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Social preferences and network structure in a population of reef manta rays

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Abstract:	Understanding how individual behavior shapes the structure and ecology of populations is key to species conservation and management. Like many elasmobranchs, manta rays are highly mobile and wide ranging species threatened by anthropogenic impacts. In shallow-water environments these pelagic rays often form groups, and perform several apparently socially-mediated behaviors. Group structures may result from active choices of individual rays to interact, or passive processes. Social behavior is known to affect spatial ecology in other elasmobranchs, but this is the first study providing quantitative evidence for structured social relationships in manta rays. To construct social networks, we collected data from more than 500 groups of reef manta rays over five years, in the Raja Ampat Regency of West Papua. We used generalized affiliation indices to isolate social preferences from non-social associations, the first study on elasmobranchs to use this method. Longer lasting social preferences were detected mostly between female rays. We detected assortment of social relations by phenotype and variation in social strategies, with the overall social network divided into two main communities. Overall network structure was characteristic of a dynamic fission-fusion society, with differentiated relationships linked to strong fidelity to cleaning station sites. Our results suggest that fine-scale conservation measures will be useful in protecting social groups of M. alfredi in their natural habitats, and that a more complete understanding of the social nature of manta rays will help predict population responses to anthropogenic pressures, such as increasing disturbance from dive-tourism.
Response to Reviewers:	Dear Ian, Thanks very much for your comments on this article. Please see below for my responses: Line 33-35: Abstract: “Our results suggest…” The importance of dive tourism is not

anticipated earlier in the abstract. Consider combining the last two sentences of the abstract into a more general statement on the implications of the study for conservation.

Ok I have changed this- dive tourism is now given as an example of an anthropogenic pressure

Lines 53-55, “Social interactions directly affect…”. Because this sentence refers to social interactions in general, and no emergence of social structure per se, move this to the end of Line 49 (after “social learning (Brown, Laland & Krause 2011).”

Done

Line 51, remove comma after “decisions”

Done

Line 58: You should make the connection between social network analysis and social structure clear here.
Ok I have added a short sentence and Croft et al. (2008) reference

Line 79: “Individual manta rays can be easily observed…” This sentence is clearly relevant to the paragraph but seems out of place here. Consider moving it to line 73, immediately after “including social preferences.”
Moved and changed this paragraph a bit to fit better

Line 78: Reference to self-awareness – it isn’t clear how this is relevant to the argument that mobulid rays are excellent candidates for studies on elasmobranch sociality.
Ok I've removed this part of the sentence and the reference for it

Line 80: Starting at “Globally, both species…”. This should be a new paragraph.
Done

Line 103: Explain what “genuine” social preferences are.
See added brackets for clarification

Line 116: Reviewer #3 requested additional information on the spatial aspects of sampling. However, I found the revised version still to be a little unclear. Was a single location within the 15 km^2 area chosen for a dive? What was the total area observed over a single 1 hr dive (or is this the 15 km^2)? Did this differ among sites?
Changed this paragraph to clarify these questions

Line 229: Please explain how you determined whether females were observed as “sexually active”? Is this based on observations of mating or other evidence such as mating scars?
I've changed line 125 in the methods to clarify this

Paragraph starting line 241: The numbering of supplementary figures 10 and 11 is consistent with the figure captions in the appendix, but not with the figures themselves.
Ok I've changed the numbering in the online system which should then update when the new manuscript is created

Line 250: Remove (or move to discussion): “This was surprising…”, as this is interpretation rather than results.
Ok I've moved this to discussion (L361-364), and changed the text there slightly

Line 288: I think it would be helpful to briefly remind the reader of the difference between social preferences and preferred associations here.
I've changed lines 281 and 282 to make this clearer.

Line 322: Please revise “Pregnant females may…” to reflect the actual reproductive statuses used (i.e., that these are females that have been observed to be pregnant, but (as I understand it) are not necessarily pregnant at a given observation).

	Changed this to 'mature' Line 332: There is a stray hyphen after “fishes” on the unmarked version Removed Line 378: add comma after “Therefore” Done **In addition, I've updated Figure 9 (map of study location and sites) using ARC GIS. I think this image is much better now. Hope that's ok

Title: Social preferences and network structure in a population of reef manta rays

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Author contributions:

RP and DF conceived the central idea of the manuscript. RP, SV, AM and RT collected and input data. RP conducted all statistical analyses with input from DF. RP was the primary author of the manuscript. DF, CB, AM and SV contributed to editing and manuscript revisions.

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Abstract

Understanding how individual behavior shapes the structure and ecology of populations is key to species conservation and management. Like many elasmobranchs, manta rays are highly mobile and wide ranging species threatened by anthropogenic impacts. In shallow-water environments these pelagic rays often form groups, and perform several apparently socially-mediated behaviors. Group structures may result from active choices of individual rays to interact, or passive processes. Social behavior is known to affect spatial ecology in other elasmobranchs, but this is the first study providing quantitative evidence for structured social relationships in manta rays. To construct social networks, we collected data from more than 500 groups of reef manta rays over five years, in the Raja Ampat Regency of West Papua. We used generalized affiliation indices to isolate social preferences from non-social associations, the first study on elasmobranchs to use this method. Longer lasting social preferences were detected mostly between female rays. We detected assortment of social relations by phenotype and variation in social strategies, with the overall social network divided into two main communities. Overall network structure was characteristic of a dynamic fission-fusion society, with differentiated relationships linked to strong fidelity to cleaning station sites. Our results suggest that fine-scale conservation measures will be useful in protecting social groups of *M. alfredi* in their natural habitats, and that a more complete understanding of the social nature of manta rays will help predict population responses to anthropogenic pressures, such as increasing disturbance from dive-tourism.

Keywords: Reef manta ray, *Mobula alfredi*, social network analysis, social preferences, generalized affiliation indices.

Significance statement

In social animals, relationships between individuals have important implications for species conservation. Like many other sharks and rays, manta rays are threatened species, and little is known about their natural behavior or how their populations are structured. This study provides evidence of social structure in a wild, free-ranging population of reef manta rays. We show for the first time that individual manta rays have preferred relationships with others that are maintained over time, and structured societies. This study extends our knowledge of elasmobranch ecology and population structuring. Results suggest that understanding social relationships in manta rays will be important in protecting populations from human impacts, and developing sustainable, localized conservation and management initiatives.

1. Introduction

Knowledge of how individual behavior drives population structure and dynamics is required to predict the response of populations to human impacts (Sutherland 1998, Sih et al. 2013). In group-living species, social interactions are a fundamental part of population ecology (Hinde 1976) important in enabling collective behaviors (Couzin et al. 2002, Couzin & Krause 2003, Sumpter 2006), such as cooperative foraging (Sih et al. 2009), predator avoidance (Ward et al. 2011) and social learning (Brown, Laland & Krause 2011). Social interactions directly affect key ecological and evolutionary processes such as disease transmission, habitat use and genetic exchange (Kurvers et al. 2014). Social animals are often able to modify their behavior depending on the status of their relationship with various social partners (Krause & Ruxton 2002). Social preferences between individuals may have profound effects on movement decisions that lead to the formation of structured social groups (Bode et al. 2011). Understanding this structure can aid conservation approaches by explaining individual behavior in the context of a population's social environment (Berger-Tal et al. 2011, Krause et al. 2014, Snijders et al. 2017). Social heterogeneity tends to produce organization of animal societies into units that respond differently to environmental conditions, such as in their foraging success (Whitehead & Rendell 2004). This is likely to cause stratification in survival and reproductive success of group members, so it can be misleading to assess population dynamics without considering the impact of this structure (Lusseau et al. 2006). Social network analysis may be used to describe and quantify social structure (Croft et al. 2008) may be particularly useful for populations in which the existence of social relationships between individuals is not immediately evident, such as in fission-fusion societies (Snijders et al. 2017).

Despite wide literature on social structuring in terrestrial vertebrates and marine mammals (e.g. Baird & Whitehead 2000, Gero et al. 2005, Lusseau et al. 2006, Wolf et al. 2007, Foster et al. 2012), there are few equivalent studies on marine fish. These are particularly lacking for elasmobranchs, despite their high potential for socially structured populations (Jacoby et al. 2010). Sharks and rays are often thought to be solitary creatures, but many species across elasmobranch phylogeny are found in groups or loose aggregations (for review see Jacoby et al. 2012). Where individuals vary in their movements and habitat preferences, some are likely to interact more than others by chance. Group formation via passive processes occurs in elasmobranchs during feeding aggregations (e.g. Heyman et al. 2001) and seasonal migrations (e.g. Heupel & Simpfendorfer 2005, Bass et al. 2016). Many elasmobranchs have developmental shifts in habitat and diet (Wetherbee et al. 2004) that may drive assortment in size- or sex-segregated groups

(Wearmouth & Sims 2008). Recently, ex-situ studies have shown that some species exhibit complex sociality, including social structure (Jacoby et al. 2010), social learning (Guttridge et al. 2013, Thonhauser et al. 2013) and individual personalities (Jacoby et al. 2014, Byrnes et al. 2016). Due to the difficulty in observing multiple interactions between wild elasmobranchs, however, quantitative analysis of the importance of social relations to the structure of their populations is lacking (but see Guttridge et al. 2011, Mourier et al. 2012). It is usually a considerable challenge to disentangle passive aggregation driven by external forces from active social preferences.

Manta rays (*Mobula spp.*) are excellent candidates for studies on elasmobranch sociality, including social preferences. Individuals can often be easily observed and accurately identified in the wild. Mobulid rays have the largest brains relative to body size of all elasmobranchs (Lisney et al. 2008), with a highly developed central nucleus that has been linked to social intelligence and formation of hierarchical social structures (Ari et al. 2011). Social recognition may be important in mate choice (Marshall & Bennett 2010). Manta rays perform group-based behaviors including collective foraging, following, breaching, copying, play and curiosity towards humans (Marshall 2008, Deakos 2010, Gadig & Neto 2014, RP pers. obs.), that are associated with social functions and reminiscent of highly social marine mammals (Bradbury 1986).

Globally, both species of manta ray (*M. alfredi and M. birostris*) are considered vulnerable to extinction (Marshall et al. 2018a, 2018b) due to evidence for recent, large-scale population declines in several regions (e.g. Rohner et al. 2017). Populations are extremely vulnerable to overfishing, among other threats such as ocean pollution, climate change and bycatch (Marshall et al. 2011a, 2011b, Lawson et al. 2014, Stewart et al. 2018), exacerbated by their extremely low reproductive output (Dulvy et al. 2014, Stevens 2016) and high mobility (Germanov & Marshall 2014, Jaine et al. 2014). Populations inhabit subtropical waters, typically those of developing nations where funding for conservation or policing initiatives is scarce, and are unlikely to receive adequate protection from small marine reserves. Indonesia is a globally significant area for both species, having some of the largest identified populations of manta rays in the world (Marshall & Holmberg 2019). Despite receiving protection throughout Indonesian waters in 2014 (Lawson et al. 2017), fishers continue to exploit mobulid rays with impunity, impacting local populations (Couturier et al. 2012, Lewis et al. 2015, Croll et al. 2016). Manta rays are an important attraction in dive-tourism (O'Malley et al. 2013, Venables et al. 2016a), and unrestricted growth of this industry may cause disturbance at known aggregation sites (Anderson et al. 2011b, Venables et al. 2016b). Understanding the nature of manta ray group and social structuring will aid the implementation of measures to mitigate any negative impacts of dive tourism in these areas.

Research on manta rays to date has focused mainly on broad population demographic and ecological studies (e.g. Marshall & Bennett 2010, Deakos et al. 2011, Marshall et al. 2011, Kashiwagi et al. 2011, Jaine et al. 2012, Couturier et al. 2014), as-well as individual-based movement tracking and behavioral studies (e.g. Dewar et al. 2008, Jaine et al. 2014, Stewart et al. 2016a, Ari et al. 2016). While these provide comprehensive baseline data for management of manta rays, considering social structure will aid a more nuanced approach, where the behavior of individuals is linked to group- or population-level responses to the environment. Recent studies have shown that individuals within shark populations exhibit large differences in movements, feeding behavior and personality (Jacoby et al. 2014, Matich & Heithaus 2015, Finger et al. 2016, 2017), suggesting that network analyses may be vital to provide reliable data for population ecology and conservation. Though several studies have provided anecdotal evidence of social behavior in manta rays (Deakos et al. 2010, Stewart et al. 2016b, Stevens et al. 2018), this is the first study to provide a quantitative description of their social organization. Our aims were to describe the temporal and spatial structure of social relations, and determine whether manta rays had genuine social preferences (caused by active choice of individuals to interact) by controlling for non-social structural factors, including location, time, phenotype and individual gregariousness. We expected to find heterogeneity in social relations, as in most social species (Foster et al. 2012). Based on previous knowledge of manta ray ecology and habitat use, we predicted that location fidelity would be an important driver of association, and individuals would have differentiated social strategies. We expected that assortment by phenotype, including sex, maturity, colour morph, and reproductive status would be important in structuring the society, potentially enabling the division of the population into distinct social communities.

2. Methods

2.1. Sampling procedure

Data on reef manta ray group compositions were collected from November 2013 to May 2018 in the Dampier Strait region of Raja Ampat, West Papua, by trained researchers diving using SCUBA equipment, or freediving- depending on the position of rays in the water column. Where exact times and locations could be verified, some records (approx. 10% of all data) were obtained by photographic uploads to 'MantaMatcher.org', an online citizen-science based catalogue (Marshall & Holmberg 2019). It was not possible to record data blind because our study involved observing animals in the field. Sightings of reef manta rays recorded at 5 sites (3 cleaning stations and 2 feeding sites) within a 20km^2 area were used to allow analysis of fine-scale social structure, with data also collected from an additional 5km^2 site that was used by manta rays for both feeding and cleaning behaviours. Sampling occasions were dives or snorkels of approx. 1h, at one of these sites, restricted to one sampling occasion at each site per day. The total area covered during a single dive or snorkel was approximately 0.5-1km^2. We alternated sampling effort by site and time to minimize environmental bias, using variables expected to influence manta ray behavior (location, tidal phase, tidal range, time, and lunar phase) (Jaine et al. 2012). See Appendix Section 1 for details of study area (Fig. 9) and sampling effort (Table 4).

