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26 **Age and sex influence social interactions, but not associations, within a killer**  
27 **whale pod**

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60 **Keywords:** centrality, homophily, *Orcinus orca*, social network, social life history,  
61 UAS

## 62 **Abstract**

63 Social structure is a fundamental aspect of animal populations. In order to understand  
64 the function and evolution of animal societies, it is important to quantify how individual  
65 attributes, such as age and sex, shape social relationships. Detecting these influences  
66 in wild populations under natural conditions can be challenging, especially when social  
67 interactions are difficult to observe and broad-scale measures of association are used  
68 as a proxy. In this study, we use unoccupied aerial systems to observe association,  
69 synchronous surfacing, and physical contact within a pod of southern resident killer  
70 whales (*Orcinus orca*). We show that interactions do not occur randomly between  
71 associated individuals, and that interaction types are not interchangeable. While age  
72 and sex did not detectably influence association network structure, both interaction  
73 networks showed significant social homophily by age and sex, and centrality within the  
74 contact network was higher among females and young individuals. These results  
75 suggest killer whales exhibit interesting parallels in social bond formation and social  
76 life histories with primates and other terrestrial social mammals, and demonstrate how  
77 important patterns can be missed when using associations as a proxy for interactions  
78 in animal social network studies.

## 79 **Introduction**

80 Individual characteristics such as sex and age often influence social relationships  
81 and underly variation in social position in animal societies. Understanding how these  
82 characteristics shape social structure under natural conditions can shed light on  
83 numerous aspects of behavioural ecology, including social life history evolution (e.g.  
84 Machanda & Rosati 2020) and the mechanisms underlying social bond formation (e.g.  
85 Gerber et al. 2020), while also providing potentially vital information about population-  
86 level processes such as gene flow and disease transmission (Kurvers et al. 2014).

87 Social network analysis has become an important tool for understanding these  
88 processes over the last two decades (Brent et al. 2011; Webber & Vander Wal 2019),  
89 however uncovering the drivers of social network structure is challenging. Studies of  
90 animal social networks require data on the rates of relevant social behaviours between  
91 identified individuals (Whitehead 2008a; Croft et al. 2008, Farine & Whitehead 2015),  
92 which often require a great deal of sampling to measure precisely (Whitehead 2008b).  
93 Furthermore, the structure of observed social networks is dependent on the  
94 behavioural definition of edges (Castles et al. 2014).

95 While social structure fundamentally arises from the patterns of repeated interactions  
96 between individuals (Hinde 1976), social interactions are often difficult to observe in  
97 free-ranging animals, as interactions may be subtle, rare, or not visible from traditional  
98 observation platforms. Therefore, many studies of social structure in free-ranging  
99 animal populations utilize association indices, measuring the probability that  
100 individuals are found within the same group or a particular spatial proximity during a  
101 sampling period (reviewed by Webber & Vander Wal 2019). As association provides  
102 the opportunity for interaction, these associations are typically assumed to generally

103 reflect patterns of interactions between individuals (Whitehead & Dufault 1999),  
104 however there is still debate over the degree to which associations can reflect true  
105 interactions (e.g. Farine 2015). Using behavioural proxies of relationships that are too  
106 broad or do not represent the relationships of interest may mask the influences of  
107 individual characteristics on social network structure.

108 In this study, we quantify the influence of age and sex on social relationships in a pod  
109 of resident killer whales (*Orcinus orca*). Previous studies of killer whale societies have  
110 suggested that individuals do not show social homophily by age or sex (Tavares et al.  
111 2017; Esteban et al. 2015; Williams & Lusseau 2006), and analyses of individual  
112 network centrality with respect to age and sex in this species have produced mixed  
113 results (Baird & Whitehead 2000; Williams & Lusseau 2006; Tavares et al. 2017). The  
114 apparent lack of age and sex structure in killer whale social networks is somewhat  
115 surprising in the context of other well-studied dolphin species, where social networks  
116 are commonly structured by age and sex (e.g. Hawkins et al. 2019; Hartman et al.  
117 2008; Elliser & Herzing 2014; Leu et al. 2020; Webster et al. 2009). This discrepancy  
118 may be due to the definitions used to construct killer whale social networks. Because  
119 killer whales live and move in stable social units, the position of individuals and the  
120 patterns of edges within association networks are likely to primarily reflect attributes  
121 and relationships at the level of the unit, rather than the individual (e.g. Ivkovich et al.  
122 2009; Williams & Lusseau 2006). This system therefore provides an opportunity to test  
123 the degree to which the use of broad-scale association patterns can mask important  
124 effects of individual characteristics in animal societies.

125 Here, we utilize unoccupied aerial systems (UAS) to quantify association (defined as  
126 individuals detected simultaneously, and therefore with the opportunity to be observed  
127 interacting), synchronous surfacing, and physical contact among individually identified

128 killer whales. In delphinids, synchrony can be beneficial during cooperative behaviours  
129 (Myers et al. 2017) and may be important for maintaining and establishing social  
130 relationships (Connor et al. 2006; McCue et al. 2020). Similarly, physical contact often  
131 signals social affiliation between closely bonded individuals (Connor et al. 2005;  
132 Dudzinski et al. 2017) and may be important for reconciliation after aggressive  
133 interactions (Weaver 2003). We hypothesized that both of these interactions would  
134 occur non-randomly between associated individuals, and that any influence of age and  
135 sex on social structure, both in terms of social homophily and individual centrality  
136 within the social network, would be more clear when analysing these interactions than  
137 when analysing associations.

138

## 139 **Methods**

### 140 *Study population*

141 The southern resident killer whales are a small (< 80 individuals), closed population  
142 inhabiting the coastal waters of the northeastern Pacific, with their core habitat being  
143 the inland waters of Washington, USA and British Columbia, Canada. This population  
144 has been subject to a complete annual census carried out by the Center for Whale  
145 Research since 1976. All individuals can be visually identified using unique markings,  
146 body shapes and sizes, and scarring.

147 The southern residents exhibit lifelong bisexual philopatry to maternal social groups.  
148 The basic social unit is the matriline, composed of close relatives with a recent  
149 common maternal ancestor. Closely related matrilineal groups form pods, larger semi-stable  
150 social groups with a shared vocal dialect (Bigg, et al., 1990; Parsons et al. 2009). This

151 population contains three pods, designated J, K, and L pod, which at the time of the  
152 study contained 22, 18 and 32 individuals, respectively.

