Kinship does not predict the structure of a shark social network

Johann Mourier[1,2,3], Serge Planes[1,2]

[1] PSL Research University, EPHE-UPVD-CNRS, USR 3278, Université de Perpignan, Perpignan, France

[2] Laboratoire d'Excellence "CORAIL," EPHE, PSL Research University, UPVD, CNRS, USR 3278 CRIOBE, Papetoai, Moorea, French Polynesia

[3] UMR MARBEC (IRD, Ifremer, Univ. Montpellier, CNRS), Sète, France

ORCID: JM, 0000-0001-9019-1717; SP, 0000-0002-5689-5371

Corresponding author:

Johann Mourier

Email: johann.mourier@gmail.com

ABSTRACT:

Genetic relatedness in animal societies is often a factor that drives the structure of social groups. In the marine world, most studies which have investigated this question have focused on marine mammals such as whales and dolphins. For sharks, recent studies have demonstrated preferential associations among individuals from which social communities emerge. Assortment patterns have been found according to phenotypic or behavioural traits but the role of genetic relatedness in shaping the social structure of adult shark populations has, to the best our knowledge, never been investigated. Here, we used a social network analysis crossed with DNA microsatellite genotyping to investigate the role of the genetic relatedness in the social structure of a blacktip reef shark (*Carcharhinus melanopterus*) population. Based on data from 156 groups of sharks, we used generalized affiliation indices to isolate social preferences from non-social associations, controlling for the contribution of sex, size, gregariousness, spatial and temporal overlap on social associations, to test for the influence of genetic relatedness on social structure. Kinship was not a predictor of associations and affiliations among sharks at the dyad or community levels as individuals tended to associate independently of the genetic relatedness among them. The lack of parental care in this species may contribute to the breakdown of family links in the population early in life, thereby preventing the formation of kin-based social networks.

Keywords: genetic relatedness, assortment, social organisation, *Carcharhinus melanopterus*, elasmobranch

INTRODUCTION

Group formation is an adaptive strategy, widespread across the animal kingdom, that can take various forms, from temporary unstable associations to long-term stable groups in complex societies (Krause and Ruxton 2002). Understanding the factors that influence the formation and evolution of social groups is important in order to understand the evolution of animal societies as well as to gain insight into population dynamics and to inform conservation strategy (Snijders et al. 2017). Associations among individuals can provide benefits to improve individual fitness, for example, by reducing predation risk or improving foraging efficiency (Krause and Ruxton 2002). While individuals can benefit by simply associating with other conspecifics (Kerth et al. 2011), the benefit of grouping can be enhanced by associating with similar individuals, also called social assortativity. By associating with individuals of the same size or the same sex, individuals are more likely to avoid conflict or harassment (Dadda et al. 2005) and their risk of predation is reduced via the confusion effect (Landeau and Terborgh 1986). Further, assorting with kin can also provide indirect fitness benefits (Hamilton 1964). Kin assortment has been shown to provide benefits in reducing aggression (Olsén and JäUrvi), increasing growth rate (Brown and Brown 1993) or allowing cooperative behaviour such as predator inspection (Milinski 1987).

Kin structuring has received extensive attention in many animal societies, especially where animals form stable breeding groups or where groups arise from the retention of offspring and delayed dispersal that facilitates the development of interactions with relative and kin-based groups (Wolf and Trillmich 2008; Hatchwell Ben J. 2010; Wiszniewski et al. 2010). In groups composed of relatives, kin selection should play a role in determining cooperation among group members (Hamilton 1964), although cooperation can arise also between non-kin (Clutton-Brock 2009). The role of relatedness in structuring animal societies that are characterised by a dynamic fission-fusion social system has been well studied in

species with parental care such as dolphins, giraffes, elephants or bats (Wittemyer et al. 2009; Wiszniewski et al. 2010; Kerth et al. 2011; Carter et al. 2013), but much less is known for species without parental care, as is the case for many species of fish (but see Croft et al. 2012). While the link between social networks and kinship has been extensively studied in terrestrial animals (Holekamp et al. 2012; Carter et al. 2013; Arnberg et al. 2015), kinship structure in social networks of marine and freshwater organisms has been primarily limited to marine mammals (Wiszniewski et al. 2010; Mann et al. 2012; Reisinger et al. 2017). Several cetacean societies show strong kin-based social network structures. However, in fishes, kin structure is less clear. Work on shoaling fish, for example, did not find kin assortment, even in species that are capable of kin discrimination (Croft et al. 2012). While sharks have recently been shown to be able to develop preferred associations and organise into structured social networks (Mourier et al. 2018), kinship has only been explored in one case study that focused on juvenile sharks (Guttridge et al. 2011) but did not find any clear influence of kinship in association patterns even for juvenile sharks, highlighting a lack of information on the potential for kin-based associations to arise in shark populations. Another study on spotted eagle rays did not find any evidence of relatedness in the formation of groups (Newby et al. 2014), although association strength was not quantified using association indices.

Overall, most studies that have explored the relationship between genetic relatedness and social interactions have focused on highly social species and in particular, on species that exhibit parental care (Wolf and Trillmich 2008; Wiszniewski et al. 2010; Kerth et al. 2011). Studying less social vertebrates should significantly improve our understanding of how social and genetic structure interact to shape the evolution of sociality in the animal kingdom.

In this study, we investigate the interaction between socio-spatial patterns and genetic relatedness in a population of blacktip reef sharks (*Carcharhinus melanopterus*) monitored over a 3-year period on the north shore of Moorea Island (French Polynesia). Sharks

represent an interesting and unique model to explore the extent to which individuals interact with genetically related associates due to ecological traits that differ from most social vertebrates. Like most social animals, sharks are now increasingly recognised as being capable of complex social interactions, developing preferred social associations (Guttridge et al. 2009; Jacoby et al. 2010; Mourier et al. 2012), showing unexpected learning abilities (Guttridge et al. 2013; Mourier et al. 2017), developing foraging strategies by associating with other species to improve predation success (Labourgade et al. 2020) and developing patterns of leadership and dominance hierarchy (Guttridge et al. 2011; Jacoby et al. 2016; Brena et al. 2018). However, contrary to many social organisms, reef sharks do not show parental care and almost all shark species drop their progeny in specific nurseries outside adult habitats and leave them to interact by themselves (Mourier and Planes 2013). These discrete nurseries are chosen to potentially provide the neonates with a safe environment where they will spend their first months of life. Recent studies suggested that females show reproductive and even natal philopatry to these particular birthing grounds (Mourier and Planes 2013; Feldheim et al. 2014), suggesting that newborn sharks may have the opportunity to develop strong relationships with close kin. When juvenile sharks reach a certain size or age, they leave their nursery to explore a wider home range (Chapman et al. 2009); they then integrate within the adult population and start interacting with older individuals, but it is not known whether they coexisted with other newborn during their juvenile stage or disperse alone. Therefore, while aggregations of kin are possible during the early stages, it is currently unknown if they persist through adulthood after dispersal. In shark populations, interactions between kin are also diluted by the presence of numerous neighbours and average relatedness quickly drops with increasing group size. In some shark species, the likelihood of associating with a related peer is reduced due to small litter size and a high mortality rate at the juvenile stage, leading to a lack of first order relatives to reach adulthood. However, in a closed

system, such as an isolated island, and in the case of blacktip reef sharks which spend their entire life cycle within Moorea (Mourier and Planes 2013), relatives will have more chances to encounter each other and to interact in social groups. Thus, in these conditions, the limited number of related pairs might decrease the risk of inbreeding.