2.2. Recording individual encounters

Individual reef manta rays were identified by standard Photo-ID methods (see Fig. 1), using unique, lifelong spot patterns on the ventral surface (Pierce et al. 2018). Rays were sexed by presence/absence of claspers, and maturity and reproductive status/sexual activity were estimated as in Marshall & Bennett (2010) using evidence from female pregnancies and mating scars, and male clasper size/calcification. Disc-width (DW) was estimated by visual comparison of manta rays to coral structures of known size. Based on 55 individual females of known maturity, size-at-maturity in the population was estimated to be 3-3.5m DW, similar to populations in Hawaii and Australia (Deakos et al. 2012, Couturier et al. 2014). Where maturity could not be determined using morphological features, females with estimated DW ≥ 3.5m were considered mature, and estimated DW ≤ 3m immature. Photographic records of each distinct encounter (sighting of an individual) were stored in an online database (www.MantaMatcher.org). For each individual, an 'encounter rate' (ER= no. sightings of individual at site, divided by no. sampling occasions at site) was calculated, and ranked by site to define individual site preferences. Sex ratios were compared at each study site using exact binomial tests. We constructed logistic mixed effects models using the glmer function of the lme4 package (Bates et al. 2014) in R version 3.4.4 (R Core Team 2018) to compare the probability of encounter of different phenotypes (sex, maturity, colour morph) at cleaning stations/feeding sites, and at individual sites, using presence/absence of individuals during a sampling occasion as the dependent variable, site and phenotype as fixed effects, and individual ID as a random effect. We used deviation coding to compare probability of encounter to a grand mean over all sites (see Appendix Section 3, Table 5).

2.3 Defining associations

Associations between individuals were defined using the 'Gambit of the Group' (GoG) (Whitehead & Dufault 1999), which assumes all individuals observed together are associated, without necessarily interacting socially. This is appropriate where individuals move between groups (Franks et al. 2010), and where direct interactions are difficult to observe regularly, but groups can easily be defined and have meaningful structure (Farine et al. 2015). Each dive was considered an independent sampling occasion (Whitehead 2008a), and all individuals observed during a dive were considered as part of the same group if a gap of <10mins between encounters occurred (this addressed difficulty in observing a highly mobile species with restricted visibility underwater). In practice, we were confident that observed associations gave an accurate representation of true structure, because groups were spatio-temporally well-defined, and it was usually possible to record the identity of all individuals seen.

Data were recorded in a group by individual binary matrix with rows representing each sampling occasion, and columns representing individuals. Network analyses were performed in R, using the asnipe (Farine 2017a), igraph (Csardi & Nepusz 2006), and tnet (Opsahl, 2010) packages. Network diagrams were drawn in Gephi 0.9.2 (Bastian et al. 2009). We calculated simple-ratio indices (SRIs) (Cairns & Schwager 1987) to measure strength of association between all pairs. The SRI is the recommended association index (AI) where calibration data are unavailable (Hoppitt & Farine 2018). SRIs were calculated within 45 sampling periods (SPs) of length 15 days. This length was chosen according to results from LAR analysis (see section 3.4), and prior knowledge of the species' movements (e.g. Marshall et al. 2008, Deakos et al. 2012), to be short enough that individuals were likely to remain in the area, but long enough to allow sufficient opportunity for swaps between groups required for independence of observations. We identified 112 individuals ≥ 10 times. All individuals observed < 10 times were removed from subsequent network analyses, because various studies suggest that prioritizing edge accuracy is preferable to including a large proportion of the population (Whitehead 2008b, Franks et al. 2010). We calculated social differentiation (S): the variability of the 'true' AIs estimated using maximum likelihood approximation (Whitehead 2008a). Values of S close to 0 indicate homogenous relationships within the population, while values near or greater than 1 indicate highly varied relationships. To determine the accuracy of AIs, and their power in testing for social relationships we calculated the correlation coefficient r, between S and the observed (measured) AIs (Whitehead, 2009) as: $r = \frac{S}{\mathrm{CV}(SRI_{ab})}$. Sufficient statistical power to test for preferred or avoided associations was accepted when $S^2 \times H > 5$, (where H is the mean no. identifications per individual) (Whitehead 2008b). Standard errors for S and r were estimated using 100 bootstrap replicates of the observed data.

2.4. Stability of identifications and associations over time

We calculated lagged identification rates (LIR) (see Appendix Section 3) and lagged association rates (LARs) (Fig. 5) to describe changes in the presence of individuals in the study area, and their relationships over time (Whitehead 1995). For these analyses we used sampling periods of one day. We used LAR rather than standardized LAR because we were confident of identifying most individuals within groups. We calculated three LARs: for all individuals; between females only; and between males only. Due to large time gaps between study seasons, a maximum time lag of 180 days was used to restrict LARs to within a single study season. We used a moving average (A) over the possible no. associations (p), multiplied by 0.25 ($A^{p0.25}$), to smooth the line ($A^{p0.25}$ (all individuals)= 3630, $A^{p0.25}$ (females)= 1208, $A^{p0.25}$

(males)= 431). We fit models describing different potential aspects of relationships within animal societies (see Appendix Section 4), and compared LAR to a null association rate (NAR- the expected rate if associations in the population were randomly distributed). Standard errors were obtained using jackknife resampling (Whitehead 1995). All LIR and LAR analyses were run using SOCPROG 2.7 (Whitehead, 2009). The most parsimonious LAR model was selected using the quasi-Akaike Information Criterion (QAICc) (Burnham & Anderson 2002, Whitehead 2007).

2.5.1. Quantifying social preferences

Social networks derived using AIs may be the result of many inter-related factors, including joint locational preferences or overlap in time (passive grouping with unknown others), individual gregariousness (active choice to form groups with unknown others), as well as individual social preferences (active choices to group with known individuals). Manta rays in this study had high location fidelity and phenotypic variation in site preferences (see sections 3.2 and 3.3). We needed to disentangle non-social factors from the social preferences that we were interested in. Researchers often use location-constrained permutations for this purpose, but these only change p-values, and do not control for bias in effect sizes, which can lead to spurious conclusions. We therefore use generalized affiliation indices (GAIs) that control for various non-social factors when constructing network weights (Whitehead & James 2015). GAIs in our study were deviance residuals (divided by the denominator of the corresponding SRI value) from a generalized linear model with a binomial error structure and log link function, with SRIs as the dependent variable, and corresponding matrix elements of predictors of pairwise association as independent variables. High positive values for GAIs indicate affiliation (dyads are more associated than expected given the structural predictor variables), and negative values indicate avoidance**.** GAIs may therefore be considered an estimate of the strength of social preference between pairs, with variation due to non-social factors statistically removed. Predictor variables used in calculation of GAIs were: site use similarity- the Euclidean distance between the encounter rate (see section 2.2) of each pair at each study site, temporal overlap (custom SRI calculated on whether pairs were observed in the study area within 14 days of each other, within sampling periods of 60 days), gregariousness (based on Godde et al. 2013, joint pairwise gregariousness was calculated as follows: $G_{ab}= \log(\Sigma SRI_a \Sigma SRI_b)$ where ΣSRI_a and ΣSRI_b are the sums of all the SRIs for individuals a and b, respectively), sex class (male/female, 1 if same sex, 0 if not), maturity class (adult/juvenile, 1 if same maturity class, 0 if not), and color morph class ('normal' or melanistic, 1 if same color morph, 0 if not). Multiple regression quadratic assignment procedure (MRQAP) tests (Dekker et al. 2007) were used to identify the relative influences of each predictor variable on associations (see Appendix Section 6, Table 8).

2.5.2. Permutation tests

We tested various hypotheses regarding preferred associations, social preferences, assortment by phenotype, and community structure by comparing observed statistics against equivalent statistical distributions produced by data-stream permutations of the observed group by individual matrix (Bejder et al. 1998, Croft et al. 2011). All tests used 1000 permutations of the data, with 100 flips per permutation. P-values were calculated by the number of times the randomized statistic was higher than the observed statistic. In all cases permutations were sufficient for p-values to stabilize. Permutation tests for SRIs were conducted on all individuals, and for GAIs were conducted on sub-networks of individuals divided by the sex and maturity of individuals, as follows: 1. Overall network (all ties between all individuals); 2. Female:Female- female ties with other females; 3. Male:Male- male ties with other males; 4. Female:Male- female ties with males; 5. Adult:Adult- adult ties with other adults; 6. Juvenile:Juvenile- juvenile ties with other juveniles; 7.

Adult:Juvenile- adult ties with juveniles. This allowed us to retain variation associated with sex or age differences within GAIs while interpreting differences in social relations between sex and age classes. For each network, we tested the hypothesis there were more preferred and avoided relationships than expected by chance. Short-term preferred relationships were indicated by a significantly lower than expected mean of all tie weights, long-term preferred relationships indicated by a significantly higher than expected SD of all tie weights, and overall preferred relationships indicated by a significantly higher CV of all tie weights (vice versa for avoided relationships), following Whitehead (2009). We used the same permutation method to find dyadic values that were significantly higher than expected within each network. These were used to build a network of estimated social preferences (Fig. 7).

2.6. Assortment by phenotype

We tested for assortment in the reef manta ray population by sex, maturity and color morph, with the null hypothesis that assortment would be no stronger than expected if relationships were random. To test for assortment whilst controlling for the structure of the dataset, we compared assortativity coefficients (ACs) calculated on observed SRIs (to check if rays assorted non-socially) and GAI values (to check if social preferences were assorted) to equivalent coefficients calculated from data stream permutations (section 2.5.2). ACs were positive if vertices of similar phenotype tended to positively connect, or if vertices of different phenotype tended to negatively connect. ACs were negative if vertices of different phenotype tended to positively connect, or if vertices of similar phenotype tended to negatively connect. GAIs had both negative values (indicating avoidance) and positive values (indicating social preference). Due to the difference in meaning of positive/negative values here, it did not make sense to calculate ACs for all GAI values combined. We therefore tested for assortment among positive and negative GAI values separately.

2.7. Community structure

We used the leading.eigenvector.community algorithm in igraph to identify community structure within the overall networks of SRIs/GAIs. This method divided networks successively into clusters, with the most parsimonious network division being that which maximized the modularity coefficient, Q (Newman 2006). Data-stream permutations (section 2.5.2) were used to evaluate whether this value was meaningful. We obtained confidence intervals for Q using the method of Lusseau et al. (2008). We assessed robustness of community assignment using a coefficient of assortativity (R_{com}), which directly assessed the degree to which empirical community assignments of nodes agreed with assignments from bootstrap replicates (Shizuka & Farine 2016). We then calculated within-community social differentiation (section 2.3) to measure social complexity in the population.

2.8. Individual network positions

To investigate social strategies and classify overall network structure, we calculated network metrics for individuals within the overall network of GAIs. This allowed us to test hypotheses that individuals of different phenotypic class (sex, maturity status, color morph) or reproductive status (females observed as pregnant at least once/females never observed as pregnant, and females observed as sexually active/never observed as sexually active) had different average network positions. We used the tnet package (Opsahl et al. 2010) in R to calculate the following metrics: weighted degree (summed weight of all connections for each individual); weighted betweenness centrality (measure of how often an individual is located on the shortest path between two others); and local clustering coefficient (measure of how complete the neighborhood of each individual is). For this analysis, all negative GAI values were treated as zeros, because we were primarily interested in the effect of direct social preferences (positive values), rather than avoidance (negative values).

Our measure of weighted betweenness favored shorter paths composed of weaker ties over longer paths with stronger ties (α tuning parameter= 0.5). We compared metrics between phenotypes by calculating the coefficient of the slope of linear models for different levels of each phenotype (Farine, 2017b). Empirical slope values were compared to equivalent random values produced via data stream permutations, that provided a null model, p-values obtained as in section 2.5.2.

3. Results

3.1. Individual identification and group structures

A total of 3411 encounters of 594 *M. alfredi* individuals were recorded over 512 sampling occasions. The highest number of sightings of a single individual was 57, with 112 individuals observed ≥ 10 times, including 70 females (43 mature, 13 immature, 14 unknown maturity) and 42 males (32 mature, 9 immature, 1 unknown maturity). A declining discovery curve (see Appendix Fig. 10) indicated that most of the total population was recorded at least once. Observed group sizes ranged from 1 to 67 individuals, with most smaller than 20 (mean 6.66 over all sites, 95% CI= 6.03-7.30), median 4 over all sites, 95% CI= 4-5). Feeding sites typically had larger group sizes, but large groups were also observed at cleaning stations (see Appendix Section 2, Fig. 11 for group size and sightings frequency data).

3.2. Site use and encounter rates

For individuals observed ≥ 10 times, especially females, encounters were much more likely at that individual's 1st preference site than any other (Fig. 2). Many individuals were observed multiple times at a single cleaning station, but infrequently or not at all at others (see Appendix Fig. 12) indicating strong site preferences. In general, female rays were more likely to be encountered at cleaning stations than males, while mature males were more likely to be encountered at feeding areas (see Appendix Section 3, Table 5). However, encounter rates at individual cleaning stations MS, MR and RSB varied considerably between sexes, with different results for each site (Fig. 3). Site MS had a strongly female-biased sex ratio (Exact binomial tests: N_{enc}= 1198, 77% female, 95% CIs 74.6%-80.1% female, p<0.001), site MR had no difference from parity (N_{enc}= 1052, (53% female, CI= 48.9%-56.8% female, p= 0.163), and site RSB (N_{enc}= 321, 40% female, CI 34.2%-46.3% female, p= 0.002) had a male-biased sex ratio.

3.3. Structure of associations

The population had moderate social differentiation (S = 0.574, SE= 0.067) and estimated AIs were a useful representation of the true AIs (r = 0.450, SE= 0.048). We had sufficient power to test the hypothesis that reef manta rays had no preferred or avoided relationships ($S^2 \times H$ = 5.59). Most pairs that had associated at least once were not strongly associated (70% of recorded associations had an SRI value of <=0.1, and only 3% had a value ≥ 0.2, median nonzero SRI value: 0.071). The highest SRI value between any pair of individuals was 0.357. Fig. 4 shows the network of associations between individuals in the context of their site preferences, which appear to be an important factor structuring associations. The network was highly connected (56.4% of possible connections realized), but connections among individuals with similar site preferences were more common and typically stronger. Manta rays with preference for site 'MS' appeared partly segregated from the rest of the population.