153

#### 154 *Field observations*

155 During the summer of 2019, we collected video observations using a small UAS (DJI  
156 Phantom 4 Pro V2) launched from a small motorized vessel (21 ft. Grady White), or  
157 using a larger aircraft (DJI Matrice 600) launched from shore. Focal subgroups (sets  
158 of whales in close physical proximity to each other which could be captured  
159 simultaneously on video) were located by observers prior to launching the aircraft.  
160 Subgroups were primarily chosen for follows based on logistical factors, such as  
161 distance from the launch point and the presence of whale watch and research vessels.  
162 Preference was typically given to larger subgroups to maximize the possible number  
163 of interactions observed over a given observation period. We correct for potential  
164 biases introduced by this preference in our permutation analysis (see below). During  
165 on-water operations, the vessel maintained a low speed (< 7 kts) when within 1 km of  
166 whales. The vessel was usually positioned behind groups of whales, at a distance of  
167 200-400 m (see Ayers et al., (2012) for details on vessel maneuvering).

168 When in the air, one crew member piloted the aircraft, while another served as a visual  
169 observer to aid in maintaining visual line-of-sight and situational awareness. A third  
170 team member was designated as a general observer, tasked with monitoring whale  
171 behaviour during research flights and assisting with operations. The aircraft  
172 maintained an altitude between 30 and 120 meters while above whales, and was  
173 typically positioned to the side of or behind the animals. The angle of the camera and  
174 position of the aircraft were adjusted to ensure a clear view of the full subgroup.

175 Operations were limited to conditions conducive to the safe operation of the UAS and  
176 clear observation of animals below the water (no rain, wind below 10 kts, sea state  
177 less than Beaufort 3). We collected footage of southern residents over 13 days. For  
178 most of these days (10/13), only members of J pod were present. To avoid spurious  
179 inferences about relationships involving K or L pod, we chose to restrict our analysis  
180 to days in which only J pod was present.

181 All data was collected under research permits issued by the US National Marine  
182 Fisheries Service (NMFS permits 21238 and 22141) and all pilots were licensed under  
183 Federal Aviation Administration Part 1077. Research was approved by the University  
184 of Exeter College of Life and Environmental Sciences ethics committee. During flights,  
185 we monitored focal groups to determine if behavioural responses occurred as the UAS  
186 approached, however no behavioural responses were observed during the study.

187

#### 188 *Video analysis*

189 We analyse all video in BORIS software (Friard & Gamba, 2016). Analysis of each  
190 video clip proceeded by first identifying all whales that were visible at any point during  
191 the video by their unique markings, body shapes and size, and scarring. Then, in  
192 random order, each whale was followed for the entirety of the video. We coded a state  
193 variable for individual visibility, indicating when each individual was on screen and  
194 identifiable. We considered individuals to be associated when they were  
195 simultaneously visible in the video (Figure 1).

196 We code physical contact as an undirected point event, recorded when individuals  
197 initially come into contact. As we were interested in patterns of affiliative social  
198 relationships, we excluded aggressive interactions such as fluke strikes and biting. We



199 also exclude observations of nursing. Potential sexual contacts were not excluded, as  
200 affiliative socialization often includes sexual behaviour in this population (Noren &  
201 Hauser, 2016; Osborne, 1986).

202 Synchronous surfacing was also coded as an undirected point event. Individuals were  
203 considered to have breathed in synchrony if they surfaced within one adult female  
204 body length (approx. 6 m) and at some point during their surfacing both individuals'  
205 blowholes were simultaneously above the water's surface. Individuals could be  
206 recorded synchronously surfacing with multiple partners in a single surfacing, however  
207 we did not use a chain-rule, and therefore synchronous surfacings were not transitive.  
208 As both interactions were coded as point events, they did not preclude one another.

209 Our sequential follow protocol generates two records of each interaction, potentially at  
210 slightly different time points. We ensured all interactions were recorded for both  
211 individuals and that all individuals were coded as visible during all of their interactions,  
212 with errors corrected by re-analyzing the video. We set the interaction time as the  
213 midpoint between the two records. The median difference in time between the two  
214 records was 0.203 seconds (IQR = 0.23) for synchronous surfacing and 0.439 seconds  
215 (IQR = 0.656) for contact.

216

### 217 *Determining age, sex, and kinship*

218 In 2019, all surviving members of J pod were born after the study began in 1976, and  
219 thus their ages (in years) are known with certainty. The sexes of all individuals in this  
220 pod were determined based on obvious sexual dimorphism in mature individuals and  
221 from genital coloration in young individuals.

222 Maternal kinship was estimated based on behaviourally defined mother-calf dyads.  
223 These relationships have been universally supported by subsequent genetic sampling  
224 (Ford et al. 2018). From known mother-calf relationships, we constructed a maternal  
225 pedigree and estimated a maternal relatedness matrix using the kinship2 R package  
226 (Sinnwel & Therneu 2020).

227

### 228 *Social network construction*

229 We constructed interaction networks by dividing each dyad's total interaction by their  
230 total observation time. Initial analysis suggested interactions did not occur in bouts  
231 (see supplementary materials), so each interactions was treated as independent. Each  
232 dyad's observation time was summarized as the total amount of time that one or both  
233 of the individuals was visible.

$$234 \quad rate_{ij} = \frac{x_{ij}}{t_i + t_j - t_{ij}} \quad (1)$$

235 Here,  $x_{ij}$  is the number of interactions observed between individuals  $i$  and  $j$ ,  $t_i$  and  $t_j$  are  
236 the total time (in seconds)  $i$  and  $j$  were visible, respectively, and  $t_{ij}$  is the amount of  
237 time both  $i$  and  $j$  were visible simultaneously. We calculate interaction rates separately  
238 for synchronous surfacings and contacts. We quantify the reliability of our interaction  
239 networks by estimating the correlation between true and observed interaction rates  
240 following Whitehead (2008b) (see supplementary materials for details).

