individual age  
257 as a random slope over individual ID to capture any among-individual variation in the change in  
258 indirect connectedness with age. We had no biological reason to expect non-linearities in the  
259 relationship between age and measures of indirect connectedness given that we were looking at  
260 changes from prime adulthood to old age and we've previously found a linear relationship  
261 between direct measures of connectedness and age [6]. Nevertheless, we fitted a model with  
262 quadratic terms for within-individual age and average age and compared that model to the model  
263 with only linear age terms using leave-one-out cross-validation in the brms package (version  
264 2.17.0) [70]. The quadratic terms never improved the model fit and so were not considered  
265 further. For the eigenvector centrality model, we logit-transformed the response variable to  
266 improve model fit and fitted a model with a Gaussian error distribution. For betweenness we  
267 fitted a model with a zero-inflated Poisson distribution. For closeness and clustering coefficient  
268 we fitted models with a Beta error distribution and a zero-one-inflated Beta error distribution,  
269 respectively.  
270

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273

*Investigating the relationship between age distribution and network structure*

274           Our analyses quantifying changes in indirect connectedness with age focused on females  
275 aged 10 and older to capture individual changes in social network position from prime age and  
276 beyond. Here we were interested in how the age distribution of a group was linked to network  
277 structure. For these analyses we therefore used our complete networks including all adult females  
278 aged 6 and older. We had three response variables of interest (three measures of global network  
279 structure) and fitted a separate model for each: mean degree, diameter, and transitivity. To ask if  
280 age distribution relates to network structure, we included the proportion of old individuals as a  
281 continuous predictor in all our models. Since 18 is the median age of death in this population and  
282 maximum lifespan is about 30 years, we considered individuals above 18 to be “old” [52,61].  
283 The proportion of old females in our 19 networks ranged from 0.03 to 0.19 (Fig. 1; Fig. S2).  
284 Given that rhesus macaques live in matrilineal groups with kin-biased behaviour [53,77], we  
285 included the average relatedness of the network as a continuous covariate to account for  
286 differences between groups in general relatedness. We also included network density (calculated  
287 as the number of existing ties in the network divided by the number of possible ties) as a  
288 continuous fixed effect in the models of diameter and transitivity to account for the fact that  
289 density can drive variation in other global network metrics. We included year as a random effect  
290 to account for yearly variation that might affect network structure. For the diameter model, we  
291 log-transformed the response variable to improve model fit. We fitted all models with a Gaussian  
292 error distribution. To account for a potential non-linear relationship between age distribution and  
293 network structure we fitted all models with a quadratic term for proportion of old individuals and  
294 compared that to the model with only linear terms using leave-one-out cross-validation in the

295 brms package (version 2.17.0; [70]). The quadratic terms never improved model fit and so were  
296 not considered further.

297  
298 **Agent-based model of the relationship between age distribution and network structure**

299         We expected that age-based changes in patterns of direct association would scale up to  
300 affect overall network structure. However, our empirical data revealed no effect of the proportion  
301 of old individuals in the network on global network metrics (see Results section below). To  
302 better understand these results, we built an individual-based model where we could manipulate  
303 age-based differences in sociality in isolation of other variables to better explore how different  
304 age distributions would be expected to affect overall network structure, and why such scaling up  
305 of age-based differences in social behaviour may not be detectable in our data. Our general  
306 approach was to simulate artificial populations that exhibited the social age-dependencies  
307 observed in the rhesus macaque system on Cayo Santiago and use these to investigate the  
308 relationship between age distribution and global network metrics. As mentioned above, adult  
309 female rhesus macaques change two aspects of their sociality with age: their number of social  
310 partners, and the proportion of partners that are kin [6]. These individual changes in sociality  
311 across adulthood lead to differences between young and old individuals in both the number of  
312 social connections and probability of connecting with kin [6].

313         The model therefore simulates social networks of varying age distributions, in which the  
314 probability that two nodes (i.e., individuals) have an edge (i.e., a grooming link) depends on the  
315 age of the individuals and their and kinship to each other. Individuals belonged to two age  
316 categories (as in the empirical analysis for global structure; old adults and young adults, hereafter  
317 “old” and “young”) and two kin categories (kin and non-kin). This gives 6 dyad types, which we  
318 denote by the age categories of the two individuals and their kinship status (e.g., old/old kin). We

319 established the linking probability (i.e., the chance of having an edge in the social network) for  
320 each dyad type based on the mean proportion of dyads of that type that had an edge across the 19  
321 empirical macaque grooming networks. The linking probability for dyads that were old  
322 individuals who were related to each other (i.e., old/old kin) was 0.33; for old/old non-kin dyads  
323 it was 0.02; for old/young kin dyads it was 0.37; for old/young non-kin dyads it was 0.05; for  
324 young/young kin dyads it was 0.27 and for young/young non-kin dyads it was 0.08. We fixed  
325 group size at 50 individuals, which approximates the mean number of adult females in real  
326 groups on Cayo Santiago (mean  $\pm$  SE = 50.7  $\pm$  3.9). Each simulated network had 10 clusters of  
327 individuals who were related to each other (i.e., kin groups) with 5 individuals in each. The  
328 number of individuals within each kin group mirrors the mean number of close adult female kin  
329 (relatedness coefficient  $\geq$  0.125) that adult female rhesus macaques have on Cayo Santiago  
330 (mean  $\pm$  SE = 5.2  $\pm$  0.87). In the model, kinship between pairs of individuals was determined by  
331 their kin group membership: individuals from the same kin group were classed as kin and  
332 individuals from different kin groups were classed as non-kin.