3.4. Stability of identifications and associations

LIRs fell steeply over the first few days, but remained stable thereafter for at least a year (see Appendix Section 4, Fig. 13, Table 6), and individuals were much more likely to be re-sighted at the same site than a different site over the full study period (1603 days). The re-identification rate at a different site to initial sighting was low, remaining constant throughout the study period. Identifications at the same location were best described using a model that indicated the occurrence of emigration (including permanent emigration from the study area) while re-identifications at a different location were best described by a model indicating a closed population (Appendix Table 6). LARs (Fig. 5) showed that time was an important influence on group structures. Among all individuals, the LAR declined slowly but gradually over several months. Re-associations between females occurred more frequently than those between males, with overall and female LAR remaining higher than equivalent null rates over several months, whereas male LAR approached the null rate after ~55 days. Models of exponential decay fit to the LAR data are shown in Table 7 (Appendix). The best fit model based on QAICc suggested that preferred relationships were important in structuring relationships between females (and among all individuals), while casual acquaintances were important in structuring relationships between males.

3.5. Tests for preferred associations and social preferences

Results of tests for association preferences (co-occurrence in time and space) and social preferences (active decisions to interact) are given in Table 1. Associations are measured by simple ratio indices (SRIs), whereas social preferences are measured by generalized affiliation indices (GAIs). The CV of SRIs was significantly higher (observed mean: 1.14, mean of random CVs: 1.10, p=0.001) than expected, indicating that reef manta rays had preferred associations. These preferences were not evenly distributed throughout the full network. Results were similar for associations between females (F:F network), mixed sex (F:M), and mixed maturity (A:J) associations indicating preferred associations within these networks. Associations between adult rays (A:A) and between juvenile rays (J:J) had CV values that were not significantly higher than expected. Associations between males (M:M), however, had a lower than expected CV, indicating that males did not have preferred associations with other males, and may tend to avoid each other.

Associations between individuals in our study may be highly influenced by non-social factors (see Fig. 4 main text, Table 8 Appendix). Our use of generalized affiliation indices (GAIs) controlled for this. GAIs gave similar results to SRIs in some cases, but not all. Generally, we found that social preferences were more common than preferred associations (see Fig. 14 Appendix). For all networks the mean of GAI values was negative, indicating that avoidance between pairs was common, particularly between males and between juveniles (the M:M and J:J GAI networks had the lowest means). The CV of all observed GAIs was significantly higher, and the mean of observed GAI values significantly lower than expected, indicating that social preferences occurred between all individuals, particularly over short (<15 day) time periods. All statistics for female:female GAIs (Network 2) were significant different to random expectation, indicating the presence of short and long-term social preferences between female rays. In contrast, for male:male GAIs, only short-term social preferences were significantly stronger than random expectations. There was also a lower percentage of preferred dyadic values between males (4.9%) than between females (8.1%). The highest percentage of preferred dyadic values was between individuals of different sex (12.6%) (Table 1C), though these appeared to be mainly short-term preferences. Social preferences were not common between adult rays (A:A network). The CV and mean for the J:J and A:J networks indicated that short term social preferences were stronger than expected between juveniles, and between juveniles and mature adults. The percentage of social preferences was similar for all three networks separated by maturity (7.3-9.0%).

3.6 Assortment by phenotype

Results for assortment by phenotype are reported in Table 2. Assortativity coefficients (ACs) for SRI values were significantly higher than expected when grouping individuals by sex and maturity, indicating that associations were positively assorted by these phenotypic attributes. There was no evidence for assortment of associations by color morph. For GAI values, the AC was significantly higher than expected (considering only positive GAI values), and significantly lower than expected (considering only negative GAI values) when grouping by sex. This indicated that same-sex pairs tended to have social preferences, and did not avoid each other. There was limited or no evidence for assortment of GAIs by maturity or color morph. Fig. 7 shows the network of social preferences by sex and maturity. While all individuals are highly connected, there is partial segregation between the sexes.

3.7. Community structuring

We found support for sub-division of the observed manta ray society into communities of individuals with stronger in-group relationships. The most parsimonious division of the association (SRI) network (Fig. 4) was into two communities with a Q_{max} value of 0.168 (95% CIs- 0.162:0.257). This indicates that the population had only a weak modular structure, but there was significantly more structure than expected if associations were random (mean of random Q_{max} values = 0.106, P= 0). Robustness of community assignment (R_{com}) for SRIs was 0.580, which is considered reliable evidence for the empirical structure (Shizuka & Farine, 2016) (see Fig. 6). Within community social differentiation was quite different for the two communities. Community 1 (S=0.393, observed CV= 0.926, correlation= 0.427) had a moderately differentiated social structure, while community 2 (S= 0.093, observed CV= 0.919, correlation= 0.100) had a strongly homogeneous social structure.

3.8. Variability in network positions

Results comparing network metrics of GAIs between phenotypes are presented in Table 3 and Fig. 8. They suggest some variation in social strategies between phenotypic groups and according to reproductive status. Juveniles had significantly higher weighted degree and weighted betweenness than mature adults, and were therefore more central in the overall network of GAIs. Females observed to be pregnant at least once during the study had significantly lower weighted betweenness, and significantly lower clustering coefficients than females with no observed pregnancies. Mature females may therefore be more segregated from the overall network than other individuals. No other metrics were significant, with similar values for degree, betweenness and clustering between individuals of different sex, color morph, and for mated and non-mated females.

4. Discussion

Reef manta rays in the Dampier Strait region of Raja Ampat, West Papua formed a complex and heterogeneously structured society, with non-random associations between individuals that divided the population into two distinct communities. Associations were the result of more than just similarities in habitat use, gregariousness, or overlaps in time, indicating that individuals actively chose to group with preferred social partners. As such, this is the first study to provide quantitative evidence for structured social relationships in manta rays. Such relationships may provide survival benefits across a range of contexts (Frère et al. 2010, Kalbitzer et al. 2017, Ellis et al. 2017). Familiarity and kin recognition over extended time periods (Griffiths & Ward 2011) have been shown to enhance the benefits of group living in fishes through antipredator effects (Chivers et al. 1995), increased foraging efficiency (Swaney et al. 2001) reduction in competition (Frostman & Sherman 2004), release of time budget constraints (Griffiths et al. 2004) and improved social learning (Lachlan et al. 1998). However, it is not yet clear to what extent sharks and rays recognize familiar individuals, including their capability for long-term social recognition (LTSR) of multiple partners and long-term memory of relationship histories.

Our results show that stable, differentiated social relationships lasting over several weeks or months are an important driver of group structures in reef manta rays, which suggests that both familiarity and LTSR are important in structuring their societies. In complex social systems, such capabilities can be essential to identify partners in reciprocal altruism, maintain social hierarchies and avoid inbreeding (Trivers 1971, Axelrod & Hamilton 1981, Bruck 2013). Simultaneous relationships with multiple partners may be required for social behaviors in manta rays, such as in initiation of mating trains and during collective feeding events. Social preferences were detected mostly between female rays, in mixed-sex relations, and between juveniles, with only weak evidence for short-term preferences between males. Time-based analyses suggested that associations between manta rays dissociated gradually over time, but often remained stable over weeks or months (particularly among females). Associations and social preferences were assorted by sex and maturity, and network metrics showed that social relationships were highly differentiated, and indicative of varied social strategies. The overall network of observed associations was weakly modular, with two main communities that had quite different structure, one having a mixed sex ratio with differentiated social relations, and the other having a highly biased female sex ratio, with homogeneous social structure. Female reef manta rays therefore appear to choose to associate mostly with other females (in more stable groups), or with males (in more dynamic groups). This decision may depend on factors such as age/maturity and reproductive status, as discussed further below. Reef manta rays did not form tight-knit social groups, such as those observed in many dolphin and larger toothed whale populations (Baird & Whitehead 2000, Cantor et al. 2015), although in several aspects our findings were comparable to social network studies on bottlenose dolphins (*Tursiops* sp.) including a recent study using GAIs (Zanardo et al. 2018). Bottlenose dolphins typically live in open and fluid hierarchical societies with fission-fusion dynamics, LTSR, and a high number of potential affiliates (Lusseau et al. 2003, Gero et al. 2005, Wiszniewski et al. 2012, Bruck et al. 2013). Social structure in these dolphins is flexible depending on environmental conditions (Lusseau et al. 2003, Karczmarski et al. 2005), enabling efficient flow of information required in foraging and predator avoidance (King & Janik, 2015). It is possible that social relationships in reef manta rays have similar structure and functions.

In addition to preferred social relationships, we found that passive aggregation and assortment of individuals with similar phenotypic attributes were important non-social factors influencing network structure. Many rays had strong philopatry to individual cleaning stations, resulting in marked differences in site sex ratios. This was surprising given the close proximity of all sites (Appendix Fig. 9c) and known wide-ranging movements of the species. Fidelity to areas of coastal reef has been described previously in *M. alfredi* in various locations (Marshall et al. 2011, Deakos et al. 2011, Jaine et al. 2014), including in Raja Ampat (Setyawan et al. 2018), but our study is novel in that it demonstrates that this can occur variably at multiple sites in close proximity (at a smaller scale than the daily movements of the species). This result suggests that broad processes such as food availability or habitat quality may not be as important as individually distinct environmental or social preferences in driving manta ray movements and habitat use at fine scales. Associations were closely correlated with individuals' site preferences. Site fidelity is often a prerequisite for sociality in gregarious animals, creating an environment for social relationships to develop (Wolf et al. 2007) and controlling the emergence of social preferences (Mourier et al. 2012). Time was also an important influence on social organization. Being present in the study at the same time was a strong predictor of association between pairs. Re-sightings were increasingly unlikely only a few days after initial sighting, but were much more likely to occur at a previously visited site over long time periods. Rather than having broad area residency (where isolation by distance might explain location fidelity), this suggests that individuals typically stayed in a certain location for hours or days, and made frequent movements in and out of the study area, returning to visit preferred sites (i.e. philopatry) over several years. It is likely that many individuals ranged widely throughout a larger area than we could cover in the scope of this study. LAR results suggested that casual acquaintances between rays were as important (or more) than preferred companionships to network structure. *M. alfredi* are known to travel up to 95km per day (Jaine et al. 2014, Duinkerken 2010) and move to deeper waters during the night (Braun et al. 2014). In Raja Ampat (Setyawan et al. 2018) and other locations (Marshall 2008, Dewar et al. 2008) visits to cleaning station sites occur mainly during daylight hours. Social structure in reef manta rays may therefore depend on daily fission-fusion dynamics. A limitation of our study is that associations between rays were only recorded at a few specific locations for short time periods during daylight hours. Preliminary observations via remotely-piloted-aircraft show that manta rays often follow each other when leaving cleaning stations or feeding areas (RP unpublished), and suggest that group structures formed in these areas are maintained outside them. Therefore, the network of associations that we recorded may underestimate true social relationships.

Sex, age and size based assortment are common in shark aggregations (Heupel & Simpfendorfer 2005, Wearmouth & Sims 2008, Guttridge et al. 2011), so it was not surprising to detect phenotypic structuring here. Sex ratios at manta ray aggregation sites are often female dominated (Marshall et al. 2011), though here we document a male-dominated site. Assortment may occur without any individual recognition capability, for example if individuals differ in behavior or motivation, they may spontaneously form closer associations to similar individuals, known as ‘self-sorting’ (Couzin 2006). Social preferences are, however, often important in creating assortative structures in dynamic systems (Croft et al. 2015), and assortative interactions suggestive of active partner preference are reported in a wild elasmobranch (Guttridge et al. 2011). Here we detected sex and maturity-based assortment of GAIs, suggesting that social preferences were a driver of assortative structuring. This could be linked to reef manta rays' reproductive strategy, which is not yet well described, but appears to be promiscuous (Stevens 2016). In several *M. alfredi* populations, most non-juvenile male and female manta rays display evidence of reproductive activity, males initiate courtship with multiple females at different times, while females may take part in mating chains with multiple males (Marshall & Bennett 2010, Deakos et al. 2012, Stevens et al. 2018, RP unpublished data). A single female manta ray has been observed to mate with two males in close succession (Yano et al. 1999). Sexual conflict in promiscuous systems is common (Parker et al. 2006) and social factors are known to be drivers of sexual segregation in elasmobranchs (Wearmouth et al. 2012). Fish are also known to avoid mating with familiar conspecifics in promiscuous systems (e.g. Simcox et al. 2005) and the use of familiarity is often varied between sexes (e.g. Griffiths & Magurran 1997, Croft et al. 2003). While both sexes may have equal ability to recognize familiar individuals, they may not have equal motivation- for example males may only behave differently towards familiar individuals in the context of mate choice (Griffiths & Ward 2006). Differences in motivation to be social in manta rays could explain why social preferences were rare between males, and why pregnant females were significantly less central and less connected to the overall population than non-pregnant females. Mature females often appeared to dominate cleaning stations, and were rarely observed performing cleaning behaviors with mature males. When females (including many pregnant individuals) were alone they were often pursued by males (RP, pers. obs.). Enabling social behavior may be a primary cause of manta ray visitations to cleaning stations, that act as 'social gathering points’ (Stevens 2016). Hierarchical social organization in these locations could allow mature females to group with preferred social partners and simultaneously avoid unwanted mating attempts by mature males. Familiarity has been shown to reduce aggression among sharks within recently established social hierarchies (Brena et al. 2018). Social gathering points could also facilitate exchange of information (e.g. regarding the distribution of ephemeral food patches) in species which appear to lack the ability to communicate over medium-long distances, for example breaching may be used as a social signal of food availability (Stevens 2016). Some elasmobranchs use body positioning and fin movements in gestural communication (Martin 2007, Sperone et al. 2012), and this may occur in reef manta rays (Stewart et al. 2016, RP unpublished). Research into the communicative capabilities of manta rays is warranted.