241 We construct an association network representing the proportion of sampling time in  
242 which individuals co-occurred in our observations:

$$243 \quad association_{ij} = \frac{t_{ij}}{t_i + t_j - t_{ij}} \quad (2)$$

244 where the variable definitions are the same as in equation 1. This index is comparable  
245 to the “simple ratio index” commonly used in animal social network analysis (Cairns &  
246 Schwager, 1987). Like other association indices, the edges in this network range from  
247 0 (never co-occurred) to 1 (always observed together). This index represents the  
248 proportion of time that individuals were detected together, not the amount of time they  
249 truly spent together; Individuals could fail to be detected while in association if they  
250 were outside of the camera’s field of view, or if they submerged to a depth where they  
251 were no longer visible. During data collection, the camera captured an area with a  
252 median maximum distance between any two recorded points of 85 m (IQR = 30; see  
253 supplementary materials for methods). This distance is comparable to previous killer  
254 whale studies where a cutoff of 10 body lengths (roughly 70 m) has been used (e.g.  
255 Williams & Lusseau 2006). Social networks construction and all further analysis was  
256 carried out in R (R Core Team 2020).

257

### 258 *Comparing associations and interaction rates*

259 We first tested whether the structure of the two interaction networks could be explained  
260 solely by dyadic association and sampling. We construct a null model for our  
261 interaction networks that maintains both individual detection history and temporal  
262 variation in the observed overall rate of interactions. For each observed interaction,  
263 we randomly sample two individuals coded as visible at the time of the interaction as  
264 the new interaction partners. We repeat this procedure 10,000 times, re-calculating  
265 interaction rates for each randomisation to generate 10,000 randomised networks.

266 We first test whether interaction rates are more variable than expected given  
267 associations. We do this by using the coefficient of variation (CV) as a test statistic.

268 The CV is a measure of the variation in interaction rates. When individuals have  
269 strongly preferred and avoided interaction partners, the CV of interaction rates will be  
270 higher than when individuals interact at random (Whitehead 2008a). We reject the null  
271 hypothesis that interactions occurred randomly between associates if the observed  
272 CV is greater than the upper 95% confidence interval of CVs from the randomised  
273 networks.

274 We additionally test whether the correlations between associations and interactions  
275 are different from expected if interactions occurred randomly by calculating  
276 Spearman's rank correlation ( $r_s$ ) between interaction rates and association indices in  
277 both the observed and randomised interaction networks. If  $r_s$  in the observed data lies  
278 within the 95% CI of  $r_s$  values from the randomised networks, we do not reject the null  
279 hypothesis that interaction patterns match those expected given random interactions  
280 between associates. If the observed  $r_s$  is lower than the lower 95% CI of the  
281 randomised values, the rates of social interaction between individuals cannot be  
282 directly inferred from patterns of association. We additionally compare these  
283 correlations to the null hypothesis of no correlation between the networks using Mantel  
284 tests, using the vegan package in R (Oksanen et al. 2019). Note that the Mantel test  
285 has a different null hypothesis than the randomization of the raw data. While our  
286 randomization of the raw data represents the null hypothesis that interactions occur  
287 randomly between associated individuals (and thus associations reflect interactions),  
288 the Mantel test proposes the null hypothesis that association and interaction rates are  
289 independent.

290

291 *Comparing surfacing and contact networks*

292 Next, we investigated whether there were structural differences in the two interaction  
293 networks. We again use randomizations to test the null hypothesis that interaction  
294 types are interchangeable, using the procedure proposed by Franz & Alberts (2015).  
295 Each observed interaction is labelled according to which type of interaction it  
296 represented in the original data. Over 10,000 permutations, these labels are shuffled  
297 and the two resulting networks are calculated. We determine whether there are  
298 differences in the CV between the networks by comparing the observed difference in  
299 CV to the distribution of differences from the randomised networks as above. We test  
300 whether the networks are less correlated than expected if interaction types were  
301 interchangeable by comparing the  $r_s$  between the observed networks to a distribution  
302 of  $r_s$  values generated from the randomised networks, as above. We also test the  
303 correlation between these two networks against the null hypothesis of no relationship  
304 using a Mantel test.

305

306 *Effects of age, sex, and kinship on edge strength*

307 We next test the role of kinship, age, and sex in the structuring of edges in the  
308 association, contact, and synchronous surfacing networks. To quantify the relationship  
309 between both synchronous surfacing and contact rates and our predictors, we use  
310 generalised linear models (GLMs), with a negative binomial error structure. These  
311 models can be expressed as:

312 
$$x_{ij} \sim \text{NB}(\lambda_{ij}, \theta) \tag{3}$$

313 
$$\log(\lambda_{ij}) = \beta_0 + \beta_1 R_{ij} + \beta_2(-|a_i - a_j|) + \beta_3(1 - |s_i - s_j|) + \log(t_i + t_j - t_{ij})$$

314 where  $\lambda_{i,j}$  and  $\theta$  are the mean and dispersion parameters for the negative binomial  
315 distribution, respectively,  $R_{ij}$  is the estimated maternal kinship between  $i$  and  $j$ ,  $a_i$  is  
316 individual  $i$ 's age in years,  $s_i$  is the sex of individual  $i$  (0 = female, 1 = male), and the  $\beta$   
317 are estimated regression parameters and the term  $\log(t_i + t_j - t_{ij})$  is an exposure term.

318 Similarly, we quantify the relationship between our predictors and association patterns  
319 with a beta regression model:

$$320 \quad \text{association}_{ij} \sim \text{Beta}(\mu_{ij}, \phi) \quad (4)$$

$$321 \quad \text{logit}(\mu_{ij}) = \beta_0 + \beta_1 R_{ij} + \beta_2 (-|a_i - a_j|) + \beta_3 (1 - |s_i - s_j|)$$

322 where  $\mu_{ij}$  and  $\phi$  are the mean and precision parameter of the beta distribution. In this  
323 model, dyadic sampling effort was included as a proportional weight in the fitting  
324 process. As there were zeros in the association data, we transformed these values  
325 following Smithson & Verkuilen (2006):

$$326 \quad y' = \frac{y(N-1)+0.5}{N} \quad (5)$$

327 Here,  $y$  are the original values,  $y'$  are the transformed values, and  $N$  is the sample size  
328 (here, the number of dyads). We fit these models in R, using the MASS package for  
329 negative binomial regression (Venables & Ripley 2002) and the betareg package for  
330 beta regression (Cribari-Neto & Zeileis, 2010).

331 We use a permutation procedure to determine the statistical significance of regression  
332 coefficients. We use the double-semi-partialling method developed by Dekker et al.,  
333 (2007) with 10,000 randomizations, using the Wald's  $Z$  as our test statistics. Our  
334 method is equivalent to multiple regression quadratic assignment procedure  
335 (MRQAP), but fitting GLMs instead of least squares regression. We therefore refer to

336 this procedure as a generalised linear model quadratic assignment procedure  
337 (GLMQAP).