To understand the assortative forces which underpin the structural properties of the system is challenging for elusive underwater animals. As the blacktip reef shark displays a high degree of site fidelity (Papastamatiou et al. 2009) and shares some of its areas with many conspecifics (Mourier et al. 2012), exploring this network holds the potential to work out the relationship between spatial, social and genetic structure in a reef shark. Size, sex and gregariousness of sharks have been shown to influence assortment at the population and community levels (Mourier et al. 2012; Mourier et al. 2017). However, whether genetic relatedness plays a role in structuring the network at both the individual and community levels remain unknown. In particular, whether sharks benefit from associating with kin remains unknown as cooperation has not been proven and social foraging may not require associations with kin to improve predation success (Labourgade et al. 2020).

We aim to describe the social structure and to determine whether sharks had genuine social preferences (caused by active choice of individuals to interact) by controlling for non-social structural factors, including space use, time, phenotype, and individual gregariousness. We then tested whether the social structure at different scales can be explained by the genetic relatedness between individuals.

MATERIAL AND METHODS

Field observations and data collection

Between 2008 and 2010, observation surveys were conducted along approximately 10km of coastline of the Northern reef of Moorea Island (French Polynesia) (Figure 1). The surveys

consisted of 40 min dives at 7 sites along a 10 km portion of reef (total = 180 dives, site 1 = 20, site 2 = 50, site 3 = 8, site 4 = 33, site 5 = 30, site 6 = 34 and site 7 = 7). Individual blacktip reef sharks were identified by photo-identification, using unique, lifelong colour-shape of the dorsal fin (Mourier et al. 2012).

Associations between individuals were defined using the ”Gambit of the Group” (Whitehead and Dufault 1999) assuming that all individuals observed together are then considered as “associated”. This approach is appropriate when individuals move between groups and direct interactions are difficult to observe, but where groups can be easily defined (Franks et al. 2010; Farine and Whitehead 2015). An experienced diver conducted a stationary visual census at each site monitored, moving and identifying sharks within a ~100 m radius area (made possible by the high visibility conditions in these tropical waters). All individuals observed during a dive were considered as part of the same group if they were encountered within 10 min periods. We are confident that observed associations represented true grouping structure, because groups were spatio-temporally well-defined and sharks were engaged into specific social behaviour (e.g. following, parallel swimming or milling; Mourier et al. 2012). To avoid the potential for weak and non-relevant associations between pairs of individuals with very low number of sightings, we used a restrictive observation threshold to include only individuals observed more than the median number of sightings (median = 14; mean ± sd = 14.92 ± 8.04; Supplementary Figure S1). Thus, all individuals seen less than 15 times were removed from the analyses to ensure that associations were estimated with high accuracy and precision.

DNA sampling and laboratory procedures

Shark fishing sessions using rod and reel and barbless hooks were conducted to obtain tissue samples for genetic analysis. Once hooked, sharks were brought alongside the boat where

164 they were inverted and placed in tonic immobility while biological data and tissue samples
165 were collected. Each shark was identified by photo-identification of the dorsal fin, sexed and
166 measured to the nearest centimeter (Mourier et al. 2012; Mourier, Mills, et al. 2013). Fishing
167 sessions were conducted directly after underwater surveys to avoid perturbations of the
168 experimental setup (Mourier et al. 2017) and to increase the chance of getting DNA samples
169 from sharks that were part of the social network. Fishing effort was maintained until sharks
170 failed to respond to the bait (generally <30 min and after catching 2-3 individuals). A fin clip
171 was collected from the second dorsal fin or anal fin and samples were individually preserved
172 in 95% ethanol and returned to the laboratory for genotyping (Mourier and Planes 2013).
173 DNA was extracted using the QIAGEN DX Universal Tissue Sample DNA Extraction
174 protocol. PCR amplification and the microsatellite loci used are described in detail in
175 previous studies (Mourier and Planes 2013; Vignaud et al. 2013; Vignaud et al. 2014). The
176 software MICROCHECKER (Van Oosterhout Cock et al. 2004) was used to test for null
177 alleles and other genotyping errors.
178 We compared the suitability of seven pairwise relatedness estimators: five non-likelihood
179 estimators (Queller and Goodnight 1989; Li et al. 1993; Ritland 1996; Lynch and Ritland
180 1999; Wang 2002) and two maximum-likelihood estimators (Milligan 2003; Wang 2007) in
181 the R package *related* (Pew et al. 2015) and determined that the triadic maximum-likelihood
182 estimator (TrioML; Wang 2007) was best suited to our microsatellite panel (Supplementary
183 materials, Supplementary Figure S2) as it showed the highest correlation (i.e. 0.831) with the
184 true values and the smallest variation around the mean for every relationship (except for full-
185 sibs). This analysis generates simulated individuals of known relatedness based on the
186 observed allele frequencies and calculates the genetic relatedness using the different
187 estimators. The correlation between observed and expected genetic relatedness was obtained

188 for each estimator, and the one with the highest correlation coefficient was selected for
189 further analysis.
190
191 **Defining associations**
192 Using R package *asnipe* (Farine 2013), we calculated dyadic association strengths (i.e.
193 associations among pairs of individuals) among photo-identified individual sharks seen in
194 groups from the spatio-temporal co-occurrences, and the proportion of time two individuals
195 were observed together at the same site given that at least one was observed, using the
196 simple-ratio association index (SRI) (Cairns and Schwager 1987). The SRI is the
197 recommended association index when calibration data are unavailable (Hoppitt and Farine
198 2018).
199 To measure the diversity of associations, we calculated the social differentiation (S) in
200 the network that is the estimated coefficient of variation (standard deviation divided by mean)
201 of the true association indices. If the social differentiation of the network is 0, then
202 relationships among members are completely homogeneous. Conversely, if the social
203 differentiation is above 1.0, there is considerable diversity in the relationships between pairs
204 of individuals within the network (Whitehead 2008). For our data, the standard error of S was
205 generated by bootstrapping (1 000 replications).
206
207 **Potential structural factors of social associations**
208 We quantified five structural factors that could affect shark association patterns: spatial
209 overlap, temporal overlap, gregariousness, and size and sex similarity for each pair of
210 individuals. Genetic relatedness was not included as a structural factor as it will be tested
211 independently when other factors are extracted.