Our study provides the first evidence for structured social relationships in manta rays, and suggests that detailed information on their social organization (including structure, dynamics, and social preferences) will help to understand their natural behaviors and response to human and environmental impacts. Social preferences may lead to formation of distinct social units that are differentially at risk of disturbance (Jacoby et al. 2012). Social structures may be adapted to current selective environments, so rapid environmental changes may have severe consequences in disrupting demographically important social processes, influencing population genetic and demographic structure. Species that occur in small, isolated populations, with a low rate of reproduction, and a high reliance on social interactions are likely to be vulnerable to sudden population crashes due to changes in social structure (Snijders et al. 2017). We recommend long-term monitoring of manta rays in the Raja Ampat marine park to understand the effects of dive-tourism, including increases in boating and SCUBA diving activities, that may cause displacement from certain locations, and changes to social and reproductive behaviors. Knowledge on social interactions and fine-scale site fidelity in manta rays may be used to prioritize the protection of key sites and develop guidelines for sustainable ecotourism. It is important, however, to stress that fine-scale monitoring and protection within small MPAs is not likely to protect these highly mobile species from target fisheries, bycatch, environmental change or ocean pollution, which are the major global dangers that manta rays face (Marshall et al. 2018a, 2018b). In the light of these more nefarious threats, network-based studies that link movements and behavior to population ecology are required. These might: combine social information with animal tracking technology (Wilson et al. 2015, Jacoby et al. 2016) or information on genetic relatedness (Frère et al. 2010); use temporal networks to investigate social stability and assortativity in the context of a changing environment (Blonder et al. 2012); determine network resilience to removal of individuals (Williams & Lusseau 2006, Mourier et al. 2017); link habitat connectivity to social connectivity (Snijders et al. 2017); or model disease, information and gene flow using a network approach (Hamede et al. 2009). Such studies will improve our understanding of the ecology and evolution of mobulid rays and other elasmobranchs, and help to provide a more holistic approach to their conservation.

Compliance with ethical standards

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Ethical approval: All applicable international, national, and institutional guidelines for conducting research on animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the corresponding author is based.

Informed consent: Research did not involve human participants.

Data availability: The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. Photographs of each encounter are available in the MantaMatcher online repository www.mantamatcher.org

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Figure captions

Fig. 1 Identification of reef manta rays; 1a) female ‘normal’ morph with distinct ventral spot pattern; 1b) mating scars on female indicating maturity; 2a) male ‘normal’ morph, with claspers; 2b) juvenile male ‘normal’ morph, with undeveloped claspers; 3) melanistic morph with distinct white patches between gills; 4) pregnant female

Fig. 2 Encounter rates over all study sites by sex (F=females, M=males), ranked by site preference. Note the much higher average values at first preference sites than other sites, indicating strong site fidelity, particularly for females. There was considerable variability in the level of site fidelity between individuals, but not between sexes

Fig. 3 Encounter rates at each of the six study sites by sex (F=females, M=males). Note the difference between attendance of males and females at the three cleaning stations ('MS', 'MR' and 'RSB'), showing marked differences in site preferences. There were a greater number of zero values at the three feeding areas ('WSA', 'ESA' and 'LDS') due to lower sampling effort there

Fig. 4 Network of SRIs. Node colors indicate individual site preferences (green: 'MS', purple: 'MR', bottle green: 'RSB', red= 'ESA', orange='WSA', blue: 'LDS'). Node size scaled by the SD of encounter rates of an individual at each site, indicating level of overall site fidelity. Edge widths represent weight of SRIs (min= 0.118, max= 0.444). Individuals with 8 or more encounters included as nodes. Only the 30% highest SRI values were included as edges to show strongest associations. Forceatlas algorithm used to construct network

Fig. 5 Lagged association rates (LAR) compared to null association rate (NAR) between all individuals, between females and between males. Bars indicate approximate standard errors generated by jackknife resampling. Females dissociated gradually, and LAR did not approach the null rate, whereas males dissociated more rapidly, and LAR approached null rate more frequently. Figure drawn in SOCPROG

Fig. 6 Network of community assortativity assignments (based on SRIs) showing how often (represented by edge widths) empirical community assignment of each pair agreed with bootstrap replicate networks. Edges <0.25 removed. Node sizes indicate maturity status: large= adult, small= juvenile, medium= unknown). Community 1 (white nodes) contained an approximately equal no. females (24) and males (34), but Community 2 (black nodes) had a strong female bias (46 females, 8 males). ForceAtlas2 algorithm used to construct network

Fig. 7 Network of social preferences (N_{edges}= 480). Node colors indicate sex (red=female, blue=male). Node size indicates that individual's centrality (measured by weighted betweenness). Edge widths represent weights of GAI values. Edge colors represent relations between females (red), between males (blue), and mixed-sex relations (purple). While all individuals are highly connected, there is clear partitioning of the network by sex. ForceAtlas algorithm used to construct network

Fig. 8 Significant differences in network metrics by phenotype, including; (a: weighted degree for adult (A) and juveniles (J), b: weighted betweenness for adult (A) and juveniles (J), c: weighted betweenness for females observed pregnant (Y) and never observed pregnant (N), d: clustering coefficient for females seen(Y) pregnant and never seen (N) pregnant)

Tables

Table 1 Tests for preferred associations and social preferences. Statistics from empirical network compared to random networks. P-values significant at < 0.025 or >0.975 (two-tailed tests). Overall preferred relationships indicated by significantly high CV, short-term (within sampling period) preferred relationships indicated by significantly low mean, long-term (between sampling period) preferred relations indicated by significantly high SD. For P-values, level of significance indicated by: ***** ≤ 0.05, ****** ≤ 0.005 (two-tailed tests). The right-most column shows % of all pairwise GAI values that were defined as preferred relationships, and means of these values.

Table 1	A) Preferred associations (SRIs)	B) Social preferences (GAIs)			C) Dyadic preferences (GAIs)
Relations Measure	Overall CV	Overall CV	Short term Mean ($\times10^{-3}$)	Long term SD ($\times10^{-2}$)	(% total) Mean ($\times10^{-3}$)
	Observed value: mean of random values, P-value				
1) Whole (n=112:112)	1.14 : 1.10 ***P= 0.001*****	-5.15:-5.44 ***P=0*****	-2.77:-2.58 ***P= 1*****	1.42 : 1.41 *P= 0.049*	(10.2%) 9.63
Interpretation: Highly significant preferred associations and social preferences (short term)					
2) F:F (n=70:70)	1.07 : 1.04 ***P= 0.022****	-5.37:-5.58 *P=0.045*	-2.57:-2.41 ***P= 0.999*****	1.38 : 1.34 ***P= 0.019****	(8.1%) 11.32
Interpretation: Preferred associations and social preferences (only network with long-term social preferences)					
3) M:M (n=42:42)	1.13 : 1.15 *P= 0.794*	-5.05:-5.25 *P= 0.146*	-3.15:-2.94 ***P= 0.978****	1.56 : 1.54 *P= 0.151*	(4.9%) 23.00
Interpretation: Only short-term social preferences. No preferred associations					
4) F:M (n=70:42)	1.21 : 1.14 ***P= 0.002*****	-5.05:-5.44 ***P= 0.002*****	-2.77:-2.61 ***P= 0.999*****	1.40 : 1.41 *P= 0.817*	(12.6%) 8.75
Interpretation: Highly significant short-term preferred associations and social preferences, not long-term					
5) A:A (n=75:75)	1.05 : 1.02 *P= 0.052*	-5.94:-6.06 *P= 0.175*	-2.40:-2.31 *P= 0.932*	1.43 : 1.40 *P= 0.039*	(7.3%) 13.71
Interpretation: No significantly preferred associations or social preferences					
6) J:J (n=22:22)	1.26 : 1.18 *P= 0.096*	-4.00:-4.85 ***P= 0.014****	-3.04:-2.58 ***P= 0.996****	1.21 : 1.21 *P= 0.468*	(8.2%) 6.27
Interpretation: No preferred associations, short-term social preferences, not long term					
7) A: J (n=75:22)	1.17 : 1.08 ***P= 0.001*****	-5.02:-5.34 ***P= 0.019****	-2.69:-2.47 ***P= 0.999*****	1.35 : 1.33 *P= 0.156*	(9.0%) 10.42
Interpretation: Strong short-term preferred associations and social preferences, not long-term					

Table 2 Tests for assortment by sex, maturity and color morph for associations (SRIs), and positive and negative affiliations (GAIs). ACs from empirical network compared to random networks. ACs that are significantly larger than expected for SRIs and positive GAIs indicate assortment by phenotype. ACs that are significantly smaller than expected for negative GAIs indicate that similar individuals do not avoid each other. For P-values, level of significance indicated by: ***** ≤ 0.05, ****** ≤ 0.005 (two-tailed tests)

Table 2	SRIs	Positive GAI values	Negative GAI values
Phenotype: Sex AC- real: random mean (sd) P-Value	0.077 : 0.025 (0.012) ***P= 0.001*****	0.101 : 0.037 (0.019) ***P= 0.002*****	-0.046 : -0.017 (0.011) ***P= 0.995*****
Phenotype: Maturity AC- real: random mean (sd) P-value	0.030 : 0.007 (0.009) ***P= 0.005****	0.028 : 0.006 0.015) *P= 0.068*	-0.030 : -0.016 (0.008) ***P= 0.98*****
Phenotype: Colour morph AC- real: random mean (sd) P-value	-0.028 : -0.006 (0.010) *P=0.969*	-0.034 : -0.006 (0.018) *P= 0.944*	0.008 : 0.003 (0.011) *P= 0.301*

Table 3 Network metrics comparing individual positions in GAI network structure by phenotype, with mean, median and confidence intervals, testing for differences between phenotype by comparing the coefficient of the observed (obs) slope of linear models to random (rand) slope models. For P-values, level of significance indicated by: ***** ≤ 0.1, ****** ≤ 0.05 (two-tailed tests)

Table 3	Weighted degree			Weighted betweenness (alpha=0.5)			Clustering coefficient		
Phenotype	Mean (95% CIs)	Median (95% CIs)	Observed slope Random slope (SD) P value	Mean (95% CIs)	Median (95% CIs)	Observed slope Random slope (SD) P value	Mean (95% CIs)	Median (95% CIs)	Observed slope Random slope (SD) P value
Female (N=70)	-0.282 (-0.34: -0.23)	-0.313 (-0.37: -0.27)	-0.074 -0.070 (0.016) P= 0.606	43.3 (28.1-58.5)	22 (14-29)	-0.110 3.400 (4.073) P= 0.802	0.487 (0.480-0.495)	0.483 (0.475-0.491)	0.006 0.006 (0.004) P= 0.480
Male (N=42)	-0.356 (-0.41: -0.30)	-0.354 (-0.47: -0.29)		43.2 (29.7- 56.7)	34 (14-29)		0.494 (0.484-0.503)	0.489 (0.483-0.501)	
Adult (N=75)	-0.314 (-0.37: -0.26)	-0.350 (-0.40: -0.29)	**0.055** **0.012 (0.020)** **P= 0.020***	37.3 (26.6- 48.0)	22 (14-32)	**19.985** **10.388 (5.322)** **P= 0.029***	0.486 (0.479-0.493)	0.483 (0.475-0.489)	0.008 0.003 (0.004) P= 0.163
Juvenile (N=22)	-0.258 (-0.35: -0.17)	-0.273 (-0.37: -0.22)		57.3 (17.9- 96.7)	33.5 (7-50)		0.494 (0.477-0.511)	0.490 (0.471-0.511)	
Melanistic (N=55)	-0.322 (-0.38: -0.27)	-0.328 (-0.40: -0.28)	-0.024 -0.029 (0.016) P= 0.384	40.3 (28.6-52.0)	27 (16-39)	-5.868 -9.975 (3.623) P= 0.122	0.488 (0.481-0.496)	0.488 (0.478-0.499)	-0.003 -0.002 (0.003) P= 0.643
Normal (N=57)	-0.298 (-0.36: -0.24)	-0.334 (-0.39: -0.26)		46.1 (28.2- 64.0)	24 (13-35)		0.491 (0.482-0.501)	0.483 (0.477-0.491)	
Pregnant (N=36)	-0.248 (-0.33: -0.16)	-0.310 (-0.38: -0.18)	-0.069 -0.056 (0.021) P= 0.724	48.0 (20.1- 75.8)	14.5 (9-32)	**-9.619** **1.176 (4.463)** **P= 0.992****	0.480 (0.470-0.490)	0.475 (0.465-0.484)	0.016 0.004 (0.004) **P= 0.005****
Not pregnant (N=34)	-0.317 (-0.38: -0.25)	-0.333 (-0.44: -0.26)		38.4 (26.1- 50.6)	25.5 (16-43)		0.495 (0.483-0.508)	0.493 (0.482-0.503)	
Mated (F) (N=39)	-0.267 (-0.35: -0.19)	-0.331 (-0.41: -0.23)	-0.034 -0.048 (0.020) P= 0.243	39.5 (15.4- 63.7)	14 (9-27)	8.552 7.661 (4.582) P= 0.428	0.483 (0.472-0.493)	0.480 (0.470-0.490)	0.011 0.004 (0.004) P= 0.063
Unmated (F) (N=31)	-0.301 (-0.37: -0.23)	-0.303 (-0.36: -0.25)		48.1 (30.7-65.4)	29 (18-50)		0.493 (0.481-0.506)	0.488 (0.474-0.499)	

Supplementary Material (marked version)