338

### 339 *Effects of age and sex on network centrality*

340 Finally, we determine the influence of age and sex on network centrality in our three  
341 networks. As using a large number of centrality measures can lead to false positives  
342 in statistical analyses (Webber et al. 2020), we choose just one index: eigenvector  
343 centrality. Eigenvector centrality depends on direct and indirect connectivity in the  
344 network; individuals with high eigenvector centrality have numerous, strong  
345 connections to individuals that are also well connected. In the remainder of the  
346 manuscript, we refer to eigenvector centrality scores simply as individuals'  
347 "centrality".

348 We fit linear mixed effects models to identify the relationship between centrality and  
349 individual attributes. These models had the form:

$$350 \quad \log(\text{centrality}_i) \sim N(\mu_i, \sigma_{\text{residual}}) \quad (6)$$

$$351 \quad \mu_i = \beta_0 + \beta_1 s_i + \beta_2 a_i + \beta_3 \log(t_i) + \varepsilon_{m_i}$$

$$352 \quad \varepsilon \sim N(0, \sigma_{\text{matriline}})$$

353 Here  $\varepsilon$  is a matriline-level random effect (with  $m_i$  indicating matriline membership),  
354 controlling for correlations in social network positions between matriline members  
355 (Williams & Lusseau 2006), and the terms  $a$ ,  $s$ , and  $t$  are as in equation 3. The term  
356 for  $\log(t_i)$  is used here to correct for the effect of sampling intensity on centrality  
357 measures (Franks & Weiss et al. 2021). Using the logarithm of centrality improved  
358 the data's adherence to the model's assumptions of normally distributed residuals  
359 and linearity, and initial visual examination suggested a log-log relationship between

360 centrality and sampling intensity was appropriate across all three networks. These  
361 models were fit using the lme4 R package (Bates et al. 2015).  
362 We test our regression coefficients using a double-semi-partialling permutation  
363 procedure (Dekker et al. 2007), with permutation constrained within matriline. We  
364 compare the observed  $t$ -values to 10,000 permutations to derive  $p$ -values. We do not  
365 test for interactions between age and sex, as double semi-partialling cannot test  
366 interaction effects.

367

### 368 *Data accessibility*

369 The processed contact, surfacing, and association networks, measures of dyadic  
370 sampling effort, estimated maternal kinship, individual attributes, and functions to  
371 conduct GLMQAP and general double-semi-partialling are included in the “aninet” R  
372 package on GitHub (<https://github.com/MNWeiss/aninet>). The raw time-series of  
373 detections and interactions, and R code necessary to reproduce all analyses, are  
374 available in the online supplementary material.

375

## 376 **Results**

### 377 *Data description*

378 Over 10 days of sampling, we collected a total of 651 minutes of video. During this  
379 footage, a median of 4 individuals were visible at any given time (interquartile range =  
380 3). All individuals were observed on at least 3 different days, and each individual whale  
381 was videoed for a mean of 125.96 minutes (SD = 57.65). Each pair of animals was  
382 observed for an average of 213.68 minutes total (SD = 58.17). While a relatively short



383 period, this is an increase in sampling relative to the only other study using UAS to  
384 construct cetacean social networks (Hartman et al. 2020). We estimate that the  
385 observed interaction rates were strongly correlated with the true interaction rates  
386 (contact  $r_{est} = 0.98$ ; surfacing  $r_{est} = 0.98$ ). During our observations, we recorded 831  
387 instances of physical contact between individuals, and 1617 synchronous surfacing  
388 interactions (Table S1). Contact and synchronous surfacing behaviours did not tend  
389 to occur simultaneously; 1.5% of contacts occurred within one second of the same  
390 pair synchronously surfacing. Pairs of whales were visible simultaneously for an  
391 average of 38.24 minutes (SD = 30.61).

392

### 393 *Comparing interactions to association patterns*

394 Rates of both interaction types were significantly more varied than expected given  
395 random interactions between associates (surfacing: Observed = 2.31, 95% CI  
396 Random = [1.09, 1.23],  $p < 0.001$ ; contact: Observed = 2.46, 95% CI Random = [1.27,  
397 1.47],  $p < 0.001$ ). Both interaction networks were significantly positively correlated with  
398 the association network under the null hypothesis of no relationship (surfacing:  $r_s =$   
399 0.79,  $p < 0.001$ ; contact:  $r_s = 0.59$ ,  $p < 0.001$ ). The interaction networks were, however,  
400 significantly less strongly correlated with the association network than expected if  
401 interactions occurred randomly between associates (surfacing: 95% CI random  $r_s =$   
402 [0.85, 0.90],  $p < 0.001$ ; contact: 95% CI random  $r_s = [0.70, 0.78]$ ,  $p < 0.001$ ).

403

### 404 *Comparison of interaction types*

405 Rates of the two interaction types did not have statistically significant differences in  
406 their coefficients of variation. (Observed difference in CV = 0.23, 95% CI Random = [-

407 0.17, 0.24],  $p = 0.07$ ). The two networks were more correlated than expected under  
408 the null hypothesis of no relationship between contact and surfacing rates ( $r_s = 0.72$ ,  
409  $p < 0.001$ ), but significantly less correlated than expected if the two interaction types  
410 were interchangeable (95% CI Random = [0.80, 0.87],  $p < 0.001$ ).

411

#### 412 *Influence of age, sex, and kinship on edge strength*

413 As expected, maternal kinship was an important predictor of association and  
414 interaction rates across all three networks (all  $p < 0.001$ ; Table S3). In the  
415 association network, neither age similarity nor sex similarity predicted edge weights.  
416 In both interaction networks, however, interaction rates were significantly related to  
417 age similarity (surfacing:  $\beta = 0.06 \pm 0.01$ ,  $Z = 5.32$ ,  $p = 0.005$ ; contact:  $\beta = 0.12 \pm$   
418  $0.02$ ,  $Z = 6.82$ ,  $p < 0.001$ ) and sex similarity (surfacing:  $\beta = 0.60 \pm 0.20$ ,  $Z = 2.98$ ,  $p =$   
419  $0.02$ ; contact:  $\beta = 1.27 \pm 0.28$ ,  $Z = 4.58$ ,  $p = 0.002$ ).