333 Each simulation round (i.e., construction and quantification of one network) proceeded as  
334 follows: We first randomly drew the number of old individuals in the group ( $n_{old}$ ) from a uniform  
335 distribution with a set range [0, 50]. We then randomly assigned all 50 group members to age-  
336 groups ( $n_{old}$  old individuals and  $n_{young} = 50 - n_{old}$  young individuals) and kin groups. This allowed  
337 the age structure of the groups to vary across the range from only young individuals (0% old) to  
338 only old individuals (100% old). We then constructed the social network by drawing links, where  
339 the chance of each dyad getting a link depended on their dyad type (linking probabilities given  
340 above). To determine whether a dyad was given a link, we extracted a random value from a  
341 binomial distribution with a sample of 1 and probability equal to the linking probability of the

342 type of dyad. If the extracted value was 1, the dyad was given a link, if it was 0, the dyad was not  
343 given a link. A schematic representation of the various steps of the model-building process can  
344 be found in Fig S3.

345 To confirm that the model was working as intended, we ran 10000 simulations (i.e., we  
346 generated 10000 networks), from which we calculated the proportion of dyads of each type that  
347 had a link. We confirmed that the means of these proportions (old/old kin = 0.33; old/old non-kin  
348 = 0.02; old/young kin = 0.37; old/young non-kin = 0.05; young/young kin = 0.27; young/young  
349 non-kin = 0.08) corresponded well to their respective empirical linking probability (see above,  
350 and Fig. S4). We also confirmed that our model was not highly sensitive to our input linking  
351 probabilities (see Supplementary Methods, Table S1, Fig. S5 for more information). Given that  
352 our input values are only estimates of the real values, robustness to these values is important for  
353 drawing general conclusions about the potential effects in the real system.

354 To investigate the general relationship between age distribution and network structure,  
355 we ran 100000 replicates of the simulation (i.e., generated 100000 networks) where we allowed  
356 the proportion of old individuals in the network to range from 0.00 to 1.00 and visualised the  
357 relationship between the proportion of old individuals and network mean degree, diameter, and  
358 transitivity. Additionally, we used the agent-based model to investigate if we should expect to  
359 find relationships between the proportion of old individuals and network metrics in the empirical  
360 analysis. To do this, we limited the proportion of old individuals in each network to between  
361 0.04 and 0.20 (mirroring the empirical variation in age distributions), and we ran 19 simulations  
362 (mirroring the 19 empirical networks). We repeated this 50 times (i.e., 50 sets of 19 networks) to  
363 gauge consistency of the results.

364

365 **Results**

366

367 **Relationship between age and indirect measures of network connectedness**

368

369 In line with our predictions, female macaques did not show any change in eigenvector  
370 centrality with age (within-individual age:  $\beta = -0.04$ ; 95% CI = -0.30, 0.24; Fig. 2A-B, Table S2).  
371 That is, as females aged, the strength of their relationships to their partners, and to their partners'  
372 partners, was stable. We did find evidence of a within-individual decline in betweenness with age.  
373 However, this effect was rank dependent and seems to be driven primarily by a decline in  
374 betweenness as high-ranking individuals got older (within-individual age:rankH:  $\beta = -0.35$ ; 95%  
375 CI = -0.41, -0.29; Fig. 2C-D, Table S3), although mid-ranking individuals also showed greater  
376 declines in betweenness with age than did low-ranking females (within-individual age:rankM:  $\beta =$   
377  $-0.14$ ; 95% CI = -0.18, -0.09; Fig. 2C-D, Table S3). Therefore, some, but not all individuals  
378 became less effective at reaching disparate nodes in the network as they got older. Individuals  
379 showed a reduction in their closeness with age (within-individual age:  $\beta = -0.18$ ; 95% CI = -0.35,  
380  $-0.02$ ; Fig. 2E-F, Table S4), meaning they were harder to reach and be reached in the network, as  
381 we predicted. Contrary to our predictions, there was no within-individual effect of age on  
382 clustering coefficient (within-individual age:  $\beta = 0.04$ ; 95% CI = -0.06, 0.14; Fig. 2G-H, Table  
383 S5). That is, individual cliquishness was stable as individuals aged.

384

385 **Relationship between age distribution and network structure**

386

387 *Empirical results*

388 Contrary to our predictions, we found no evidence that groups with a greater number of  
389 old individuals were structured differently from groups with fewer old individuals. There was no  
390 overall effect of the proportion of old individuals in the group on mean degree ( $\beta = -2.76$ ; 95%



391 CI = -10.24, 5.25; n = 19; Fig. 3A, Table S6), or network diameter ( $\beta = -0.12$ ; 95% CI = -3.93,  
392 3.67; n = 19; Fig. 3B, Table S7). Therefore, networks were not more sparsely connected as the  
393 proportion of older animals increased. Older networks were also not more clustered or cliquish,  
394 as measured by transitivity ( $\beta = 0.20$ ; 95% CI = -0.29, 0.70; n = 19; Fig. 3C, Table S8).

### 395 396 *Agent-based model results*

397 Different group demographics in age appeared to have important consequences for  
398 network structure in our simulations (Fig. 4; Fig. S6). Specifically, our 100,000 simulations  
399 where we allowed the proportion of old individuals in the network to range from 0.00 to 1.00  
400 showed that, as the proportion of old individuals in the population increased, mean degree (i.e.,  
401 the mean number of partners that each individual associated with) decreased (Fig. 4D), and the  
402 diameter of the network (i.e., the longest path length in the network) increased (Fig. 4E), both as  
403 expected. Network transitivity (i.e., the degree of clustering in the network; Fig. 4F) showed  
404 little variation in relation to age distribution.