Figure 1

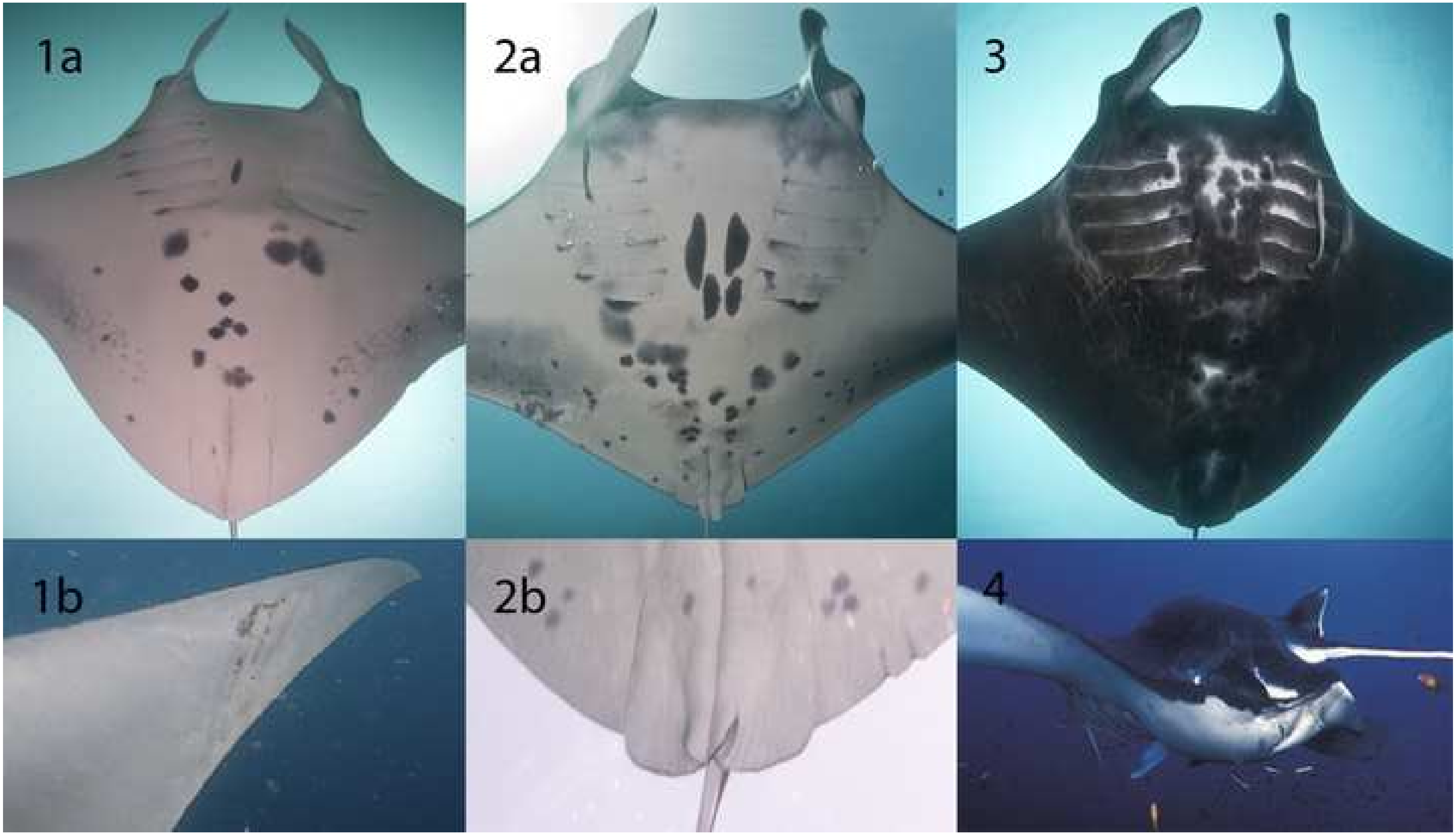


Figure 2

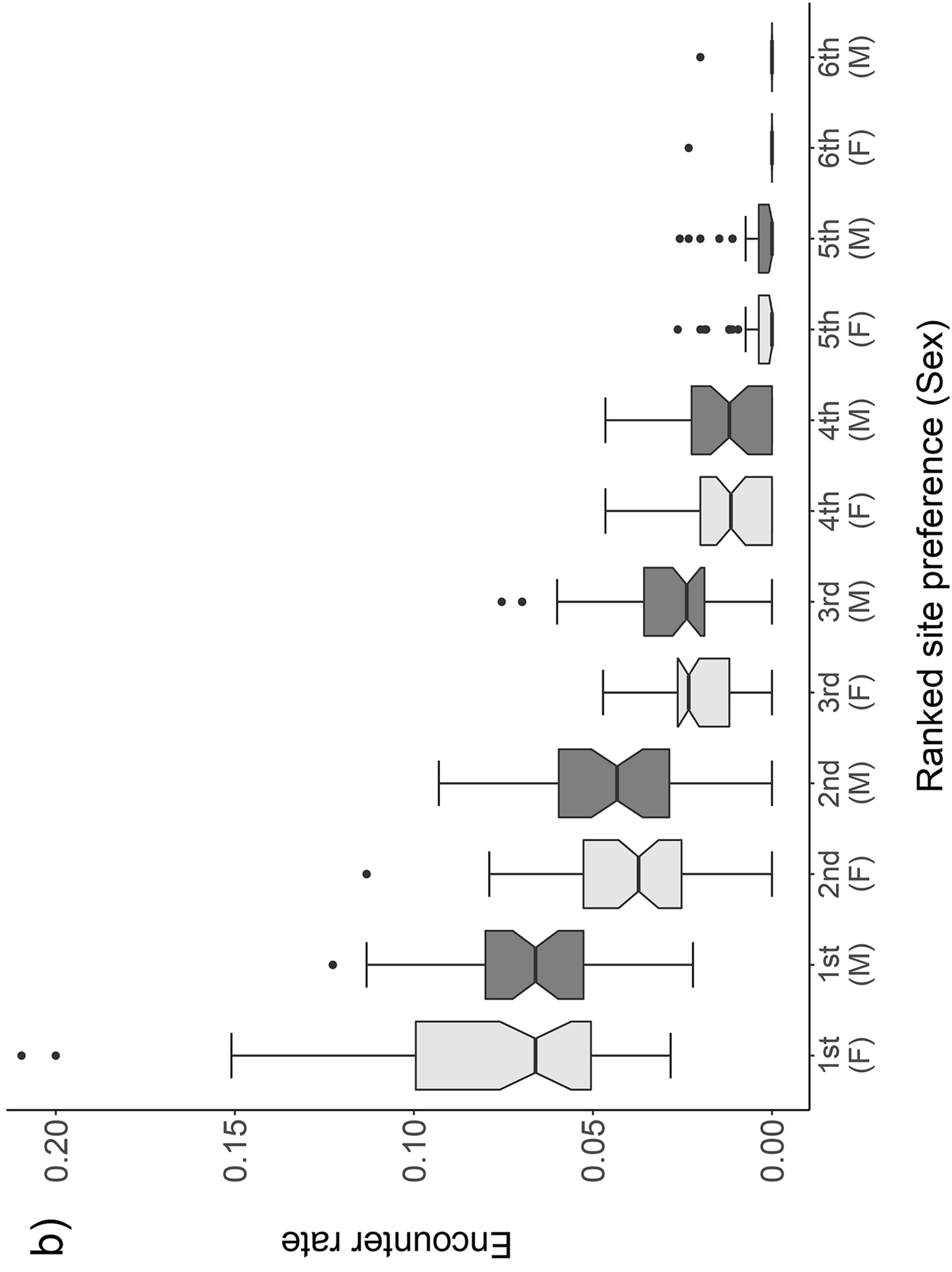
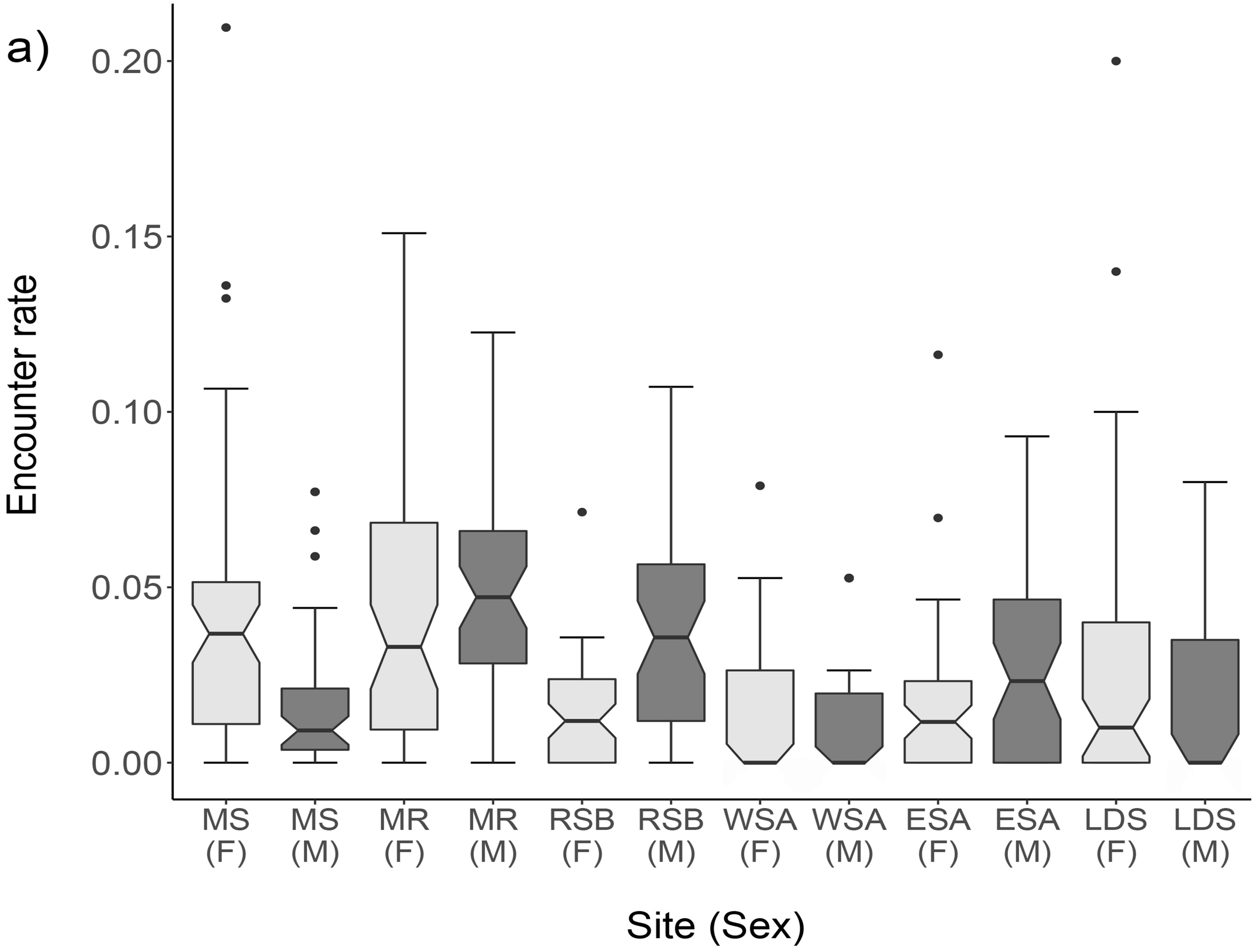

b)
Encounter rate
0.00
0.05
0.10
0.15
0.20
1st (F)
1st (M)
2nd (F)
2nd (M)
3rd (F)
3rd (M)
4th (F)
4th (M)
5th (F)
5th (M)
6th (F)
6th (M)
Ranked site preference (Sex)

Figure 3


a)
Encounter rate
0.20
0.15
0.10
0.05
0.00
MS (F)
MS (M)
MR (F)
MR (M)
RSB (F)
RSB (M)
WSA (F)
WSA (M)
ESA (F)
ESA (M)
LDS (F)
LDS (M)
Site (Sex)

Revised Fig 4.

Figure 5

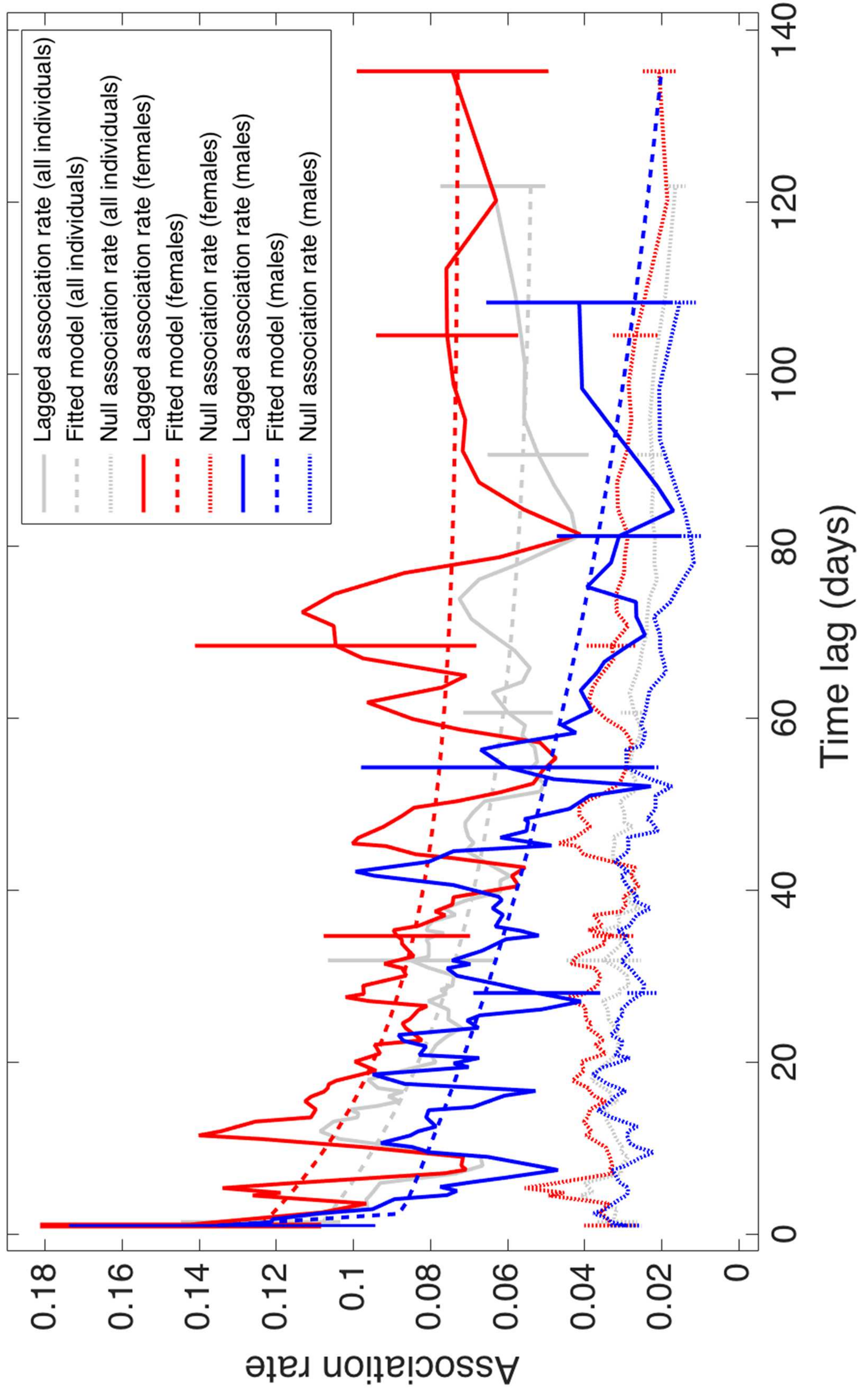
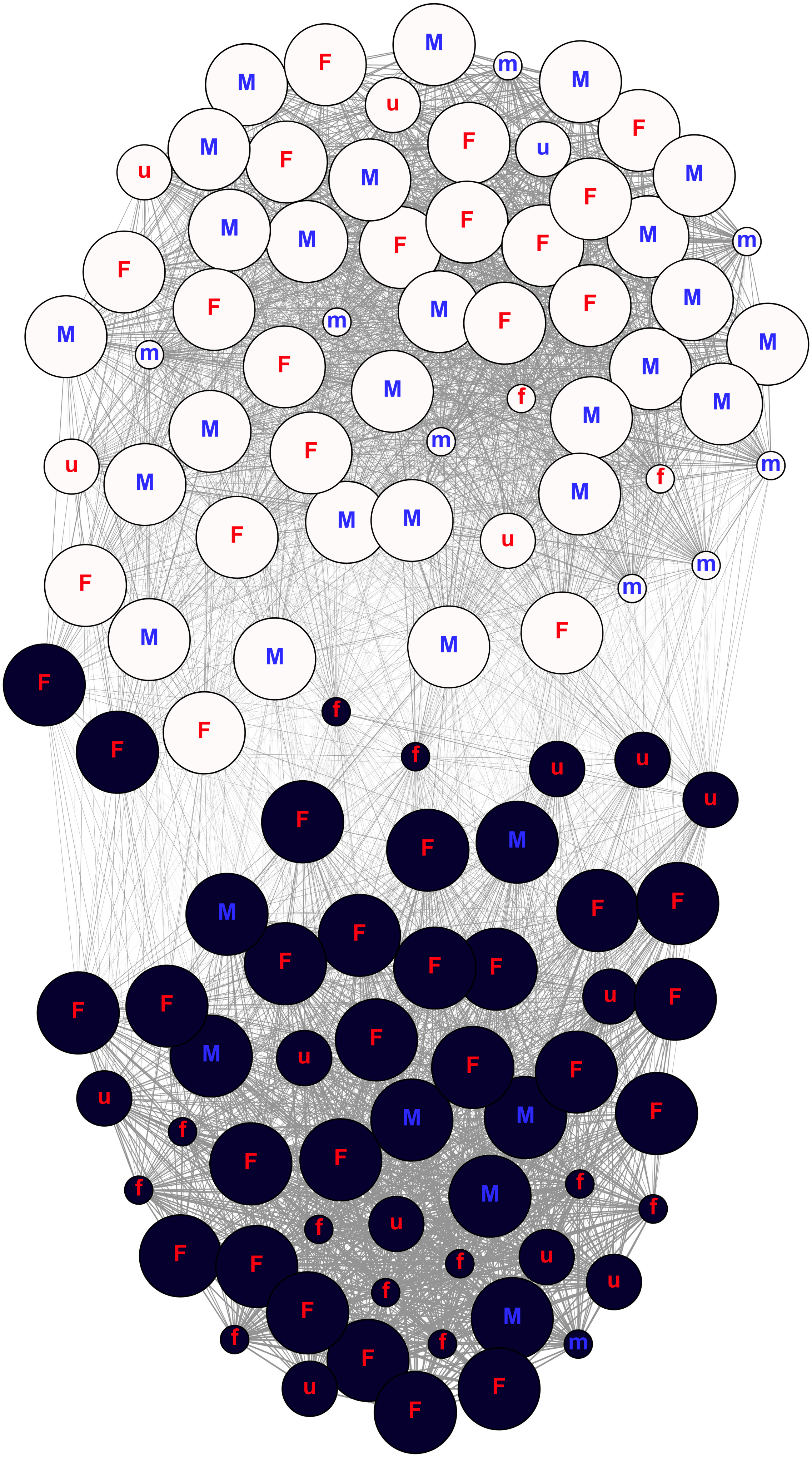