420

#### 421 *Influence of age and sex on social centrality*

422 Across all three networks, increased sampling intensity was related to greater  
423 observed centrality (all  $p < 0.04$ , Table S4). In the synchronous surfacing and  
424 association network, we found no evidence that age or sex influenced centrality (all  $p$   
425  $> 0.05$ ; Table S4). However, in the contact network, we found statistically significant  
426 effects of age and sex on centrality. There was a negative correlation between age  
427 and centrality ( $\beta = -0.03 \pm 0.01$ ,  $t = -3.30$ ,  $p = 0.006$ ), and males were less central  
428 than females ( $\beta = -0.58 \pm 0.16$ ,  $t = -3.59$ ,  $p = 0.004$ ).

429

## 430 **Discussion**

431 In this study, we observed direct social interactions in a killer whale pod to better  
432 understand the role of age and sex in structuring social relationships. Associations  
433 were not strongly organized by age or sex, but were primarily structured by matrilineal  
434 kinship. In contrast, both synchronous surfacing rates and physical contact rates  
435 showed significant assortment by age and sex. In addition, we found evidence that  
436 younger individuals and females were particularly central in the contact network,  
437 suggesting age and sex related variation in social strategies, a pattern that was not  
438 clear in the association or synchronous surfacing networks.

439 The potential issues with using association to quantify social structure have been  
440 extensively debated in the methodological literature (Whitehead & Dufault 1999;  
441 Castles et al. 2014; Farine 2015; Carter et al. 2015), however they have rarely been  
442 addressed in cetaceans and other aquatic species (but see Leu et al. 2020 and  
443 Lusseau 2007) or in the context of detecting the influence of individual attributes on  
444 network structure. Our results demonstrate how inferences about network structure in  
445 relation to individual characteristics can be missed when using association indices as  
446 a proxy for interaction rates. The effects of age and sex on the strength of network  
447 edges were only clear when analysing interaction rates, rather than associations,  
448 supporting previous studies which found no assortment by age or sex in killer whale  
449 association networks across multiple populations (Williams & Lusseau 2006; Esteban  
450 et al. 2015; Tavares et al. 2017). This suggests that while age and sex are important  
451 determinants of social interactions, these effects are difficult or impossible to detect  
452 from association patterns. While physical contact and synchronous surfacing were  
453 highly correlated, they were not interchangeable, and age and sex effects on social  
454 centrality were only found in the contact network. This suggests that physical contacts,

455 which can only be consistently observed from the air in this system, may provide  
456 greater power for analysing individual social affiliations. This result adds to a growing  
457 body of work demonstrating the power of UAS for studying cetacean sociality  
458 (Hartman et al. 2020; Nielsen et al. 2019; Ramos et al. 2020).

459 There are several mechanisms that could drive the observed correlations between  
460 age, sex, and social structure. One hypothesis relates to energetics and behavioural  
461 budget, a factor that has frequently been proposed to explain sexual segregation in  
462 terrestrial ungulates (Ruckstuhl 2007). Adult male killer whales are considerably larger  
463 than females, and thus have greater energetic requirements (Noren 2011) and spend  
464 more time foraging (Tennessen et al. 2019), which may drive males' lower social  
465 centrality. This may also lead to decoupled behavioural states between the sexes,  
466 contributing to assortment by sex in the interaction networks. Similarly, young  
467 individuals have a large portion of their energetic needs met by nursing (Newsome et  
468 al. 2009) or from prey sharing (Wright et al. 2016), which may lead to greater time  
469 spent socializing, primarily with other young individuals. Further work may shed light  
470 on how killer whale groups, which are composed of individuals with highly  
471 heterogenous energetic requirements, maintain cohesion.

472 The finding that killer whales become less social as they age aligns with social life  
473 histories found in other social mammals. In humans and non-human primates,  
474 individuals become less social and maintain fewer relationships as they age,  
475 potentially due to adaptive social selectivity or senescence (Machanda & Rosati 2020;  
476 Wrzus et al. 2013). Our results suggest that decreased sociality with age may be more  
477 widespread among social mammals, including killer whales. This apparent similarity  
478 between primate and killer whale social life history is particularly interesting given the  
479 convergent reproductive life histories in killer whales and humans (Johnstone & Cant

480 2010). Individuals may also actively form important relationships and social skills at a  
481 young age, as in other matrilineal societies (Chiyo et al. 2010; Goldenberg et al. 2016).  
482 While further work is needed to explore these and other possible mechanisms, our  
483 results demonstrate that killer whales may be a powerful system for testing hypotheses  
484 about the evolution of sex differences in sociality and social life histories in mammals.

485 These results may also have conservation implications for this population. Previous  
486 studies have highlighted the potential role of infectious disease risk in killer whale  
487 population dynamics (Gaydos et al. 2004; Raverty et al. 2017), and both contact and  
488 synchronous surfacing have been identified as disease transmission pathways in  
489 cetaceans (Leu et al. 2020). Our results suggest that young, female individuals may  
490 be at greater risk of exposure to skin-borne pathogens, such as cetacean poxvirus  
491 (Van Bresse et al. 1999). The assortment of both synchronous surfacing and  
492 physical contact by age and sex suggests that the impacts of any given disease  
493 outbreak may be spread unevenly between demographic classes, spreading to  
494 individuals of similar age and sex of the initially infected whale.

495 A limitation of the current study and method is that social interactions can only be  
496 observed by UAS when they occur relatively close to the surface. In addition, only a  
497 single social group was studied. Further studies using animal-borne devices may  
498 provide additional data on interactions that occur deeper in the water column, and  
499 analysing the full population may reveal further patterns.

500 Our results demonstrate how potentially important patterns in social relationships may  
501 only emerge at very fine scales. As association-based social networks are ubiquitous  
502 in studies of numerous terrestrial and aquatic systems, our results strongly suggest  
503 that, where possible, association data should be combined with analyses of relevant

504 social interactions when analysing social relationships. In particular, when individual  
505 movement patterns are primarily governed by membership to stable social units,  
506 analysing direct interactions may be crucial for uncovering individual level drivers of  
507 social structure.

508

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524

## 525 **Author Contributions**

526 MNW, DPC, MAC, DWF, SE, and KCB conceived of the project. MNW, DAG, SY,  
527 PD, and SKW performed fieldwork. MNW conducted video analysis with assistance  
528 from DKE. MNW performed statistical analysis, with input from DWF, DPC, CG,  
529 MLKN, SE, and PD. MNW drafted the manuscript with input from all authors.