212 For each individual, an encounter rate (i.e., no. sightings of individual at site, divided by
213 no. sampling occasions at site) was calculated by site to define individual spatial utilization
214 (Supplementary Figure S3). We then generated a Bray-Curtis similarity matrix of space use
215 to construct a matrix of spatial overlap between individuals using R package "vegan" (Dixon
216 2003).

217 Individuals using an area at the same time are more likely to be associated with each
218 other. The study period corresponds to a total of 28 months between February 2008 and June
219 2010. The temporal overlap was calculated as the custom SRI calculated on whether pairs
220 were observed in the study area within sampling periods of 60 days.

221 Gregariousness was calculated following Whitehead and James's (2015) correction,
222 where the gregariousness predictor between two individuals (*a* and *b*) is the log of the sum of
223 the association indices involving *a* (except the *ab* index) multiplied by the sum of those
224 involving *b* (except the *ba* index): $G_{ab} = \log(\Sigma SRI_a \Sigma SRI_b)$ where ΣSRI_a and ΣSRI_b are the
225 sums of all the SRIs for individuals *a* and *b*, respectively.

226 Shark length was classified into size classes ranging from 1 to 6 (1: TL < 110 cm; 2:
227 110-119 cm; 3: 120-129 cm; 4: 130-139 cm; 5: 140-150 cm; 6: TL > 150 cm). For sex and
228 size similarity, we constructed a binary matrix in which elements $a_{ij} = 1$ when individuals *i*
229 and *j* were of the same class and $a_{ij} = 0$ otherwise (sex class, 1 if same sex, 0 if not; size class,
230 1 if same size class, 0 if not).

231

232 **Influence of structural factors on social associations**

233 We quantified the contribution of all five structural factors in driving social patterns with
234 a multiple regression quadratic assignment procedure (MRQAP) modified by Farine (2013)
235 that enables null models built from pre-network data permutations to be used in conjunction
236 with a MRQAP regression. This approach was shown to be more accurate than classic

237 MRQAP procedures (Farine 2017). We assessed possible linear relationships between the
238 social associations and the structural factors using the SRI association matrix as the
239 dependent variables and the matrices representing pairwise similarity of each of the five
240 structural factors as independent variables. We used 20,000 permutations to build randomized
241 distributions to compare with the empirical coefficient. The *P*-values were the proportion of
242 the estimated coefficient regression which were smaller or greater than what would have been
243 expected by chance. We used the *mrqap.custom.null* function from *asnipe* R package (Farine
244 2013) to run MRQAP tests in R v. 3.3.0 (R Core Team 2019).
245
246 **Removing the effects of structural factors from associations**
247 We developed generalized affiliation indices (GAI, Whitehead and James 2015) to
248 remove the effects of the significant structural factors from the associations and test the
249 existence of true affiliations between dyads (i.e. active association preferences). For this, we
250 fitted a binomial generalized linear model (GLM) with the unfolded SRI matrix as the
251 dependent variable, and the significant structural factors selected from the MRQAP as
252 independent variables. GAI represents the assortment of individuals not explained by the
253 significant structural factors and corresponds to the deviance residuals of the model. The
254 model was: SRI ~ TO + SO, where SRI is the association matrix, TO is the temporal overlap
255 matrix and SO is the spatial overlap matrix (as only TO and SO were significant factors in the
256 MRQAP, Table 1).
257
258 **Social preferences and null models**
259 We used a null model to test both for social preferences and the significance of the
260 observed network modularity. We generated 20,000 randomized association and affiliation
261 networks based on 25,000 data-stream permutations of the raw observation data with a

262 swapping algorithm (Bejder et al. 1998). We permuted the empirical group-by-individual
263 matrix constraining the number of groups, individuals and occurrences (matrix dimension
264 and fill), group size (row totals) and individual frequency of observation (column totals). To
265 minimize the effect of initial values potentially correlated to the empirical data, we removed
266 the first 5,000 randomized matrices. From the randomised group-by-individual matrix, we
267 calculated a simple-ratio index association matrix, with which we built a generalized
268 affiliation index using the same predictors selected via MRQAP for the empirical data. We
269 used a modified version of R codes available from Machado et al. (2019) to build null models
270 and to calculate SRI, GAI and modularity.

271 We compared the standard deviation (SD) of the observed simple-ratio index (SRI) and
272 the SD of the observed generalized affiliation index (GAI) with the distribution of the SD of
273 corresponding randomized SRI and GAI matrices generated by the null models detailed
274 above. An observed SD significantly higher than the null expectation indicates the presence
275 of preferred and avoided associations and affiliations. We also tested for strongly connected
276 social communities by comparing the empirical modularity (Q) (Newman 2006) of SRI and
277 positive GAI matrices with that of the randomized matrices. Empirical SD and Q values were
278 considered statistically significant if they fell outside the 95% confidence interval of their
279 randomized distributions.

280

281 **Genetic relatedness, social structure and sex differences**

282 To assess whether relatedness differs for same-sex dyads, we constructed three binary
283 matrices (0,1), each encoding the presence of a certain dyad type (female–female, male–male
284 or female–male). We then tested for a correlation with the relatedness matrix using three
285 Mantel tests (20,000 permutations), via the vegan R package (Dixon 2003).

286 For each type of dyad (female–female, male–male or female–male), we then tested for a
287 correlation between the SRI and GAI matrices and the pairwise genetic relatedness among
288 sharks using Mantel tests and compared the test statistics to those of the 20,000 permuted
289 networks.

290 We also compared the gregariousness of individual sharks between the sexes. For this,
291 we used two measures of gregariousness: node degree (or binary degree) which is the number
292 of direct neighbours each individual is connected to in the network and node strength (or
293 weighted degree) that is the sum of associations of an individual. We then used these network
294 metrics in order to determine whether males and females differed in their gregariousness. We
295 constructed generalized linear models (GLMs) to test how sex affected the observed network
296 degree (degree ~ sex) and strength (strength ~ sex). We ran these same models with
297 randomized permutations of the network data to evaluate statistical significance (Farine and
298 Whitehead 2015; Farine 2017).