405 Importantly, these global metrics did not always exhibit linear relationships with network  
406 age (as might have initially been intuitively expected). The potential for non-linearity is  
407 important for understanding when the effects of age on network structure might be the most  
408 pronounced and most detectable in the real world. In particular, the increase in network diameter  
409 with an increasing proportion of old individuals showed an accelerating trend (Fig. 4E). That is,  
410 the relationship between network diameter and proportion of old individual was stronger (i.e., the  
411 slope was steeper) when the proportion of old individuals in the network was high, suggesting  
412 that effects of age on network structure might be most detectable when, for example, greater than  
413 50% of the individuals in the network are old. While we did not find any clear change in  
414 transitivity with the proportion of old individuals in the network, there was also some evidence

415 of an accelerating trend at the higher end of the age distribution. These metrics (transitivity,  
416 diameter) are driven to a greater extent by modularity in networks and the non-linear relationship  
417 could arise from the kin-biased nature of the relationships in our (modelled) study system. We  
418 also observed that transitivity and network diameter were more variable when there was a greater  
419 proportion of old individuals in the network. This suggests that changes in network structure  
420 with changing age distribution might be unpredictable, for example, networks might become  
421 more clustered or less clustered as the population gets older. Overall, these results suggest that  
422 compared to networks with more young individuals, networks with more old individuals are  
423 sparser and less cohesive, and can take on more varied structures.

424 When we limited the sample size and variation in age distribution to those of the  
425 empirical data (i.e., 19 networks where the proportion of old individuals was only allowed to  
426 vary between 0.04 and 0.20) we observed no clear change in network structure as the proportion  
427 of old individuals in the network increased (Fig. 4G-I).

## 428 429 **Discussion**

430  
431 Age has begun to emerge as an important attribute shaping the social decisions of  
432 individuals [6,7,14]. This implies that age is a potentially significant feature underlying the  
433 behaviour of animals in collectives. Here we have shown that age-based changes in social  
434 behaviour are likely to have important consequences for an individual's position within the wider  
435 social network and may scale up to influence network topology. As female rhesus macaques  
436 aged, they showed declines in some, but not all of their indirect measures of connectedness. But  
437 despite age-based changes in both direct connectedness [6] and indirect connectedness (this  
438 paper) we detected no effect of age distribution on the overall structure of rhesus macaque  
439 networks. The agent-based model gives insight into this surprising result, as it implies that age-

440 based differences in social behaviour do necessarily, as expected, scale up to affect network  
441 structure, but that these effects may be nonlinear and so may not always be easily detectable.

442 In line with our predictions, we found no evidence for changes in eigenvector centrality  
443 with age. This was expected because, despite reducing their number of social partners, female  
444 rhesus macaques maintain the amount of time they engage in social interactions as they get older  
445 [6], allowing them to continue to have strong connections to some of their partners, and  
446 (indirectly) to the partners of their partners. A similar pattern has been observed in a population  
447 of wild rhesus macaques in China whereby older individuals had fewer partners but exhibited  
448 similar weighted eigenvector centrality to those of younger individuals [34]. Unexpectedly, we  
449 did not find any evidence that clustering coefficient increased as individuals aged in this  
450 population. Females increase their preference for grooming kin as they age [6], suggesting that  
451 within-group (e.g., homophilic) tendencies increase with age, which should lead to greater  
452 clustering as females from the same matriline would cluster together in the network. However,  
453 although kin-biases increase with age, they exist for females of all ages [58]. It is therefore  
454 possible that ties with kin are the main driver of clustering coefficient scores regardless of age.  
455 The loss or removal of a few non-kin relationships as an individual ages could thus have a  
456 relatively minor impact on their clustering coefficient, leading to stable values for this metric  
457 across the adult lifespan. In general, the stability of weighted eigenvector centrality and  
458 clustering coefficient across the adult lifespan suggest that older animals can remain socially  
459 central and well-integrated in some respects, despite other aspects of their social life changing  
460 (e.g., fewer partners overall, and the patterns observed below). Old individuals may therefore  
461 continue to reap some of the advantages of social relationships [5].

462           As predicted, we found declines in betweenness and closeness with age, although some  
463 of these results were rank dependent. As individuals got older, particularly those that were higher  
464 ranking had less influence on and became less well-connected to the wider network.  
465 Betweenness and closeness are associated with an individual's level of reassociation tendency  
466 and within-group association [51]. In other words, the more likely individuals are to reassociate  
467 with the same partners, and to select partners of similar characteristics to themselves, the less  
468 they mix with the wider network and the less likely they are to connect distinct subgroups (i.e.,  
469 have high betweenness) or be easily reached by all others in the network (i.e., have high  
470 closeness). We've previously shown that ageing rhesus macaque females have fewer partners,  
471 but engage with those partners more often, and increase their preference for close relatives. In  
472 other words, while mean dyadic association strength to associates increases with age, mixing  
473 with the wider network should decline [6]. Our betweenness and closeness results seem to reflect  
474 these underlying changes in behavioural patterns. The declines in betweenness with age were  
475 rank dependent, with mid-ranking and high-ranking rhesus macaque females showing a greater  
476 decline in betweenness with age than low-ranking individuals. This may simply be due to a floor  
477 effect – because low ranking individuals have such low betweenness to begin with, there is little  
478 capacity for further decline with age.