530

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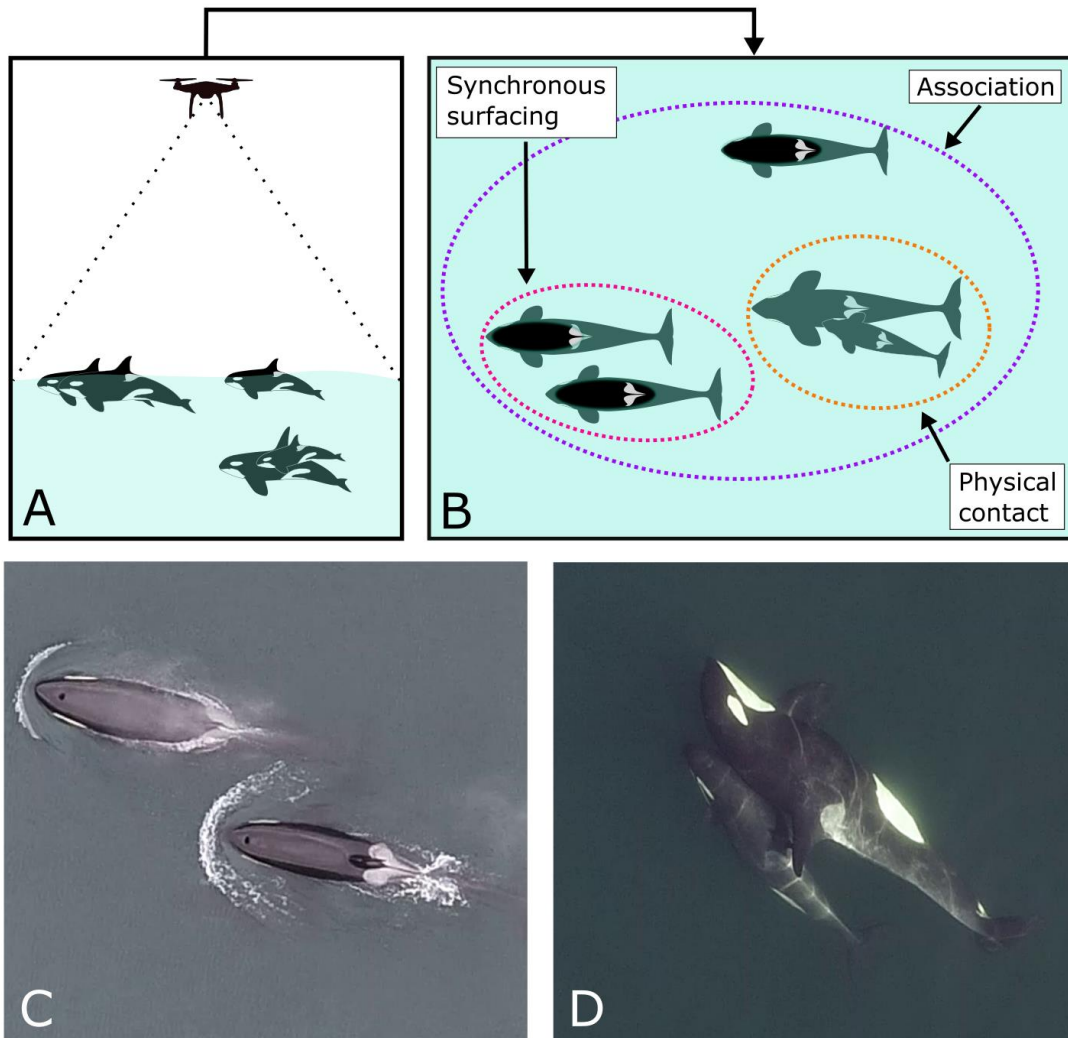
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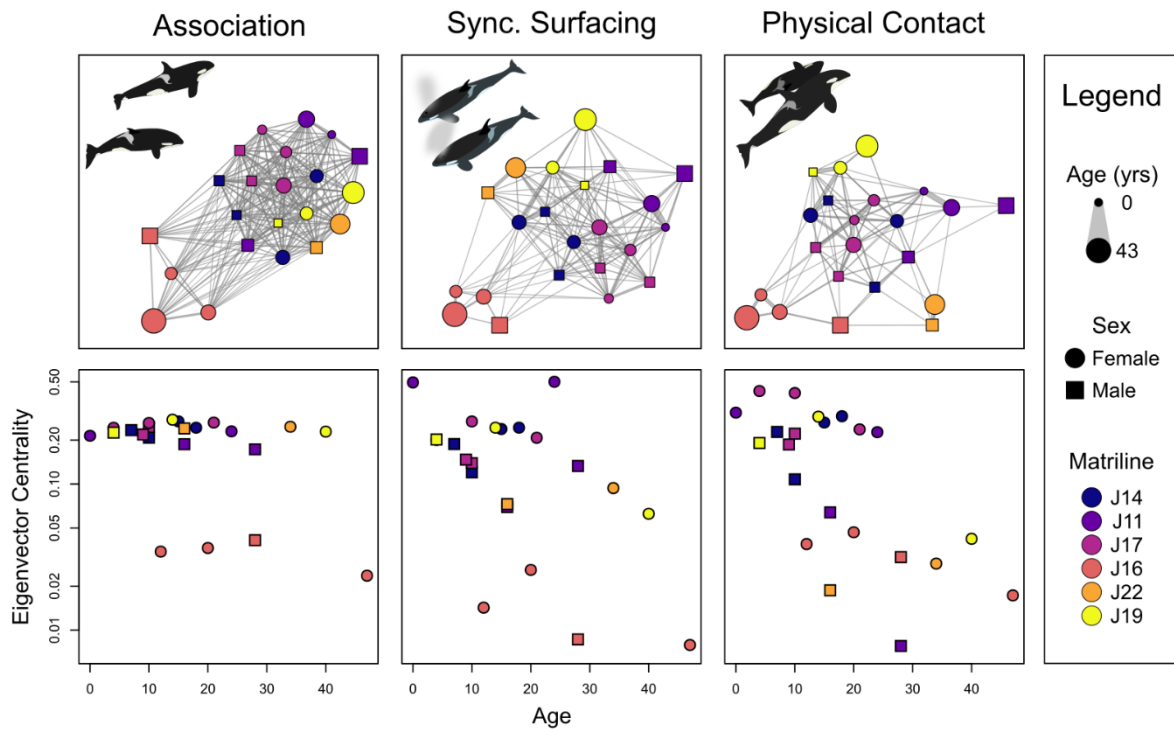
726

727 **Figures**



728

729 **Figure 1.** Observing killer whale social interactions using UAS. A-B: The aircraft is  
730 flown over focal killer whale sub-groups (A). All individuals detected simultaneously  
731 were considered to be associated, and both synchronous surfacing and physical  
732 contact interactions were recorded between identified individuals (B). C-D: Example  
733 video stills of synchronous surfacing between individuals J36 and J47 (C) and physical  
734 contact between individuals J44 and J53 (D). Killer whale side profiles based on  
735 illustration by Chris Huh, used under a CC BY-SA 3.0 license  
736 (<https://creativecommons.org/licenses/by-sa/3.0/>).