299 To determine whether individuals within groups (size class and communities) were more
300 or less closely related than expected, we compared the observed values for each group against
301 a distribution of expected relatedness values generated by randomly shuffling individuals
302 between groups for 1000 permutations, where size was kept constant, using the R
303 package *related* (Pew et al. 2015). If the observed mean relatedness was greater than that of
304 the permuted data, then the null hypothesis which predicted that the mean within-community
305 relatedness is random, was rejected.

306 If only a few closely related individuals were present, then it is possible that their within-
307 community overabundance compared to between social communities might not be detected
308 using mean coefficient of relatedness (Buston et al. 2009). In turn, we verified whether the
309 proportion of closely related pairs was higher within than between social communities using
310 a chi-squared test following the same approach as the preceding analysis with mean

311 relatedness. We compared the χ^2 statistics of the observed difference in proportions of
312 relatedness values above a certain threshold between within- and between-communities to
313 that of expected relatedness values generated by randomly shuffled individuals between
314 community groups for 1000 permutations and keeping size constant. We tested with a
315 threshold relatedness value of 0.25 corresponding to the theoretical relatedness of half-sibs.
316

317 # RESULTS

318 **Data summary**

319 Of 241 catalogued sharks (150 males, 91 females; Mourier et al. 2012), 49 (36 males, 13
320 females) were observed on more than 15 occasions (mean resightings = 14.92 ± 8.04 SD,
321 Supplementary Figure S1). A total of 225 adult sharks were genotyped from the studied area.
322 From the 49 sharks included in our social network analyse, 87% (43) were genotyped.
323 Therefore, 43 individuals (30 males, 13 females) were included in the remaining analyses.
324 This resulted in 156 observed groups (mean group size = 8.60 ± 4.92 SD). From the 17
325 microsatellite markers taken from our previous study (Mourier and Planes 2013), the
326 presence of null alleles was detected at Cli12 which was then removed from our dataset for
327 further genetic analyses. We conducted the genetic analyses with 16 loci (Supplementary
328 Table S1).
329

330 **Social structure**

331 The social differentiation of the population was higher than 1 (S ± SE = 1.474 ± 0.037),
332 revealing a diverse range of associations and a well-differentiated society. The most
333 significant predictors of shark associations were the temporal and spatial overlaps, which
334 explained 94% of the total variance in SRI (MRQAP results, Table 1).

We rejected the null hypothesis that sharks associate randomly, as the observed SD of SRI was higher than the random SD. When GAI removed the influence of temporal and spatial overlaps from SRI, we also rejected the null hypothesis of random affiliations (Figure 2a) demonstrating the presence of preferred social affiliations. At the population level, the modularity (Q) of the association (SRI) and affiliation (GAI) networks were higher than expected by chance (Figure 2b). While the three communities from the SRI network had distinct use of space, some communities from the GAI network had similar spatial distributions (e.g., communities yellow and purple, Figure 2c).

Crossing of genetic relatedness and association patterns

When testing for kin-biased relatedness, adult male-male (MM), female–female (FF) and male-female (MF) dyads did not have clear higher or lower genetic relatedness (Mantel test: MM, r = -0.012, n = 31, P = 0.061; FF, r = -0.019, n = 12, P = 0.685; MF, r = 0.023, n = 43, P = 0.259). In addition, mean genetic relatedness was not higher within than between size classes (mean r = 0.043, random 95% CI = 0.058-0.065, P = 0.88; Supplementary materials, Table S2). While individuals were relatively spatially clustered, genetic relatedness appeared much more homogeneously distributed across individuals and space (Mantel test between matrices of spatial overlap and genetic relatedness: r = 0.011, n = 43, P = 0.351; Supplementary Figure S4).

Average pairwise relatedness among individuals was 0.062 ± 0.001 (mean ± SE) ranging from 0 to 0.774. Associations were only significantly positively correlated with genetic relatedness between males (Mantel test: r= 0.103, P = 0.026) but no significant correlation was found between GAI and genetic relatedness for any sex dyad (Table 2). Males were generally more gregarious than females, as they significantly interacted with more

individuals (higher degree) but did not have stronger relationships (higher strength) (Table 3, Figure 3).

Within-community relatedness estimate was inferred for each community and index (SRI and GAI, Table 4). Relatedness within all communities was not higher than expected if communities were randomly organized (SRI network: within mean ± SE = 0.071 ± 0.005, between mean ± SE = 0.058 ± 0.003, P = 0.093; GAI network: within mean ± SE = 0.060 ± 0.005, between mean ± SE = 0.063 ± 0.005, P = 0.722) (Table 4).

Among the 903 potential pairs, 39 (4.31%) had values higher than 0.25. In addition, there was no higher proportion of close relatives within than between communities for relatedness value r > 0.25 for SRI (chi-squared test: $n_{within/between}$ = 17/ 22, d.f. = 1, χ^2 = 0.928, P = 0.119) and GAI (chi-squared test: $n_{within/between}$ = 8/35, d.f. = 1, χ^2 = 0.386, P = 0.326) (Figure 4).

Together, these results suggest that no differences exist for within- and between-community membership with respect to the genetic relatedness of their members.

DISCUSSION

We found a fine-scale social structure in blacktip reef sharks in Moorea. Taking into account the confounding effects of 5 structural variables (spatial and temporal overlap, gregariousness, size and sex), which are known to influence association patterns (e.g. Godde et al. 2013; Diaz-Aguirre et al. 2019; Machado et al. 2019; Perryman et al. 2019), we found that blacktip reef sharks in Moorea had both preferred associations and affiliations. However, social proximity was not predicted by the genetic relatedness between sharks both at the association, affiliation and community levels. At the dyad level, only male-male associations, but not affiliations, were slightly correlated with genetic relatedness. In addition, individuals had low probabilities of interacting with a close-kin which could explain the lack of influence of kinship in structuring the social network in this population. These results therefore suggest