479           Generally, our findings demonstrate that how indirectly connected an individual is to  
480 their social world can change across their lifespan. How an individual is positioned in the wider  
481 social environment can modulate their exposure to information [26,31], parasites [18,77], and  
482 pathogens [20–22]. Individuals with high betweenness and closeness occupy a critical position in  
483 the acquisition and transfer of 'goods' within a network [17,54,78]. Decreases in both of these  
484 measures of indirect connectedness with age may benefit aged individuals who may experience

485 greater susceptibility to disease or illness as a result of immunosenescence [79]. Such benefits  
486 need not imply that individuals actively change complex network positions with age. By  
487 changing simple behavioural rules or processes with age, changes in polyadic ties with age are  
488 likely to emerge [51]. Measures of indirect connectedness have been linked to fitness proxies  
489 including future social status [80,81], survival [82,83], and reproductive success [32,64,81].  
490 Indirect network metrics can be an even stronger predictor of fitness proxies [17,32] than  
491 measures of direct connections and may more strongly reflect the underlying behavioural rules  
492 that give rise to individual differences in sociality [51]. As such, documenting how ageing shapes  
493 the polyadic social world may be particularly relevant for understanding how changes in  
494 sociality across the lifespan influence patterns of senescence and fitness in later life.

495         While age is clearly associated with changes in the behaviour and social connectedness of  
496 animals living in groups [10,13,14], including in this population of rhesus macaques [6,60], we  
497 did not find any empirical evidence that age impacts the overall structure of those groups. We  
498 found no relationship between age distribution and network mean degree, diameter, or  
499 transitivity in the observed macaque data. This was surprising to us given that we expected that  
500 age-based changes at the individual level would scale up to the network level. That is, it should  
501 be self-evident that a network with more old individuals who each interact with fewer partners  
502 would, for example, have a lower mean degree. Given that we did not find empirical evidence of  
503 this, we used an agent-based modelling approach to try to understand why these results might  
504 emerge and whether under a scenario where everything else is equal, we could recreate these  
505 expected effects on network structure.

506         By modelling age-based differences in two interaction patterns (number of social partners  
507 and the tendency to link with kin) based on the age-based changes we observed in the female

508 macaques [6], we found that the age composition of a group can have important consequences  
509 for its cohesiveness and connectedness. As predicted, mean degree declined and diameter  
510 increased as the proportion of old individuals increased, while transitivity exhibited no strong  
511 relationship to age-distribution. Interestingly, these effects did not necessarily scale in the linear  
512 manner that might be expected in response to a linear increase in proportion of old individuals in  
513 the network. Network diameter showed a steeper increase as networks became older, suggesting  
514 that the strength of the effect, and thereby the ability to statistically detect an effect in a real-  
515 world case, might depend on where along the continuum of age distributions one's data lie. The  
516 combination of this and a limited sample size could potentially have led to the null result in our  
517 empirical analysis. This interpretation is supported by the fact that when we limited the age  
518 variation and sample size (number of networks) of our model to match that of the empirical data  
519 (i.e., only ran the model for 19 simulations and allowed the proportion of old individuals in the  
520 network to range between 0.4-0.20) there was no clear relationship between the proportion of old  
521 individuals and network structure.

522         The results of our model suggest that populations made up of very large numbers of  
523 young, or old, individuals may have detectable levels of divergence in network structure,  
524 whereas populations within a smaller range of age distributions may not. Sample size also  
525 appears to have played an important role in our ability to detect an effect of network age on  
526 network structure. Each “bout” of 19 networks (simulations) produced a slightly different result.  
527 Sometimes slopes were positive, sometimes negative, sometimes flat, suggesting there is a fair  
528 amount of stochasticity in our ability to detect the true effect when the sample size is small, even  
529 in the model world where there are no other confounding factors. While nineteen rhesus  
530 macaque networks from 6 groups collected across 8 years represents a considerable investment

531 of research time and effort, it may not have been enough to detect a clear pattern. However, it is  
532 also possible that our empirical results reflect a true null result if there are processes occurring  
533 that our model has not accounted for. Our model is a simplistic version of the real world and  
534 does not fully replicate the complete suite of changes that might occur as individuals age. For  
535 example, our model does not allow for potential rewiring between nodes which might occur if  
536 younger individuals choose to build new ties in response to the loss of ties with older individuals.  
537 Such rewiring could explain why some measures of network structure do not change despite  
538 individual declines in sociality with age.

539         While the general result from the agent-based model was expected, these simulations  
540 help to inform our understanding of the empirical data and offer us a glimpse into how age-based  
541 differences in sociality may affect network structure and when these effects might be detected.  
542 The fact that, even in our simplified model where there is nothing to obscure individual linking  
543 probabilities from scaling up to affect global network metrics, changes in some measures of  
544 network structure appear most likely to be detected in very old populations raises the question of  
545 when such effects are likely to be detectable in wild systems. The macaques of Cayo Santiago  
546 are a managed population that are food supplemented and have no predators. As such the  
547 proportion of old individuals seems likely to be higher than in many wild populations and aligns  
548 with other natural but non-predated systems (e.g., red deer [84]) where the proportion of old  
549 individuals in the population appears to top out at about 20%. Our model suggests that the effects  
550 of age on network structure are also present at this lower end of the age-distribution, but are less  
551 strong, or negligible, for some network measures. Hence, detecting an effect in real systems  
552 could necessitate large amounts of data. We note, however, that the effect on the network  
553 measures (the shapes of the curves) will depend both on how sociality changes with age, and the

554 social organisation of the system (such as relatedness patterns), and while other systems may be  
555 similar to the one here investigated in these regards, making predictions for detectability of  
556 social ageing effects in general would require more comprehensive modelling.