737

738 **Figure 2.** Network structure and social centrality in a resident killer whale pod. Panels  
 739 show sociograms (top) and eigenvector centrality measures (bottom) for (from left to  
 740 right) association, synchronous surfacing, and physical contact networks. Edge  
 741 thicknesses in the sociograms are proportional to association or interaction rate, and  
 742 nodes are placed according to the ForceAtlas2 algorithm (Jacomy et al. 2014). Across  
 743 all plots, node shape indicates sex and node color indicates matriline membership,  
 744 and node size in the sociograms indicates individual age (as shown in the legend).  
 745 Note the log scale for the y-axis in the lower plots.

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754 Supplemental materials for:  
755 Age and sex influence social interactions,  
756 but not associations, within a killer whale  
757 pod

## 758 **Supplementary methods**

### 759 *Estimating maximum distance captured*

760 We use the field of view of the camera lens and the flight records stored by the UAS  
761 to estimate the maximum distance between any two points in the video. Given the  
762 drone's vertical field of view  $\theta$  and horizontal field of view  $\phi$  (in degrees), the drone's  
763 altitude  $w$  (in meters), and the camera gimbal's pitch  $p$  (in degrees from a straight  
764 down view), we estimate the locations of the corners of the frame relative to the  
765 drone, which we set as the origin.

766 We first calculate the distance to the top of the screen  $y_1$  and the bottom of the  
767 screen  $y_2$ :

$$768 \quad y_1 = \tan\left(p + \frac{\theta}{2}\right)w$$

$$769 \quad y_2 = \tan\left(p - \frac{\theta}{2}\right)w$$

770 The widths of the top of the frame ( $a$ ) and the bottom of the frame ( $b$ ) can then be  
771 calculated as:

$$772 \quad a = 2 \cdot \tan\left(\frac{\phi}{2}\right)\sqrt{y_1^2 + w^2}$$

$$773 \quad b = 2 \cdot \tan\left(\frac{\phi}{2}\right)\sqrt{y_2^2 + w^2}$$

774 The x coordinates for the top two corners of the frame are then  $\{-a/2, a/2\}$ , while the  
775 x coordinates of the bottom two corners are  $\{-b/2, b/2\}$ . We then have our four points  
776  $x = \{-a/2, a/2, -b/2, b/2\}$ ,  $y = \{y_1, y_1, y_2, y_2\}$ . We measure the distances between all  
777 four points, recording the maximum distance. We record this for all flight records  
778 during the study period during which the video was active, and report the median  
779 along with the 25% and 75% quantiles.

780

### 781 *Bout analysis*

782 In order to test whether interactions could be broken into bouts, we measured the  
783 waiting times between observed interactions between dyads in each video clip. If  
784 interactions between dyads occurred in bouts, we would expect these waiting times  
785 to arise from a mixture of two exponential distributions, one representing the waiting  
786 time within bouts, and the other representing waiting times between bouts. In  
787 contrast, if interactions did not occur in bouts, we expect these waiting times to fit a  
788 single exponential distribution (Langton et al. 1995). We fit these two models in the  
789 flexmix package in R (Gruen & Leisch 2008). For both interaction types, we then  
790 compare these models using the Bayesian information criteria (BIC). Lower values of  
791 BIC indicate that the model is a better fit to the data, penalized for model complexity.

792 In both interaction types, model comparisons suggested that the mixture of two  
793 exponential distributions fit the data less well than the single exponential distribution,  
794 with differences in BIC  $> 10$  (Table S2). We therefore analysed each interaction as  
795 an independent event, rather than measuring bouts of interaction.

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**Table S2.** Model selection for exponential mixtures

Interaction type	Model	BIC
Synchronous surfacing	Single exponential	6679.487
	Two exponentials	6692.541
Physical contact	Single exponential	3806.613
	Two exponentials	3818.561

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802 *Estimating reliability of interaction networks*

803 We assume that our observed interaction counts  $x$  are drawn from a Poisson  
804 distribution where the rates themselves are drawn from a gamma distribution with  
805 shape parameter  $k$  and scale parameter  $\theta$ . The expected number of observed  
806 interactions is then the true rate multiplied by the sampling time ( $t_{ij}$ ).

807 
$$x_{ij} \sim \text{Poisson}(\lambda_{ij}t_{ij})$$

808 
$$\lambda_{ij} \sim \text{Gamma}(k, \theta)$$

809 We are interested in estimating the correlation between the true rates  $\lambda_{ij}$  and the  
810 estimated interaction rates  $\frac{x_{ij}}{t_{ij}}$ .

811 We estimate the parameters of the underlying Gamma distribution by fitting a  
812 negative-binomial distribution with mean  $\mu$  and dispersion  $\phi$  to the observed  
813 interaction counts:

814 
$$x_{ij} \sim \text{NB}(\mu t_{ij}, \phi)$$

815 We use our negative binomial fit to extract the estimated shape and scale  
816 parameters of the underlying Gamma distribution:

817 
$$p = \frac{\phi}{\phi + \mu}$$



818  $\theta = \frac{1-p}{p}$

819  $k = \phi$

820 The mean and variance of the underlying Gamma distribution are then

821  $\text{Mean}(\lambda) = k\theta$

822  $\text{Var}(\lambda) = k\theta^2$

823 Therefore, the coefficient of variation of the true interaction rates (social  
824 differentiation,  $S$ ) is:

825  $S = \frac{\sqrt{k\theta^2}}{k\theta} = \frac{1}{\sqrt{k}}$

826 Following equation 4 in Whitehead (2008), we then estimate the correlation between  
827 the observed and estimated interaction rates ( $r_{est}$ ) as