384 that genetic relatedness does not drive the structure of the social network in this shark
385 population.
386 Compared to previous work conducted on this population (Mourier et al. 2012) which
387 only analysed social structure through associations among sharks, the present study also
388 considered the effects of two structural variables to estimate affiliation indices. Affiliations
389 are an increasingly used method to investigate the true social interactions experienced by
390 animals (Whitehead and James 2015), in particular by considering the strong correlation that
391 can exist between space use overlap and association indices in a variety of taxa (e.g., Mourier
392 et al. 2012; Carter et al. 2013; Best et al. 2014). In our study, the network built from
393 associations using the simple ratio index (SRI) was composed of three main communities
394 relatively spatially separated and only low overlap (Figure 2). When removing the influence
395 of spatial and temporal overlap from association patterns, the network built from the
396 generalized affiliation indices (GAI) revealed five communities that were less spatially
397 separated. This means that associations between sharks were the result of more than just
398 similarities in habitat use or overlaps in time, indicating that individuals actively chose to
399 group with preferred social partners. The differences between the three SRI communities in
400 the present study and the four communities found in Mourier et al. (2012) can be due to the
401 high threshold we used that may highlight only string relationships and the use of SRI instead
402 of HWI. To our knowledge, only one study on elasmobranchs has investigated social
403 structure using GAI, demonstrating that manta rays also preferred affiliations (Perryman et al.
404 2019). Individuals' site preferences and being present in the study at the same time was a
405 strong predictor of association between pairs. Site fidelity is often a prerequisite for sociality,
406 creating an environment for social relationships to develop and the emergence of social
407 preferences. However, the presence of preferred social affiliations demonstrates that sharks
408 show active social preferrences that do not rely on preferrences for sites and periods. Our

409 study confirms that the observed shark social structure resembles that of a fission-fusion
410 society characterized by an open and fluid social structure, long-term social recognition and a
411 high number of potential affiliates, which is flexible depending on environemental
412 conditions.

413 Among the adult sharks in our population, there was a generally low level of
414 relatedness, and only a small number of dyads had close familial relatives. Interactions
415 frequently occurred between distant kin and non-kin. This implies that the social structure
416 among adult blacktip reef sharks was not based on associations between close kin as
417 demonstrated by our analyses which compared association and affiliation patterns with
418 genetic relatedness among dyads at the pairwise or community levels. This is confirmed by
419 the low number of close kin available for each shark in the population (< 6 % pairs with r >
420 0.25), thereby limiting the probability of an individual to encounter a family member and to
421 develop strong associations with them. The lack of genetic relatedness structure within size
422 classes and the lack of decreasing genetic relatedness as sharks grow also suggests that
423 juveniles are unlikely to leave their nursery ground with other kin. If young sharks were
424 developing and maintaining strong bonds with their littermates throughout their entire life,
425 we would have expected to find high mean relatedness and high proportion of close kin
426 across all size classes. The low relatedness we found within each size class indicates that
427 sharks favoured associations with non-kin. These results can be explained in part by the life
428 history and life cycle of blacktip reef sharks. In fact, in contrast to most social animals that
429 show some forms of family structure and parental care, female reef-associated sharks such as
430 blacktip reef shark, leave their pups in their nursery after birth (Mourier and Planes 2013).
431 Moreover, litter size in this species does not exceed five pups (Mourier, Mills, et al. 2013)
432 while litter size in Moorea was limited to a maximum of two pups (Mourier and Planes
433 2013). In addition, blacktip reef sharks follow a yearly breeding cycle with females giving

434 birth every year and potentially being fertilized by multiple males within or across years,
435 which increases the probability of having maternal and paternal half-siblings. Our ongoing
436 long-term nursery monitoring shows that capture probabilities rapidly decline after March
437 (unpublished data), 2 to 3 months after parturition, which suggests a dramatic mortality rate
438 within the nursery areas during the first months of life (i.e. survival rate expected to be
439 inferior to 50% during the first year of life). Together with a small litter size and absence of
440 parental care, this high mortality rate, which is common in many shark species, is likely to
441 limit the opportunity to find family members and develop strong affiliations with close
442 relatives at adulthood. Even in nurseries, juvenile lemon sharks did not clearly assort by
443 relatedness (Guttridge et al. 2011), even if the probability of finding a relative is higher for
444 this species with a larger litter size. When juvenile sharks grow, they progressively explore
445 their environment and increase their home range (Chin A et al. 2013), creating an opportunity
446 to find related individuals such as parents or maternal half-siblings from previous
447 reproductive seasons. At adulthood, our results confirm that preferred associations and
448 affiliations are not driven by genetic relatedness as sharks are associating with conspecifics of
449 variable genetic distances. This suggests that sharks might not have the ability for kin
450 recognition simply based on visual or olfactory cues and that kin-based preferred associations
451 and affiliations may only develop within nursery areas from increased familiarity with
452 littermates, or that they are not seeking for associations with related individuals. Through
453 investigation of social groups of spotted eagle rays *Aetobatus narinari* in Florida, Newby et
454 al. (2014) found no kin-structure in the social organization, although the analysis was based
455 on group composition rather that quantitatively inferred using association indices. However,
456 our results revealed that males sighly preferred to associate with other related males but this
457 tendency was not confirmed for affiliations (accounting for spatial and temporal structural
458 components). This suggests that genetic relatedness among males was spatially structured

459 and that males may disperse less than females. The lack of differences in relatedness between
460 males and females suggests that the risk of inbreeding might be low if these interactions
461 represented potential mating pairs and not only social bonds.
462
463 The emerging literature suggests that genetic structure of animal social networks can
464 vary dramatically, from highly cohesive kin-based groups like African elephants (*Loxodonta*
465 *africana*) (Archie et al. 2006) or spotted hyenas (*Crocuta crocuta*) (Holekamp et al. 2012), to
466 groups with moderate levels of genetic relatedness due to limited dispersal like the Galápagos
467 sea lion (*Zalophus wollebaeki*) (Wolf and Trillmich 2008) or the eastern grey kangaroo
468 (*Macropus giganteus*) (Best et al. 2014), or to groups with little to no genetic relatedness like
469 guppies (*Poecilia reticulata*) (Croft et al. 2012), the common raccoon (*Procyon lotor*)
470 (Hirsch et al. 2013) or migratory golden-crowned sparrows (*Zonotrichia atricapilla*)
471 (Arnberg et al. 2015). These patterns of variation provide opportunities to explore how
472 ecological factors interact with kinship to produce variations in the structures of animal
473 societies. Kinship is expected to promote the evolution of cooperation and sociality in
474 animals (Hamilton 1964). However, our understanding of the evolution of sociality results to
475 a great extent from the study of closed societies, in which interactions mainly involve
476 relatives and can hence be explained by kin selection (Hamilton 1964). However, the kin
477 selection theory has recently been challenged by results from studies showing that fitness
478 benefit can emerge in social groups composed mainly of non-relatives (e.g., Cameron et al.
479 2009; Riehl 2011; Wilkinson et al. 2016). In many natural populations, dispersal tends to be
480 limited, favouring local competition between neighbours and the emergence of a social
481 component, whether it be selfish, aggressive, cooperative or altruistic (Lehmann and Rousset
482 2010). But how social behaviours translate into fitness costs and benefits depends
483 considerably on life-history features, as well as on local demographic and ecological

484 conditions. The fission – fusion social dynamics lead to unstable group membership, and
485 dispersal and occasional recruitment of unrelated individuals lead to low average relatedness
486 in groups. Then under such conditions, selection is not expected to favour kin recognition
487 mechanisms based on familiarity alone.