Lagged association rate (all individuals)
Fitted model (all individuals)
Null association rate (all individuals)
Lagged association rate (females)
Fitted model (females)
Null association rate (females)
Lagged association rate (males)
Fitted model (males)
Null association rate (males)
Association rate
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Time lag (days)
0
20
40
60
80
100
120
140

Figure 6


M
F
m
M
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M
F
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Figure 7

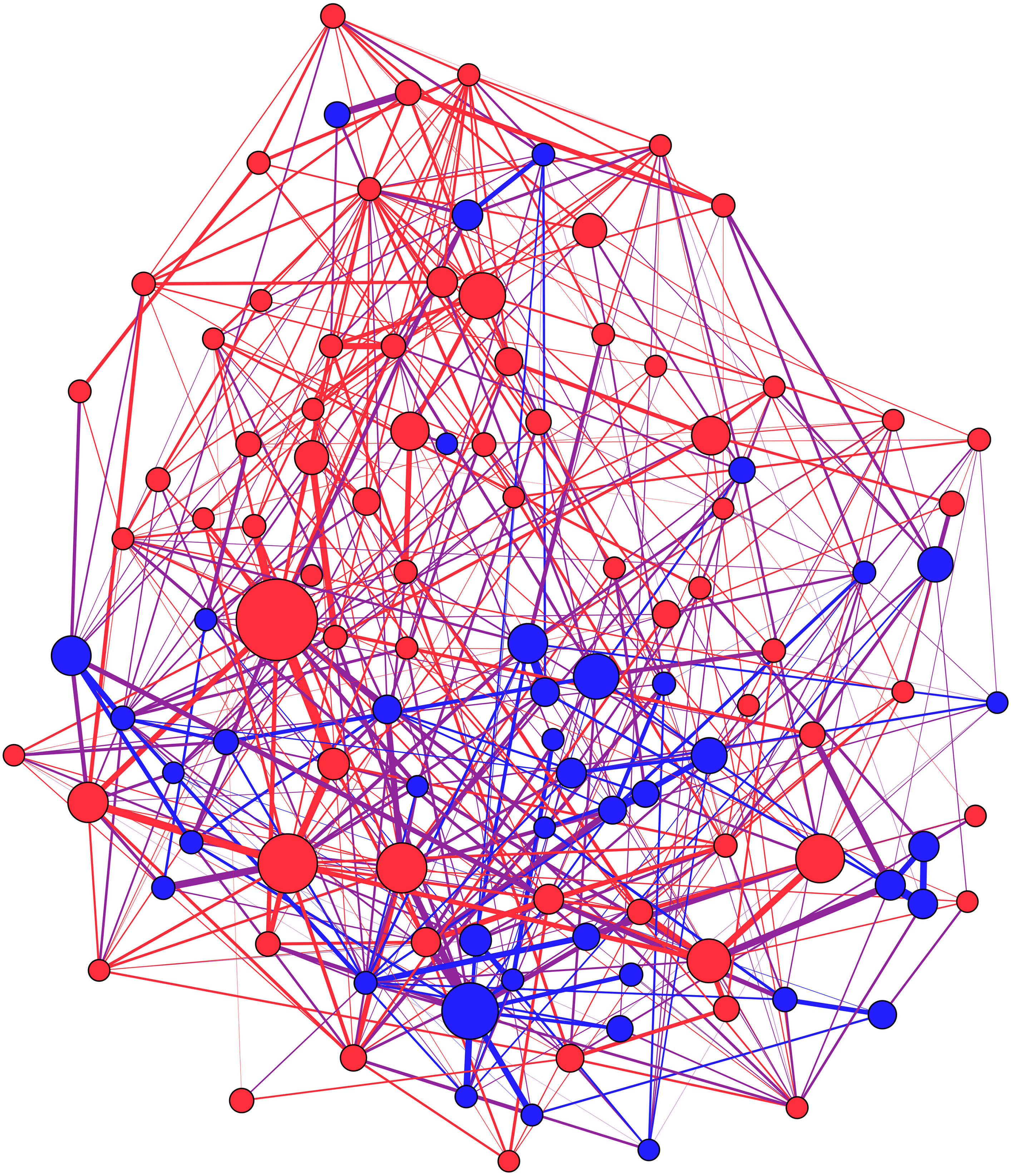
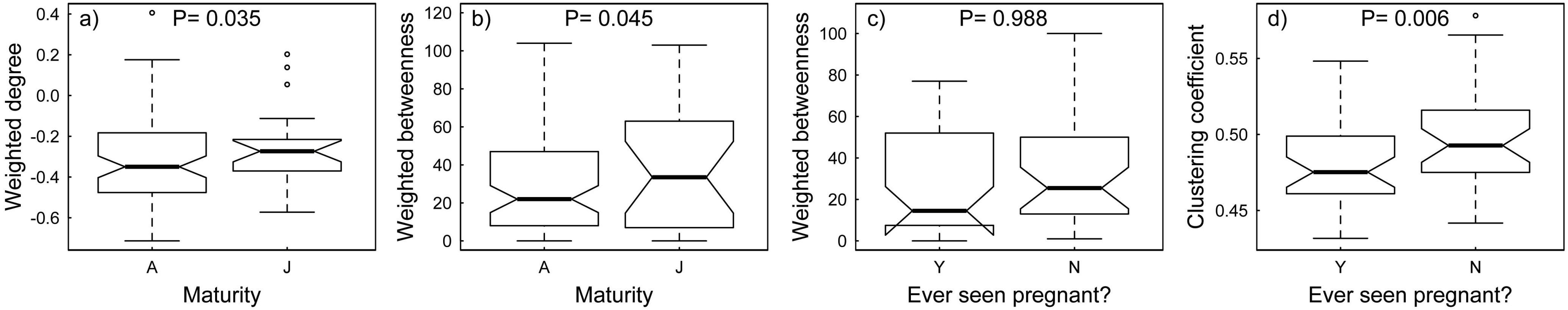
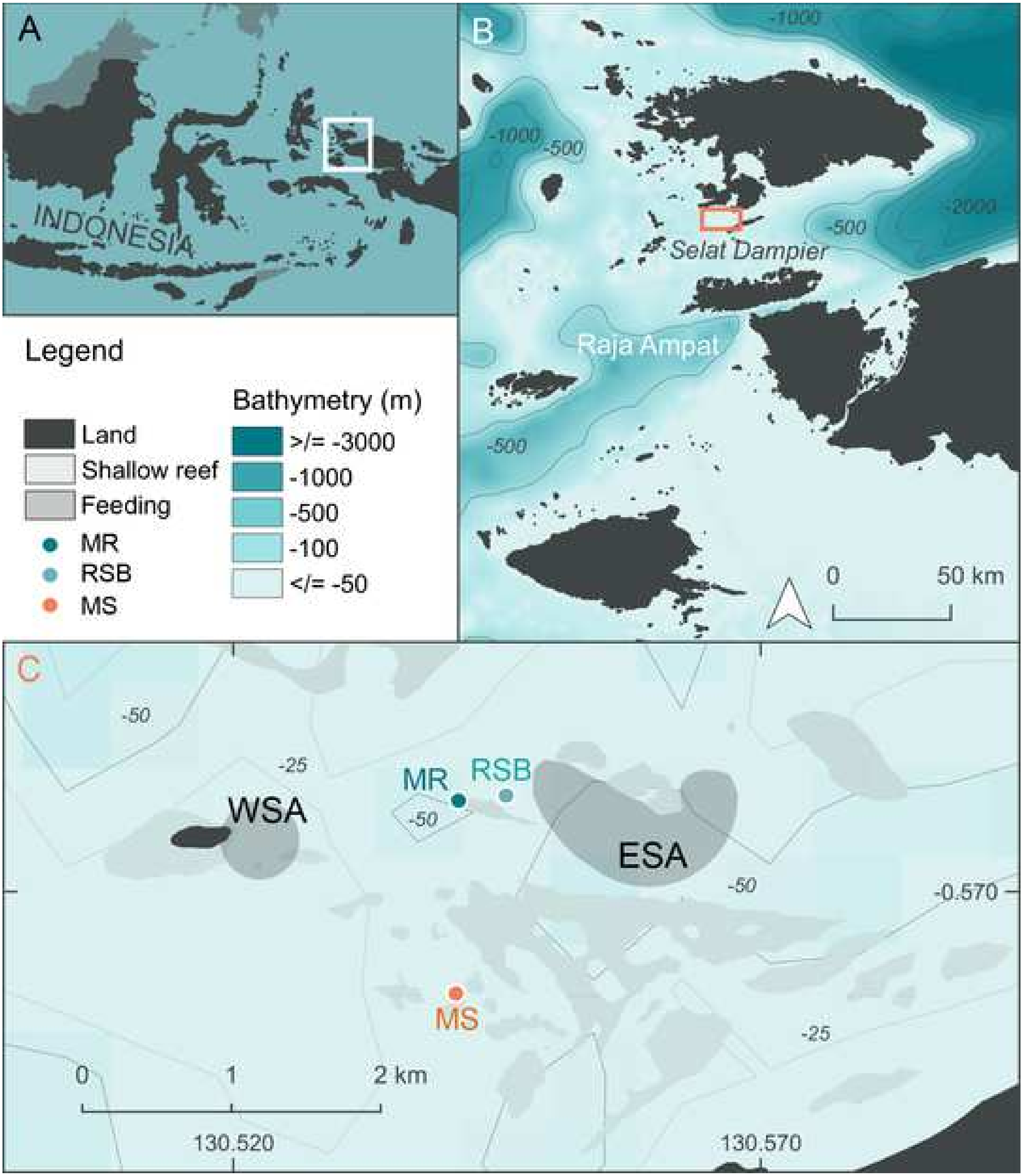


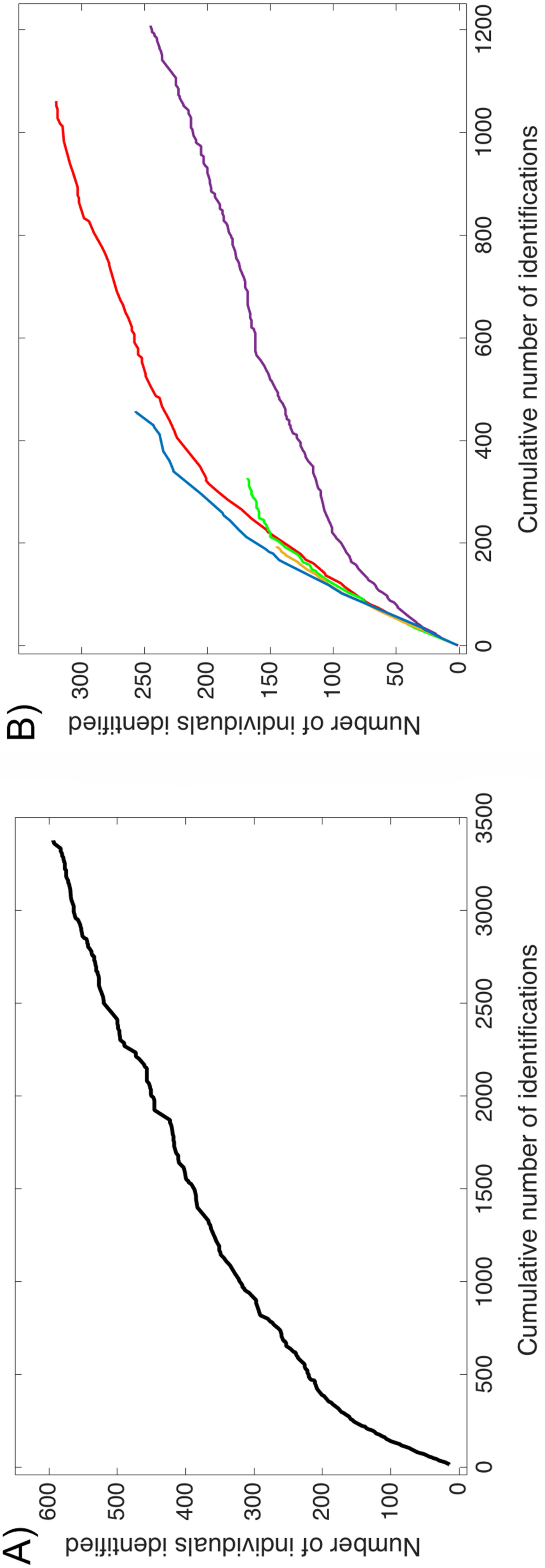
Figure 8


a)
P= 0.035
Weighted degree
0.4
0.2
0.0
-0.2
-0.4
-0.6
A
J
Maturity
b)
P= 0.045
Weighted betweenness
120
100
80
60
40
20
0
A
J
Maturity
c)
P= 0.988
Weighted betweenness
100
80
60
40
20
0
Y
N
Ever seen pregnant?
d)
P= 0.006
Clustering coefficient
0.55
0.50
0.45
Y
N
Ever seen pregnant?