828  $r_{est} = \sqrt{\frac{1}{1 + \frac{1}{S^2 \times G}}}$

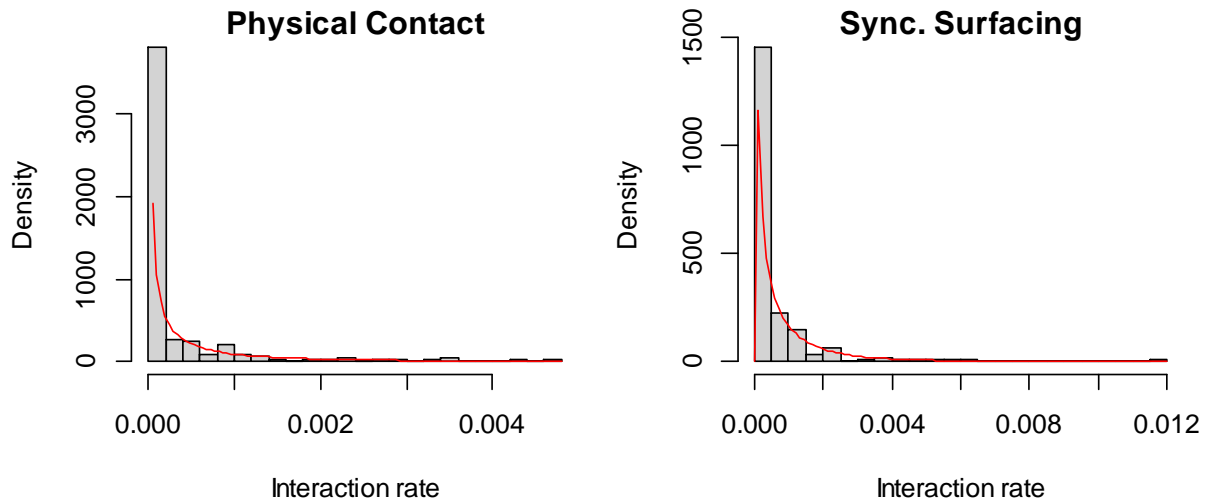
829 where

830  $G = \frac{\sum_i \sum_j x_{ij}}{N(N-1)}$

831 In order to assess whether this a reasonable estimate, we plot the empirical  
832 distribution of interaction rates against the estimated gamma distributions. For both  
833 interaction rates, the fitted Gamma distributions appear to be reasonable  
834 approximations of the empirical interaction rates, allowing for sampling noise (Figure  
835 S1).

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839 **Figure S1.** Empirical distributions of interaction rates compared to fitted gamma  
 840 distributions. Grey histograms indicate the observed distribution of estimated  
 841 interaction rates, and the red lines are the estimated density of the Gamma distribution  
 842 fit using maximum likelihood.

843

844 *Permutation analysis for centrality in mixed effect models.*

845 We adopt a double-semi-partialling approach for testing the fixed effects in our mixed  
 846 effect models of social centrality. For each fixed predictor  $X$ , we partial out the  
 847 covariance between  $X$  and all other fixed predictors  $Z$  by fitting the linear model

848 
$$X = \beta Z + \varepsilon$$

849 and extracting the residuals  $\varepsilon$ . We then replace  $X$  with  $\varepsilon$  in the original model, and  
 850 carry out 10000 permutations of these residuals. To account for matriline  
 851 membership, we permute these residuals within matriline. We repeat this procedure  
 852 for each predictor, using the  $t$ -value as the test statistic to derive  $p$ -values for all fixed  
 853 predictors.

854

855 **Supplementary results**

856

857 **Table S1** Summary of attributes and observation effort for each individual in J pod in  
 858 the summer of 2019.

Matriline	ID	Birth Year	Sex	Observation time (min)	Sync. surfacings	Contacts
J11	J27	1991	M	85	63	4
	J31	1995	F	206	315	91
	J39	2003	M	121	77	45
	J56	2019	F	203	302	141
J14	J37	2001	F	137	232	119
	J40	2004	F	173	218	114
	J45	2009	M	134	134	58
	J49	2012	M	163	195	95
J16	J16	1972	F	28	18	9
	J26	1991	M	46	14	17
	J36	1999	F	37	29	28
	J42	2007	F	34	20	20
J17	J35	1998	F	166	227	105
	J44	2009	M	159	139	75
	J46	2009	F	219	259	190
	J47	2010	M	145	163	99
	J53	2015	F	181	223	190
J19	J19	1979	F	86	50	15
	J41	2005	F	131	219	120
	J51	2015	M	140	176	78
J22	J22	1985	F	77	93	30
	J38	2003	M	99	68	32

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**Table S3.** GLMQAP results for each response network.

Response	Family	Predictor	Estimate	Std. Error	Z	$p^*$
Association	Beta	Kinship	3.54	0.48	7.38	<b>&lt;0.001</b>
		Age similarity	0.02	0.01	4.00	0.071
		Sex similarity	0.14	0.11	1.33	0.188
Synchronous surfacing	Negative binomial	Kinship	6.40	0.46	13.91	<b>&lt;0.001</b>
		Age similarity	0.06	0.01	5.32	<b>0.005</b>
		Sex similarity	0.60	0.20	2.98	<b>0.020</b>
Physical contact	Negative binomial	Kinship	8.91	1.12	7.97	<b>&lt;0.001</b>
		Age similarity	0.12	0.02	6.82	<b>&lt;0.001</b>
		Sex similarity	1.27	0.28	4.58	<b>0.002</b>

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\* $p$ -values derived from 10,000 permutations of predictor residuals

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**Table S4.** Regression analysis of eigenvector centrality.

Network	Predictor	Estimate	Std. Error	$t$	$p^*$
Association	Sampling	0.44	0.14	3.15	<b>0.038</b>
	Age	0.00	0.003	0.09	0.965
	Sex	-0.01	0.06	-0.11	0.808
Synchronous surfacing	Sampling	1.68	0.21	7.89	<b>0.011</b>
	Age	-0.01	0.01	-0.94	0.300
	Sex	-0.34	0.17	-2.01	0.066
Physical contact	Sampling	1.88	0.35	5.40	<b>&lt; 0.001</b>
	Age	-0.03	0.01	-3.30	<b>0.006</b>
	Sex	-0.58	0.16	-3.59	<b>0.004</b>

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\* $p$ -values derived from 10,000 permutations of predictor residuals within matriline

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872

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