488 Therefore, contrary to the kin selection hypothesis which predicts stronger associations
489 among kin, sharks tended to assort randomly according to relatedness. As kinship does not
490 explain the strength of social affiliations in blacktip reef sharks, the question remains as to
491 how and why sharks form preferred associations and affiliations organised in social
492 communities (Mourier et al. 2012). Although cooperation has been mainly explained in the
493 context of kin selection, there might be potential benefits of non-kin sociality in blacktip reef
494 sharks such as for other animals in which association with non-kin emerges via reciprocal
495 altruism (Carter and Wilkinson 2013; Wilkinson et al. 2016). While evidence of shark
496 cooperation has not been confirmed, gregarious behaviour can have several benefits in sharks
497 (Jacoby et al. 2012), including increased foraging success by hunting in groups (Weideli et al.
498 2015; Mourier et al. 2016), protection from predators (Mourier, Planes, et al. 2013), or
499 increased tolerance relationships and reduced aggression rate (Brena et al. 2018).
500 Heterospecific foraging associations have been found to develop and increase predation
501 success (Labourgade et al. 2020), which suggests that sharks can benefit from hunting
502 associations without associating with kin. These benefits do not necessarily imply kin
503 selection and can simply build on the development of familiarity from repeated interactions.
504 Social structure in reef sharks can arise from multiple simple ecological factors such as the
505 distribution of resources in space and time leading to aggregations of individuals even in the
506 absence of benefits of direct social affiliation (Ramos-Fernández et al. 2006) or mitigation of
507 the cost of unnecessary aggression when competing for resources mediated by individual
508 recognition (Brena et al. 2018). Regardless of the exact cause of social preferences in reef

sharks, the absence of kinship as an important factor in structuring association patterns suggests that there are important benefits of sociality in sharks that we still need to uncover. With an increasing use of social network analyses applied to shark populations (Mourier et al. 2018), future work on social networks and genetic relatedness in different populations or species is necessary to confirm our results and to improve our understanding of population dynamics in sharks and the evolution of sociality.

SUPPLEMENTARY MATERIAL

Supplementary information including two tables and four figures can be found online.

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Tables

Table 1: Multiple Regression Quadratic Assignment Procedure and the influence of all structural variables on shark social associations. Matrices representing structural variables (predictors) were regressed against the association matrix (SRI) using a subset of the individuals in the population (n = 43) to which genetic relatedness was available. TO: temporal overlap; SO: spatial overlap; Gregariousness: typical number of associates based on (Godde et al. 2013); Size and Sex: binary matrices where individuals of the same size/sex classes are represented by 1, and different classes by 0. Adjusted R^2 indicates how much of the variation on association indices was explained by the predictors. Significant predictors in which *P*-values are given by the proportion of times the empirical regression coefficient was smaller or greater than the null expectancy from 20,000 randomisations (*P*–values are complementary, totalling 1) are indicated in bold. We considered all predictors were significant when $\beta \leq r$, thus $P > 0.95$ (**).

Period (SRI)	Predictors	Regression Coefficient (β)	*P (β≥r)*	*P (β≤r)*	Adjusted R^2
All	**TO**	0.5534	1.000**	<0.001*	94%
	SO	0.1069	1.000**	<0.001*	
	Gregariousness	-0.0018	<0.001	1.000	
	Size	0.0057	0.9101	0.0895	
	Sex	-0.0025	0.0003	0.9996	

753 **Table 2** Results of Mantel test for the correlation between the simple-ratio association (SRI)
754 and generalized affiliations (GAI) matrices and the pairwise genetic relatedness among
755 individual sharks for each period and each sex relationship. Observed estimates were
756 compared to those of 20,000 estimates from the randomized networks and significant p-
757 values are indicated in bold.

Index	SRI		GAI	
	Estimate (rho)	p-value	Estimate (rho)	p-value
Male-male	0.1028	**0.0267**	0.0404	0.4187
Female-female	-0.0653	0.5767	0.0361	0.7644
Male-female	0.0136	0.8291	-0.0240	0.7050

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761 **Table 3** Effects of sex on shark gregariousness (degree and strength) in the social network.

		Coefficient	SE	*t* statictic	P_{rand}
Degree	*Intercept*	17.308	1.800	9.613	
	Sex (male)	4.726	2.156	2.192	**< 0.001**
Strength	*Intercept*	4.493	0.468	9.596	
	Sex (male)	0.369	0.560	0.660	0.548

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770 **Table 4** Community level information on structure, association and affiliation indices, and
771 genetic relatedness. For each social index (SRI and GAI) and each community, are reported
772 number of community members (no. of individuals), mean index value, mean genetic
773 relatedness and p-values of the tests for within-between differences in relatedness.

Index	Communities	Modularity Q	No. of individuals	Mean index (SD)	Mean r (SE)	*p-values*
SRI	Overall	0.493	43	0.133 (0.210)	0.071 (0.005)	0.093
	Red		14	0.487 (0.178)	0.071 (0.009)	0.267
	Yellow		9	0.256 (0.307)	0.073 (0.016)	0.24
	Green		20	0.282 (0.194)	0.069 (0.006)	0.11
GAI	Overall	0.312	43	-0.028 (0.126)	0.060 (0.006)	0.722
	Red		1	/	/	/
	Yellow		12	0.078 (0.147)	0.056 (0.010)	0.707
	Green		6	-0.003 (0.155)	0.043 (0.015)	0.735
	Cyan		13	0.022 (0.127)	0.066 (0.009)	0.415
	Purple		11	0.053 (0.140)	0.061 (0.013)	0.408

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Figure legends:

Figure 1 Map of the study location indicating the monitored sites along the 10 km reef edge of the North coast of Moorea.