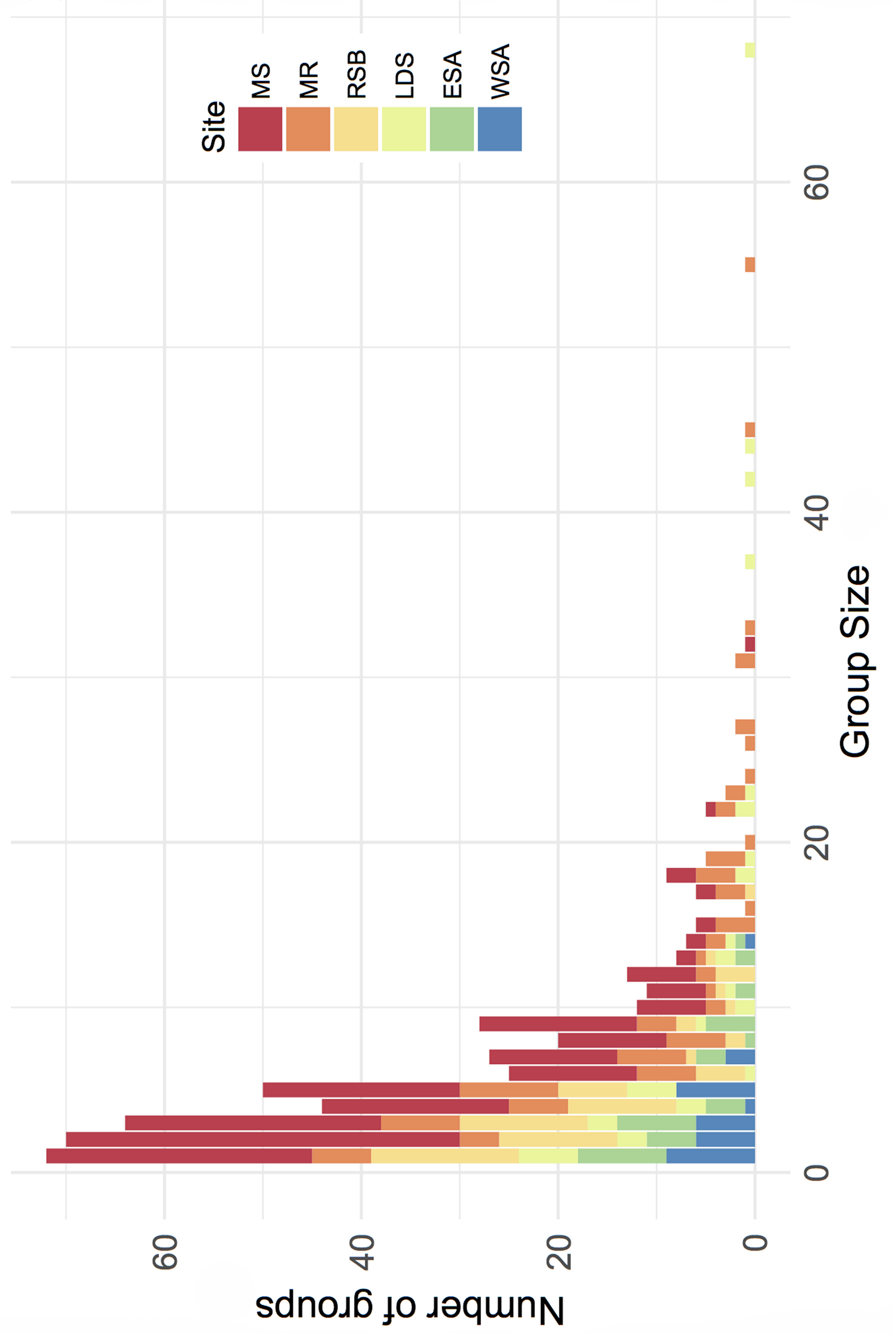
Revised Supplementary Figure 9



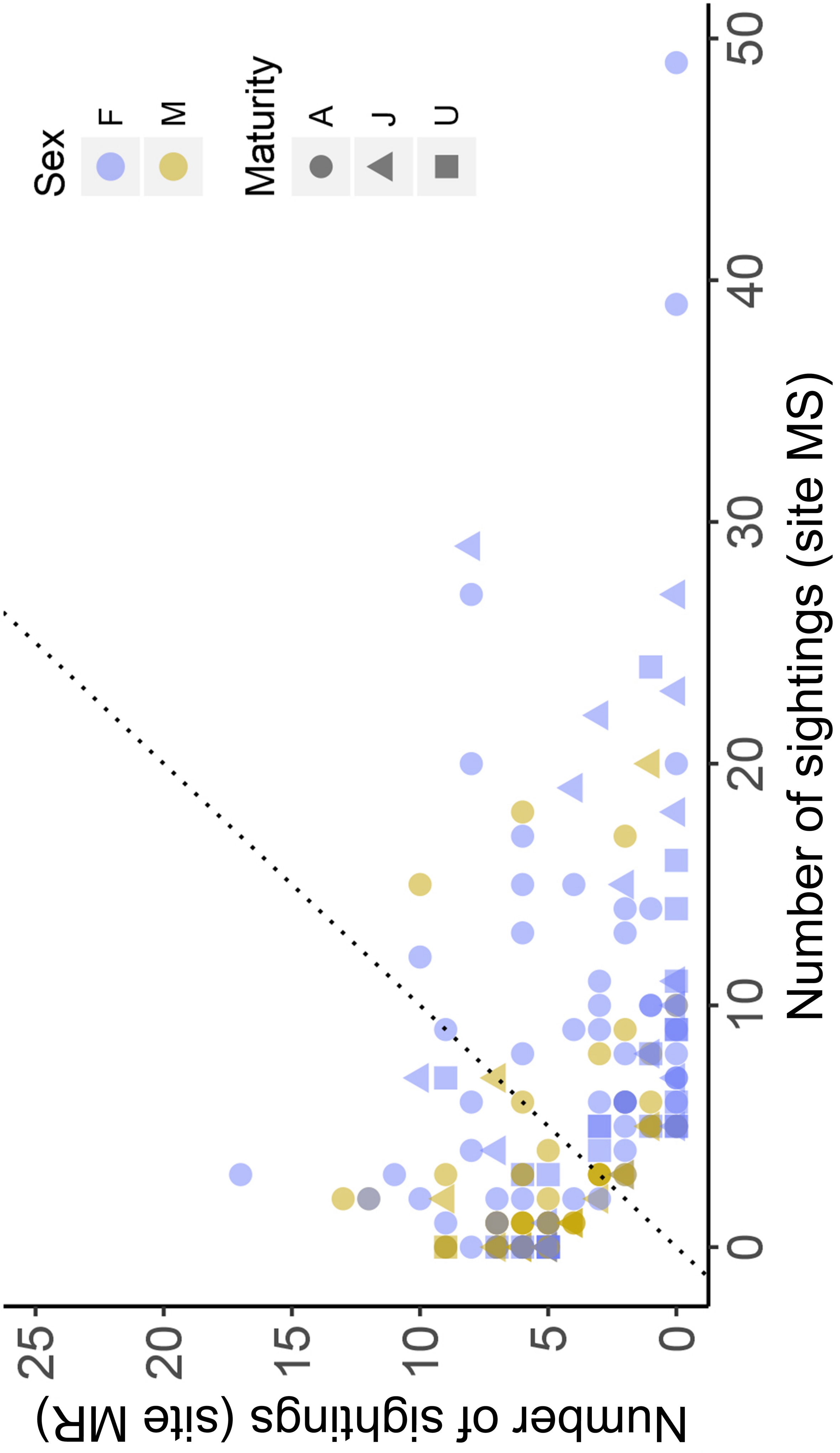
Supplementary Figure 10



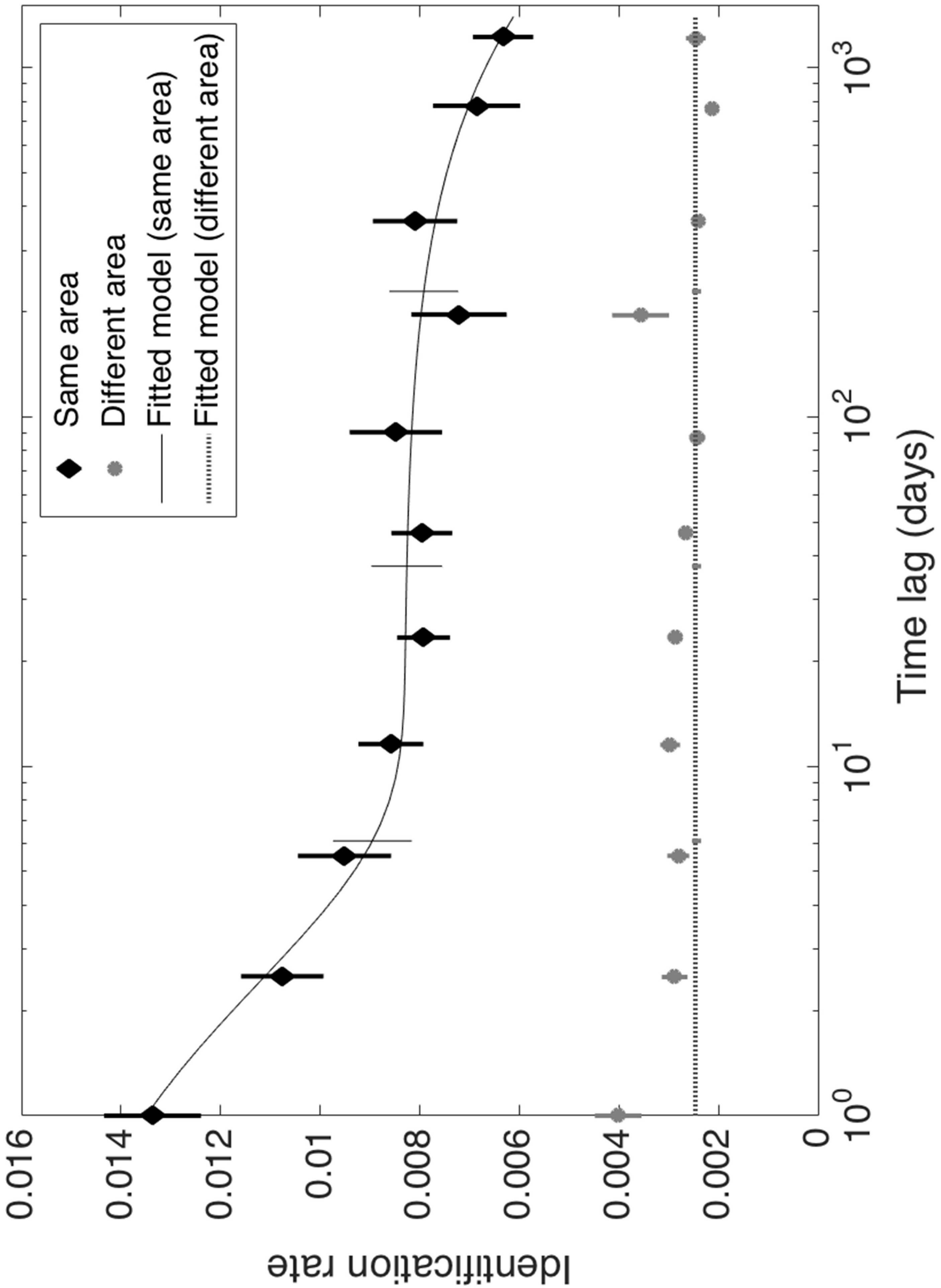
Supplementary Figure 11



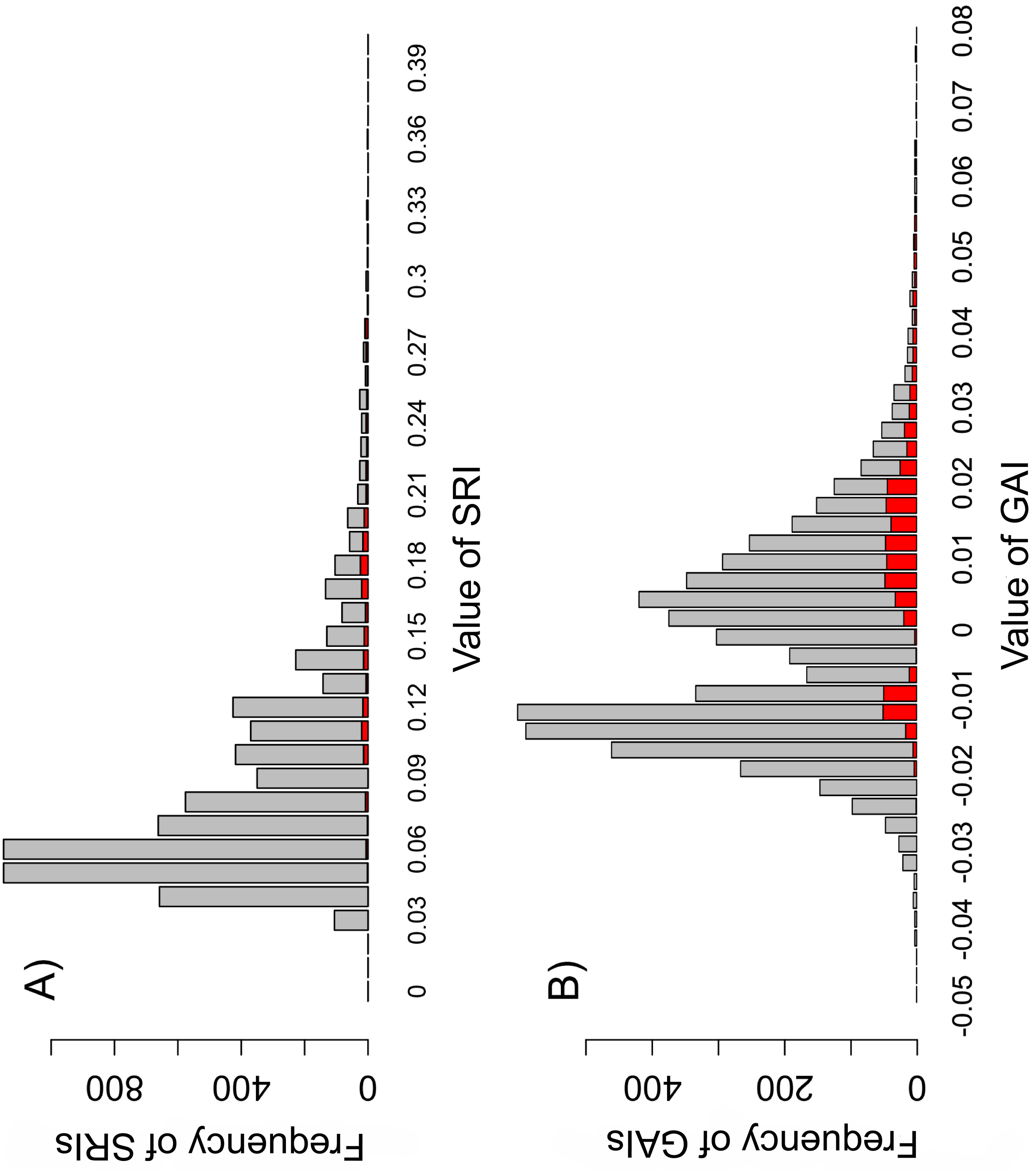
Supplementary Figure 12



Supplementary Figure 13



Supplementary Figure 14



(Perryman comments on each review point in bold)

Reviewer #1: General comments:

This study utilizes an extensive photo ID data set to quantify the social structure of Indonesian manta ray populations over a period of five years. Given the wealth of such data for manta rays at various locations across the world, it is nice to finally see social network analyses employed to explore the drivers of frequently-speculated, but never explicitly tested, social behaviours in mantas. I congratulate the authors on a very nice study, that is well written and thorough in it's analysis. I particularly like the structured approach to disentangling the spatial and social drivers of aggregation (i.e. cleaning stations and phenotypic assortativity are clearly important factors in the network structure), including individual preference for gregariousness and true social preferences established using the GAI methodology. The result is a balanced and seemly robust description of temporally stable, preferred social relationships and structured societies that reflect the
relative (social and physical) complexity of the environment these mantas inhabit. I'm sure this will be a well cited study.

I don't have a huge amount of comments, and this reflects the quality of the paper, not brevity on my part. I hope the minor comments below are useful.

David Jacoby

Abstract

L28: I think it's important to also include the location with this information here as well.
Added location (L28-29, markup version)

Introduction

The introduction is informative and well written.

L90-92: While I agree with this, the study does not really address any of these things and therefore it makes this sentence seem a little obsolete.
I have changed this sentence to fit better with the actual research performed (L90-92, markup version)

Methods

L116: Change 'with a maximum of one dive...' to 'restricted to one dive...'
Changed this (L125 in markup version)

L130-132: Presumably, the model included area type (cleaning or feeding). I see that this was tested (from the results) so this detail should be included here.

I have added analysis of cleaning stations vs. feeding sites to Appendix Table 5. Have also changed L139-142 and L272-273 (markup version) and supplementary info lines 60-63 to incorporate this

Results

L246: Although there is likely to be some influence of landmass on likelihood/frequency of movements between sites (looking at the map at least)?

I have changed L271-274 (markup version) to emphasise the closeness of sites and known wide movements of manta rays. Also changed one sentence in Discussion (L401- markup version) to clarify that the distance between sites is less than manta rays are known to move in a day.

L248: Was encounter rate between site types explicitly tested? Perhaps I've missed something but it is not clear whether this was tested but would be interesting to know whether mantas showed fidelity to cleaning stations or feeding locations (or neither).
Yes, this is dealt with above (see response to L130-132 comment)

L315-317: Can you really be confident here of determining which individuals were pregnant during the course of the study? I understand that some individuals were observed to be pregnant during the diver surveys but for others that were sighted once or relatively infrequently (i.e. resightings were further apart than the typical gestation period for this species), these are unknown so can the claim that pregnant females socially segregate truly be tested given the time aggregated nature of the network analysis? I'd be interested to get the authors opinions on this.

We can be confident of this in most cases. All individuals in the network analysis were sighted at least 10 times, and most were sighted at least once per 4-6 month research season. The gestation period in manta rays is around 13 months, with pregnancy visibly obvious after a few months. For most individuals, their sighting histories were such that we can be sure that if they were never observed as pregnant, then they never became pregnant

during the study. I have changed Methods 243-245 (markup version) to clarify how we defined observed as pregnant/never observed as pregnant.

Discussion

L339: It would be interesting to know whether female social stability, reportedly stable over a period of weeks to months, occurs more or less stable at different times of year. Future studies looking at assortativity of temporal networks would certainly be an interesting line of questioning in the context of a changing environment.

I have added a sentence about this to the discussion (L476-477, markup version), and reference (Blonder et al. 2012)

Reviewer #3:

Manta rays are known to be gregarious and form frequent and sometimes large aggregations at specific locations, and for specific purpose (e.g. feeding, cleaning or mating), but no study has yet investigated if these gathering patterns result from passive or passive social choices. This study represents the first to explore the hypothesis that manta rays can form preferred social associations and some form of social structure using a robust dataset. I really enjoyed reading this paper and discovering the results that emerged from this study. The paper is well written, and the analytical approaches are strong and robust.

However, in some sections the manuscript lacks a few details. I do not have major concerns, but I provided some specific constructive and positive comments (listed below) that hopefully will help in improving the quality of the manuscript.

Specific comments:

Line 71: not sure that it is the good citation. Did not you mean this one:
Guttridge, T. L., Gruber, S. H., DiBattista, J. D., Feldheim, K. A., Croft, D. P., Krause, S., & Krause, J. (2011). Assortative interactions and leadership in a free-ranging population of juvenile lemon shark Negaprion brevirostris. Marine Ecology Progress Series, 423, 235-245.

Correct, I have changed this (L71, markup version)

Line 76: I am not aware of evidence for cooperative foraging in manta rays? Do you rather mean collective foraging?

Yes, I have changed to 'collective' Having looked into this thoroughly there is no study in primary literature that claims mantas cooperate (i.e. work together for mutual benefit).

Although 'piggyback' and 'cyclone' feeding (see Stevens et al. 'Guide to Manta and devil rays of the world', Stevens Doctoral thesis 2016) certainly appear likely to be cooperative behaviours (apparently cyclone feeding only occurs in anti-clockwise direction which might suggest it is a learned social behaviour where individuals intend to work together, rather than individuals merely taking advantage of disturbance to plankton caused by others' movements.

Line 106: which ones? e.g. sex, size, ..etc
Added these (L114-115, markup version) and changed L111

Line 110: insert "from" after "where collected"?
Done (L120, markup version)

Line 129: which phenotypes? could you add a list?
Done (L139-140, markup version)

Line 137-138: it is not clear: do you define group as all individuals observed within a 10 min period? What is the spatial rule of defining groups (i.e. what is the inter-individual distance to be considered as a group? or what is the area of sampling observed groups - i.e. radius?
I have clarified this in the text (L150-151, markup version)

Line 144: insert "the" after "The SRI is"