557 Future work in other systems, conditions, and contexts could reveal consequences of age-  
558 based changes in sociality for network structure that are even more stark. For example, greater  
559 differences between age classes in the overall probability of forming a social tie may be expected  
560 in societies that experience selective disappearance of more social individuals or where declines  
561 in sociality with age are exacerbated by partners dying and not being replaced (which we do not  
562 observe in this system [6]). The kin structure of populations is also likely to be important if the  
563 probability of connecting decreases with age but there is no compensatory increase in the  
564 probability of forming ties with kin. This could lead to stronger absolute effects on global  
565 network metrics, including substantial changes in transitivity, and thus would likely have further  
566 consequences for network connectivity and spreading processes. While our analyses bin  
567 individuals into age categories of “old” and “young”, there may be much more nuanced effects  
568 of age on network structure if the full age distribution of a population or group is taken into  
569 account.

570 It is also important to recognize that the results presented here only reflect how changes  
571 in female sociality across adulthood are expected to influence adult female social networks.  
572 Understanding how social networks of entire groups are affected by age-based changes in  
573 behaviour, more broadly, will necessitate incorporating an understanding of the patterns of social  
574 ageing in both sexes, as well as an understanding of how interactions with juveniles shift as  
575 adults get older. While much less is known about the social ageing trajectories of males, some  
576 studies suggest that they show lower levels of connectedness at older ages, similar to those



577 observed in females [13,33]. But even in cases where social ageing trajectories are similar across  
578 the sexes, changes in socio-sexual interactions with age in addition to shifting interactions  
579 between age classes are likely to produce much more complex network dynamics than observed  
580 here, necessitating further research.

581         Despite these limitations, our study provides a first glimpse into the effects that age-based  
582 changes in behaviour might have on network structure, offering a deeper understanding of the  
583 potential importance of demographic changes for the structure and function of collectives. Much  
584 attention has been given to the potential for the social structure of populations to be affected by  
585 the removal of older individuals, for example through practices like trophy hunting or fishing  
586 [85,86]. This is relevant given that older individuals can play a critical role in their social groups  
587 through leadership [4,39], intergenerational transfers [40], and the stabilisation of social  
588 relationships [87]. Despite the importance of the loss of older individuals from networks, our  
589 results suggest that asking what happens when populations contain large numbers of older  
590 individuals may be an equally salient question.

591         In humans, population ageing is poised to be one of the most significant social  
592 transformations of the 21<sup>st</sup> century, with the global number of older persons projected to more  
593 than double over the next three decades [88], facilitated by falling fertility rates and increasing  
594 longevity [89,90]. Meanwhile, in other group-living species, anthropogenic challenges, including  
595 climate change, poaching, disease outbreaks, and pollution, among others, are likely to cause  
596 major population declines and demographic shifts [91,92]. The consequences of declining  
597 fertility and/or increasing mortality rates may be further exacerbated by the concomitant shifts in  
598 age structure and resulting implications for network structure and function. For instance, declines  
599 in cohesiveness and structural connectedness in older networks may limit or slow the transfer of

600 information [24,93], restrict the potential for cooperation [94] or reduce the stability of  
601 populations [30], feeding back to further limit population growth. Alternatively, such changes  
602 could reduce the vulnerability of populations to infectious diseases or parasites [30,95] or  
603 enhance cooperation if network modularity is increased [96]. Consequently, through its effects  
604 on network structure, shifting age demography may have broader implications than previously  
605 appreciated for group dynamics and persistence and warrants further research.

606

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620 **Data availability:** All data and code associated with the analyses will be made publicly available  
621 on the Figshare Repository following acceptance of the manuscript.