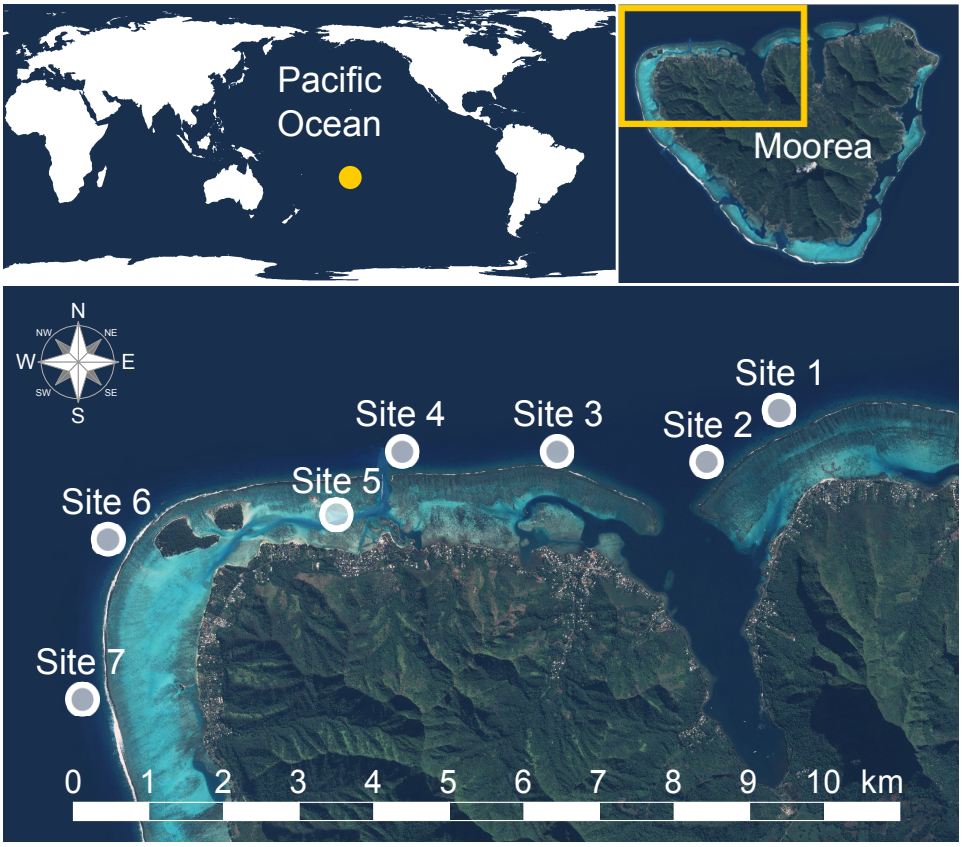


Figure 2 Shark social preferences at the individual and population levels. Nodes (N = 43; male:female = 30:13) representing photo-identified individuals are proportional to their size and colour-coded by social modules; individuals are connected by links whose thicknesses are proportional to SRI in the association networks (left panel), and to GAI removing confounding factors in the affiliation networks where only positive GAIs are plotted (right panel). In the density plots, red dots denote statistically significant observed values, shaded distributions indicate null expectancy and blue whiskers indicate 95% confidence intervals. The shark social network is characterized by (a) significant standard deviations (SD) of SRI and GAI indicating social preferences and (b) significant modularity (Q) indicating social

division. In (c) are represented the density distribution of sightings of social community members.

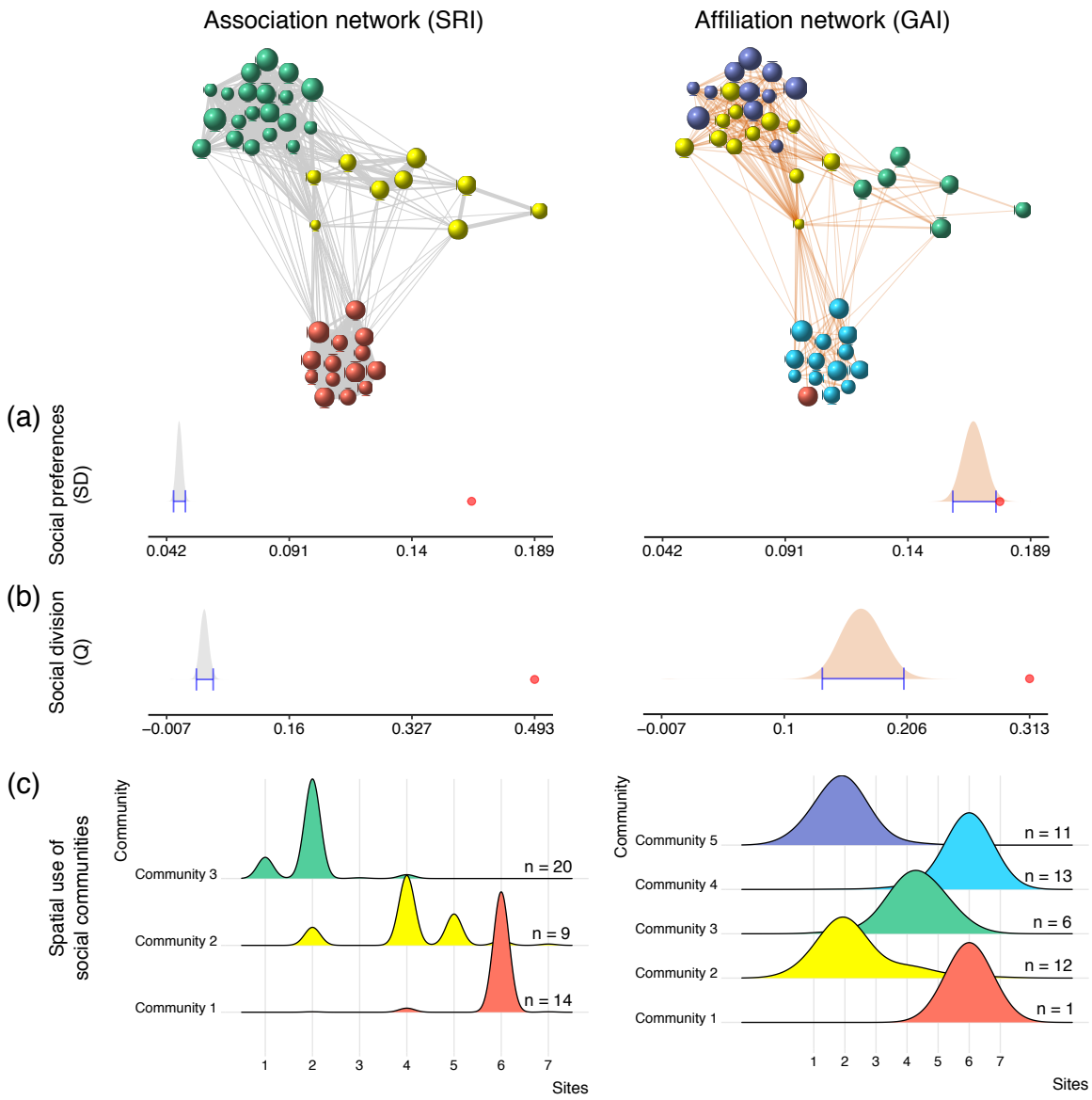
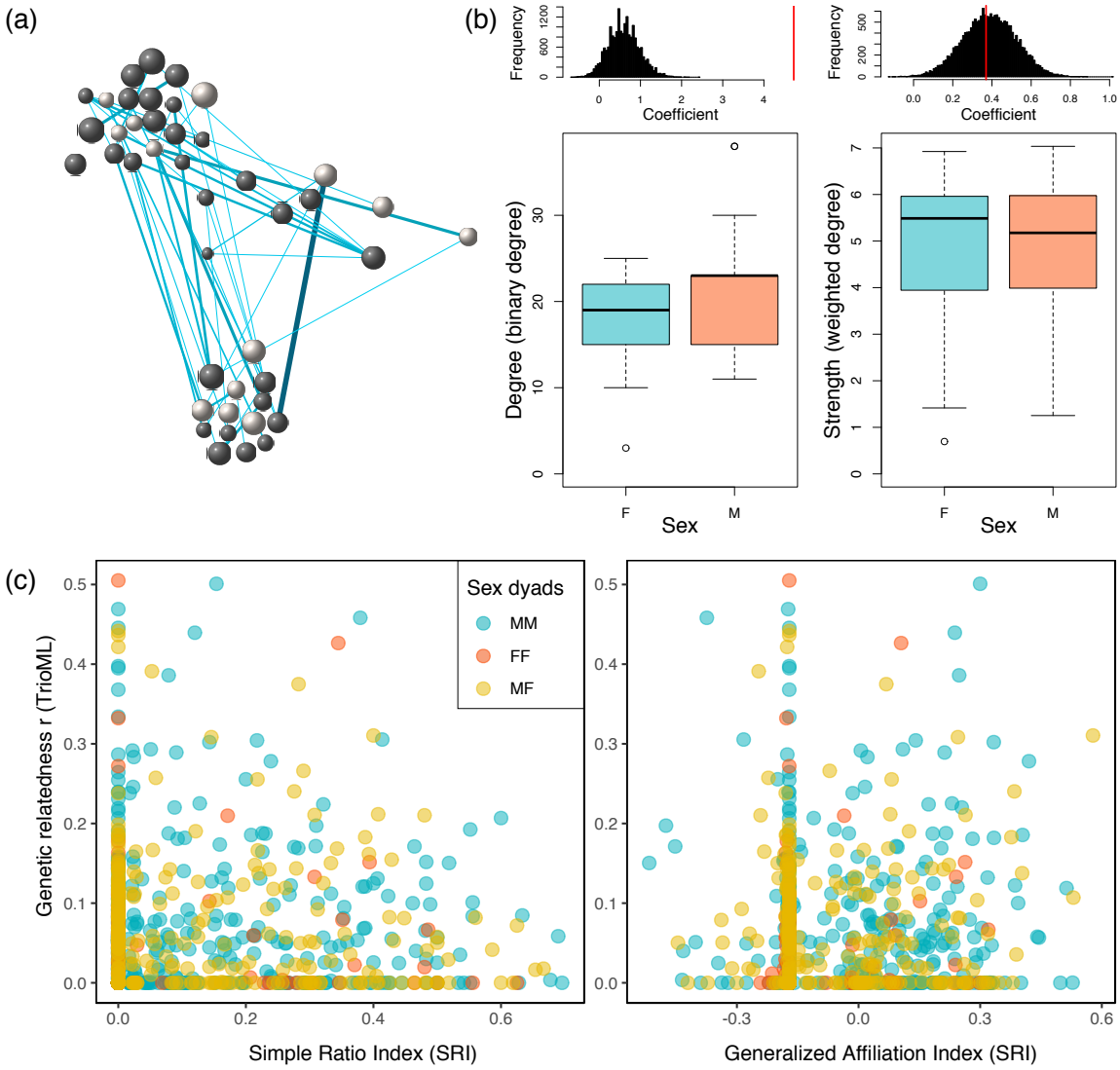