Done (L158, markup version)

Line 184: briefly explain how Godde et al. 2013 define gregariousness, within the parenthesis for example
Done (L201-202, markup version)

Line 206-207: it is not clear to me why you did this as you then test for assortment using data-stream permutations? Why using both node-based and data-stream permutations to test for significant assortment?
Yes this is a good point, as I have used data-stream permutations I have now removed the node-based method (L225, markup version) and results of this (Appendix section 9)

Line 226: these phenotypes may have changed during the study period... how did you take this into account?
I have clarified the division of rays by reproductive status (L244-245, markup version) as this was not clear. Unfortunately in the scope of this type of study it was not possible to take into account the dynamics of reproductive status on network dynamics. Nevertheless- we noticed that pregnant individuals in particular regularly grouped together, so I wanted to

test for an effect of reproductive status on network structure. The only way to do this was to divide the female population into those that we had observed to be pregnant at some point, and those that we had never observed as pregnant. As stated above, I believe the high resighting rate we achieved compared to long female gestation period gives us good reason to believe that we did not 'miss' many pregnancies, though this may have occurred for a few individuals. It is not the ideal method but was the only way I could think to test this

Discussion: Explaining the presence and structure of communities is lacking in the discussion. I suggest adding a short paragraph or few sentences on discussing what these communities and membership can mean in the context of associations in this population.

I have expanded on this in L375-379 (markup version), and slightly changed L356 (markup version)

Line 325-328: you can add foraging efficiency?

Done (L361, markup version), and added Swaney et al. (2001) to reference list

Line 334: again, can we really call this cooperative? I think evidence is lacking so collective feeding might be more adapted here.

Changed to 'collective feeding' (L371, markup version)

Line 366: I think you can also add that the limit of your study is that it monitors only associations occurring at a sample of locations within the species space use and only during the day, so the network you found and strength/duration of associations may be underestimated, as some manta bonding may be maintained at night and/or when manta rays leave the monitored locations...

Thanks, yes I have added a couple of sentences about this (L418-421, markup version).

Line 392-393: clear hierarchy have been also found in sharks in specific contexts with clear recognition mechanisms of individuals and their behaviour without necessarily based on phenotypic traits (see Brena et al 2018 for an example)

Brena, P. F., Mourier, J., Planes, S., & Clua, E. E. (2018). Concede or clash? Solitary sharks competing for food assess rivals to decide. Proceedings of the Royal Society B: Biological Sciences, 285(1875), 20180006.

Thanks, I have added a sentence on this (L444-445, markup version) to the discussion and included the suggested reference

Line 395: again is cooperative is the right term (unless I am not unaware of a reference showing evidence for cooperation in manta)? I suggest you to look back at the definition of cooperative.

Removed this sentence (L460, markup version) and changed L447-460 to fit better.

Line 414-415: I am a bit surprised about this last sentence which is not really relevant with the main findings of the study. Is finishing the paper with changing the public mind about manta to improve conservation (even if this will certainly contribute to) really representative of your findings.

Ok I have removed this sentence (from L481, markup version)

Figure 4: maybe increase the scaling of edge weights to better show the differences between associations in the network.

Done

Table 2 and Table 3: maybe add the confidence intervals or SD of random values

Done

Thankyou very much to both reviewers for your constructive and useful feedback

Response to Editor comments
Rob Perryman 30/05/19

Dear Ian,

Thanks very much for your comments on this article. Please see below for my responses:

Line 33-35: Abstract: “Our results suggest…” The importance of dive tourism is not anticipated earlier in the abstract. Consider combining the last two sentences of the abstract into a more general statement on the implications of the study for conservation.

Ok I have changed this- dive tourism is now given as an example of an anthropogenic pressure

Lines 53-55, “Social interactions directly affect…”. Because this sentence refers to social interactions in general, and no emergence of social structure per se, move this to the end of Line 49 (after “social learning (Brown, Laland & Krause 2011).”

Done

Line 51, remove comma after “decisions”

Done

Line 58: You should make the connection between social network analysis and social structure clear here.
Ok I have added a short sentence and Croft et al. (2008) reference

Line 79: “Individual manta rays can be easily observed…” This sentence is clearly relevant to the paragraph but seems out of place here. Consider moving it to line 73, immediately after “including social preferences.”
Moved and changed this paragraph a bit to fit better

Line 78: Reference to self-awareness – it isn’t clear how this is relevant to the argument that mobulid rays are excellent candidates for studies on elasmobranch sociality.
Ok I've removed this part of the sentence and the reference for it

Line 80: Starting at “Globally, both species…”. This should be a new paragraph.
Done

Line 103: Explain what “genuine” social preferences are.
See added brackets for clarification

Line 116: Reviewer #3 requested additional information on the spatial aspects of sampling. However, I found the revised version still to be a little unclear. Was a single location within the 15 km^2 area chosen for a dive? What was the total area

observed over a single 1 hr dive (or is this the 15 km^2)? Did this differ among sites?
Changed this paragraph to clarify these questions

Line 229: Please explain how you determined whether females were observed as “sexually active”? Is this based on observations of mating or other evidence such as mating scars?
I've changed line 125 in the methods to clarify this

Paragraph starting line 241: The numbering of supplementary figures 10 and 11 is consistent with the figure captions in the appendix, but not with the figures themselves.
Ok I've changed the numbering in the online system which should then update when the new manuscript is created

Line 250: Remove (or move to discussion): “This was surprising…”, as this is interpretation rather than results.
Ok I've moved this to discussion (L361-364), and changed the text there slightly

Line 288: I think it would be helpful to briefly remind the reader of the difference between social preferences and preferred associations here.
I've changed lines 281 and 282 to make this clearer.

Line 322: Please revise “Pregnant females may…” to reflect the actual reproductive statuses used (i.e., that these are females that have been observed to be pregnant, but (as I understand it) are not necessarily pregnant at a given observation).
Changed this to 'mature'

Line 332: There is a stray hyphen after “fishes” on the unmarked version
Removed

Line 378: add comma after “Therefore”
Done

****In addition, I've updated Figure 9 (map of study location and sites) using ARC GIS. I think this image is much better now. Hope that's ok**