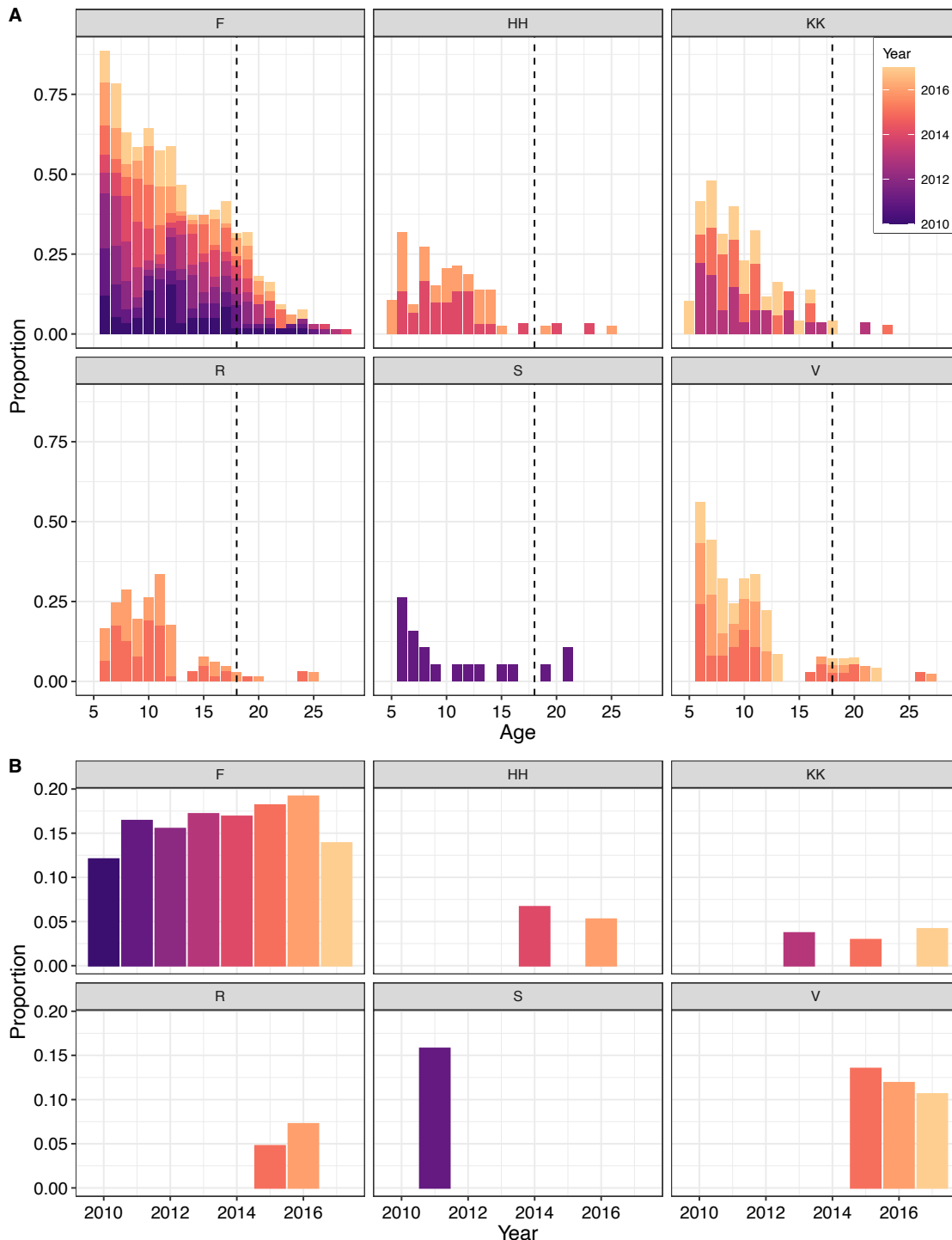
622 **Competing Interest Statement:** The authors declare no competing interests.

623 **Table 1.** Predictions for how indirect measures of connectedness are expected to change with  
 624 age in female rhesus macaques from Cayo Santiago and how global network metrics are  
 625 expected to change with increasing proportions of old individuals in the population.

<b>Network Metric</b>	<b>Definition</b>	<b>Prediction</b>	<b>Rationale</b>
<b>Indirect network metrics</b>			
<b>Eigenvector centrality</b>	Measures how well connected an individual is in the network to individuals who are themselves well connected.	Remain stable with increasing age	Females retain strength of connections to partners as they age.
<b>Betweenness</b>	Calculates the number of shortest paths between others in a network that pass through an individual. Individuals with low betweenness have low capacity for linking discrete clusters in the network.	Decrease with increasing age	Females increase their probability of interacting with strong, stable partners and kin. Therefore, females increase their tendency to reassociate with existing partners and have higher within-group association tendencies as they age.
<b>Closeness</b>	Measures the inverse distance to all other individuals in the network. The lower an individual's closeness score, the more difficult it is for them to reach others or be reached.	Decrease with increasing age	
<b>Clustering</b>	Measures cliquishness or subgrouping. A high clustering coefficient indicates that an individual's partners are highly connected to each other.	Increase with increasing age	
<b>Global network metrics</b>			
<b>Mean degree</b>	The average number of ties that each individual has to others in the network.	Decrease with increasing proportion of old individuals	Older females have fewer social partners.
<b>Diameter</b>	Measures the overall connectedness of the network. Networks with a larger diameter are less connected.	Increase with increasing proportion of old individuals	
<b>Transitivity</b>	The degree of clustering in the network.	Increase with increasing proportion of old individuals	Older females cluster more with kin.