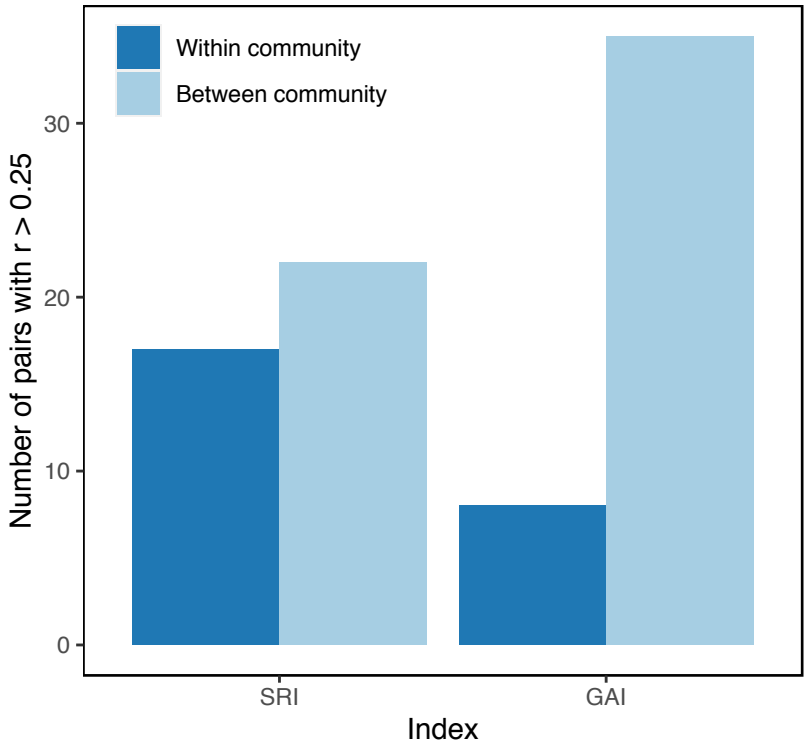
Figure 3 (a) Genetic network using the same layout as in Figure 2 where nodes (N = 43; male:female = 30:13) are proportional to individual size and colour-coded by sex (males in grey and females in white) and edges are proportional to genetic relatedness in the genetic network (only close kin are plotted, i.e. r >0.25). (b) Differences in gregariousness (degree and strength) of individual sharks between males and females (colours: pink indicates

females and blue indicates males). Comparison of the coefficient from the GLM based on the observed data (red vertical line) and the frequency distribution of coefficients from the same model based on the randomized data are indicated over each box plot to report significance of the difference. (c) Relationship between association and affiliation indices and the triadic likelihood estimator (TrioML) of genetic relatedness in male-male, female-female and male-female pairs.



806 **Figure 4** Numbers of close kin (r > 0.25, the expected value of half-sibs) within and between

807 social communities for association (SRI) and affiliation (GAI) indices.



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