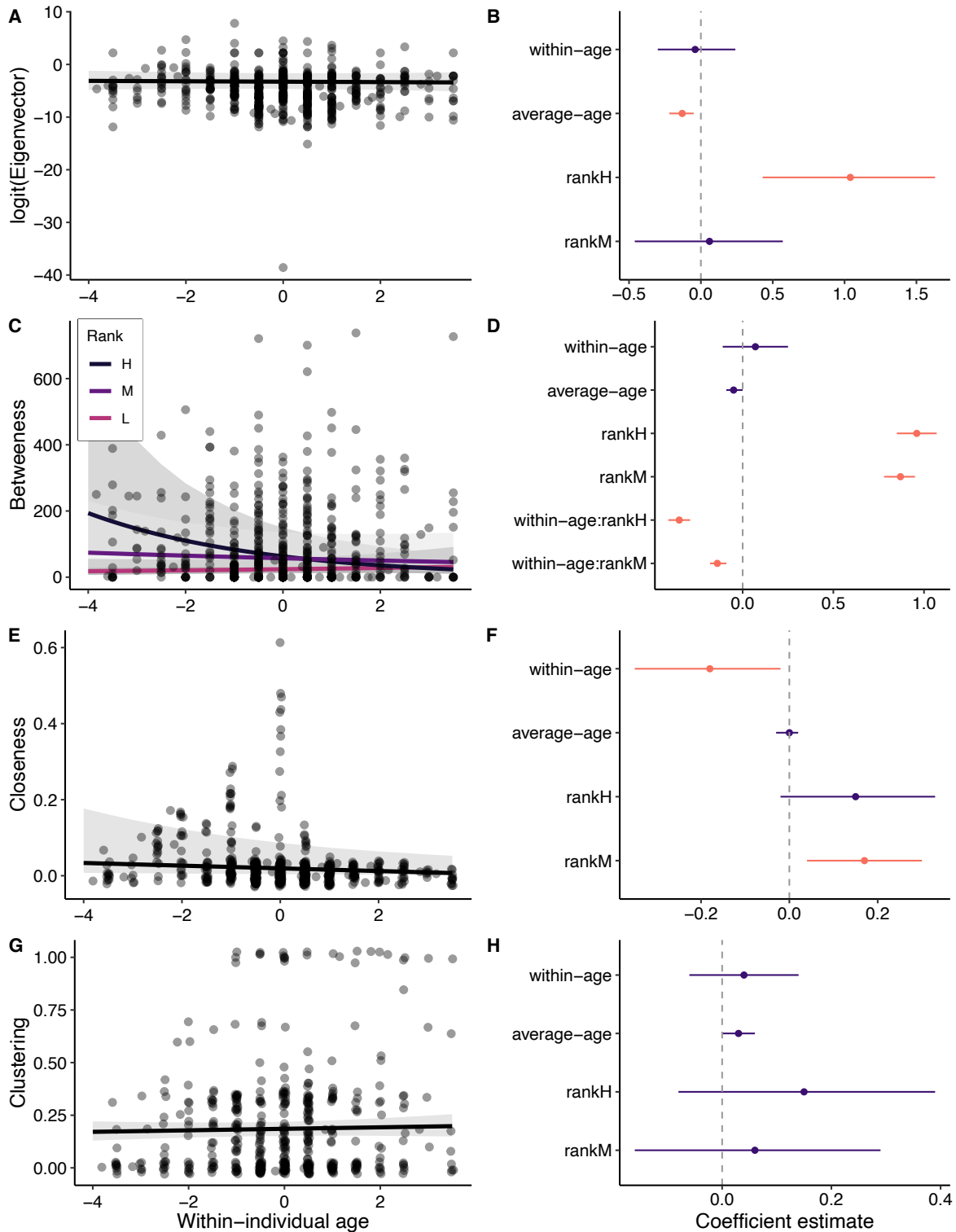
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632 **Figure 1. (A)** Distribution of ages in each of the 6 empirical macaque groups for each year that  
633 those groups were observed (19 networks total observed between 2010-2017). The data are  
634 presented as a stacked bar chart, so to compare the proportion of x-year-olds in a single group  
635 across years one should compare the height of coloured bars within a single age. The dotted  
636 black line at age 18 indicates the median age of death in this population and the cut off at which  
637 we considered individuals “old” for the sake of calculating the proportion of old individuals in  
638 the group. See also Fig. S2. **(B)** Proportion of old individuals in each group for each year that  
639 group was observed. Years with no bars indicate years in which the group was not observed.  
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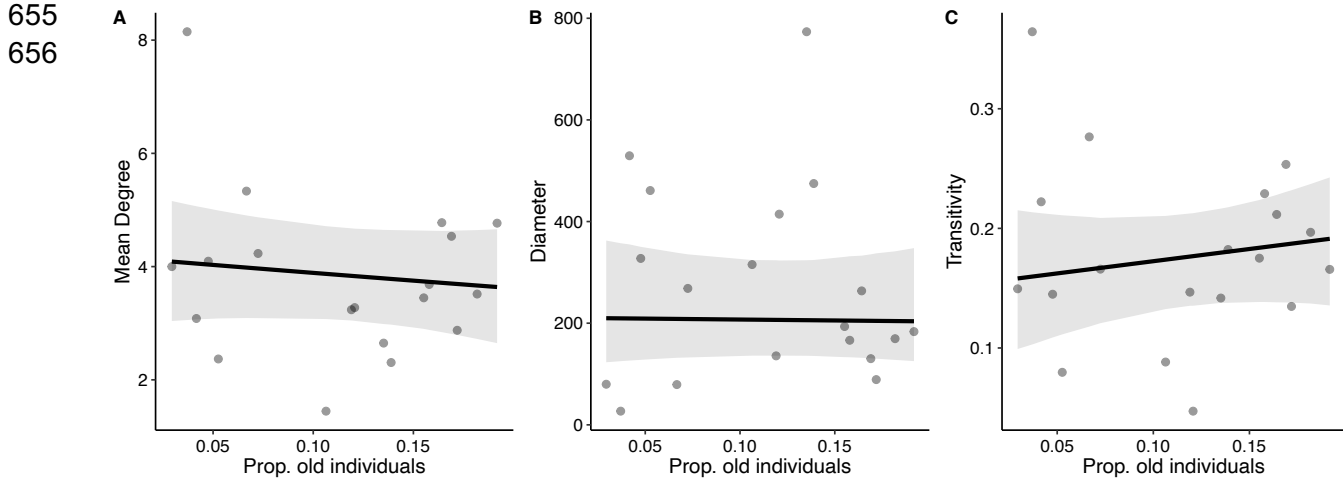


642 **Figure 2.** Relationship between within-individual changes in age and indirect measures of  
643 connectedness including (A & B) eigenvector centrality, (C & D) betweenness, (E & F)  
644 closeness, and (G & H) clustering coefficient in female rhesus macaques. In A, C, E, G the  
645 points represent raw data. Shaded grey bars indicate 95% confidence intervals around the  
646 predicted values. In B, D, F, H effect sizes and 95% credible intervals for all fixed effects and  
647 interaction terms are shown. Instances where the 95% CI overlaps zero are coloured in purple.

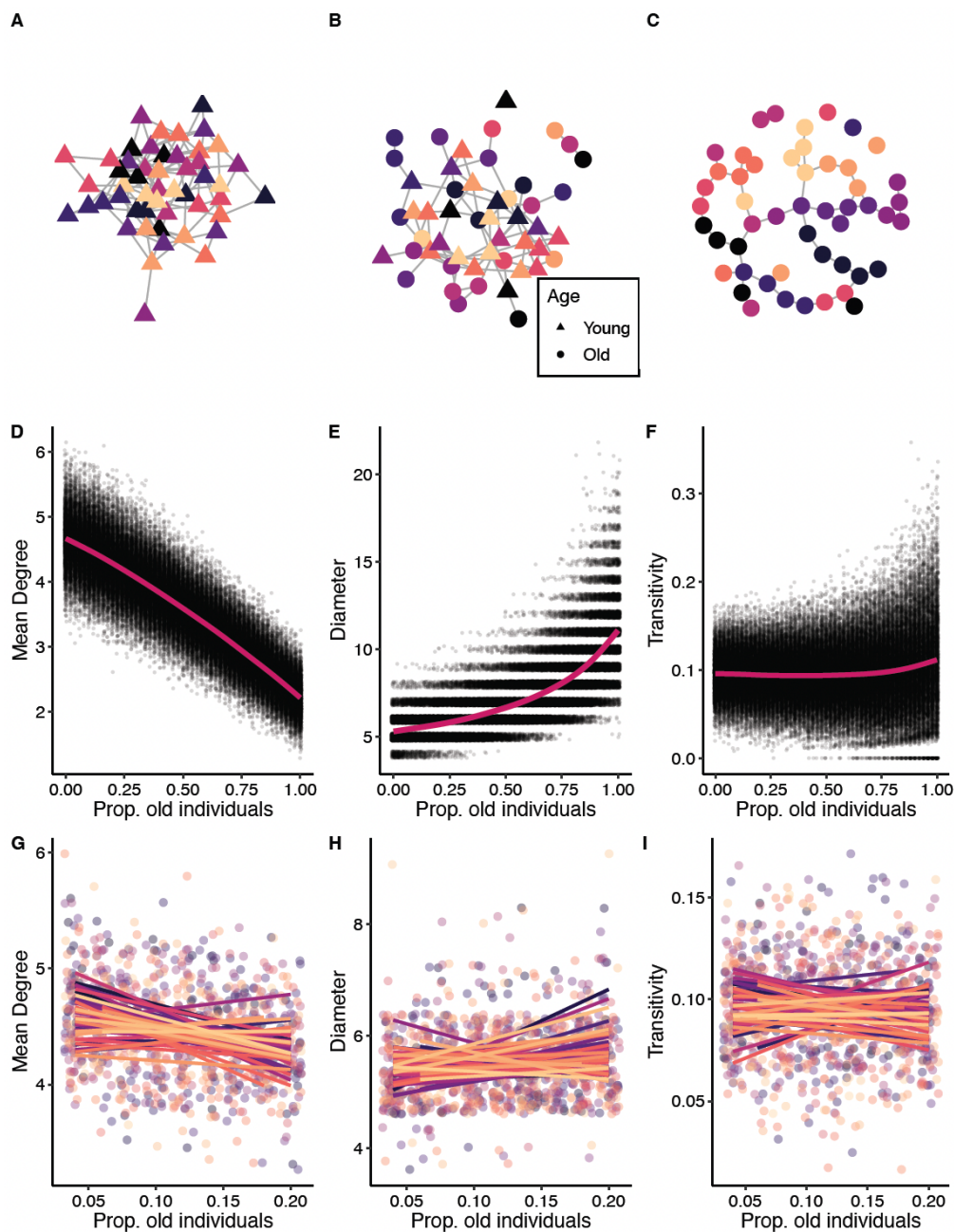
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651 **Figure 3.** The relationship between the proportion of old individuals in female rhesus macaque  
652 networks and: (A) mean degree, (B) network diameter, and (C) network transitivity. Points  
653 represent raw data and shaded grey bars indicate 95% confidence intervals around the predicted  
654 values.



657 **Figure 4.** (A-C) Example networks from the agent-based model illustrating differences in  
658 network structure with the proportions of old individuals in the network equal to 0 (A), 0.5 (B)  
659 and 1 (C). Node colour represents kin groups where nodes of the same colour belong to the same  
660 kin group. (D-F) Results from the agent-based model showing relationship between the  
661 proportion of old individuals and (D) mean degree, (E) diameter, and (F) transitivity. Data points  
662 from the 100K simulations are shown with a small amount of jitter introduced to show  
663 overlapping points and are fitted with a smoothing term. (G-I) Relationship between the  
664 proportion of old individuals and (G) mean degree, (H) network diameter, and (I) transitivity  
665 based on 19 simulations from the agent-based model where the proportion of old individuals in  
666 the population was restricted between 0.04 and 0.20. We re-simulated these 19 networks with  
667 limited age variation 50 times to help ensure our results were robust. Each colour represents a  
668 different ‘bout’ of 19 networks. Data points are shown fitted with a linear smoothing term.  
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