



Small effects of family size on sociality despite strong kin preferences in female bottlenose dolphins

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The quantity and quality of individual social relationships is a fundamental feature of social structure for group-living species. In many species, individuals preferentially associate with close relatives, which can amplify social benefits through inclusive fitness. Reproductive variation, dispersal and other factors may nevertheless impact relative kin availability, especially for species with slow life histories. As such, variation in family size can affect the social integration of the individual. Here, we investigated the effects of family size on female sociality in a population of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in Shark Bay, Australia. This population exhibits high fission–fusion dynamics, with females varying widely in gregariousness and both sexes remaining philopatric, providing females with both matrilineal and nonmatrilineal kin as potential associates. We used genetic relatedness data obtained from a large single nucleotide polymorphism (SNP) panel and a spatially explicit null model to measure females' propensities to form affiliations with both related and unrelated individuals. We found that females had strong social preferences for matrilineal close (first, second and third degree) kin, but also significant preferences for nonmatrilineal close and more distant kin compared to unrelated individuals. Despite these preferences, we found only small effects of kin availability on individual social position. Stronger and more consistent effects were attributable to individual foraging ecology, although much of the variation remains unexplained. Overall, our models suggest that while female dolphins have strong kin preferences, their social connectivity is not determined by family size; rather, individual foraging strategies and high fission–fusion dynamics enable a diverse repertoire of social strategies to coexist within a population.

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Social species are expected to favour kin associations as a mechanism to maximize their inclusive fitness benefits through group living (Hamilton, 1964; Smith, 2014). However, even in the presence of kin, members of some species form social relationships with nonkin that positively affect individual fitness (e.g. humans, *Homo sapiens*: House et al., 1988; feral horses, *Equus caballus*: Cameron et al., 2009; Indo-Pacific bottlenose dolphins, *Tursiops aduncus*: Frère, Krützen, Mann, Connor, et al., 2010; greater anis, *Crotophaga major*: Riehl & Strong, 2018). In cases where at least one

sex does not disperse, individuals may simultaneously maintain strong associations with both close relatives and unrelated individuals through fission–fusion (e.g. bats: Metheny et al., 2008; dolphins: Frère, Krützen, Mann, Watson-Capps et al., 2010; Möller et al., 2006).

Even though individuals may prefer associating with kin, they can experience different levels of kin availability or family size. Social bonds with unrelated individuals might serve as a compensatory mechanism to fulfil the need for social support of individuals without kin (Carter et al., 2017; Chakrabarti et al., 2020; Silk, Alberts et al., 2006), or may simply be formed because individuals follow familiarity rules and form bonds based on spatial overlap without explicit regard to relatedness (Cantor & Farine, 2018; Widdig,

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2007). In some species that show strong social bonds with kin, family size functions as a measure of social integration and social support (e.g. Silk, Alberts et al., 2006; Silk, Altmann et al., 2006) and has been shown to correlate positively with fitness outcomes (Brent et al., 2017; Lynch et al., 2019). Determining the relationship between family size and social environment in long-lived, polygynandrous species with multiple overlapping generations can be daunting due to the difficulty in detecting all salient kin relationships, leaving the effects of demographic processes on sociality understudied (Shizuka & Johnson, 2019). Nevertheless, investigating how the landscape of potential social partners impacts partner choice and subsequent variation in individual gregariousness will bolster understanding of the evolutionary drivers of social relationships (Seyfarth & Cheney, 2012).

Shark Bay bottlenose dolphins are an ideal system in which to test questions regarding social partner choice patterns. The Shark Bay dolphin society is large and relationally complex, with highly differentiated social relationships (Strickland et al., 2017) and an array of social phenotypes (Evans et al., 2021). Adult males form lifelong relationships with alliance partners (Connor & Krützen, 2015), exhibit a variety of multilevel alliance structures (Connor et al., 2011) and have long been studied as a model system for understanding the evolution of social intelligence (Connor, 2007). Female relationships and social structure, on the other hand, have been characterized as relatively loose and labile (Frère, Krützen, Mann, Watson-Capps et al., 2010; Smolker et al., 1992), primarily driven by kinship or shared reproductive status (Frère, Krützen, Mann, Connor, et al., 2010; see also Möller et al., 2006). Individual females range from being as gregarious as males to almost completely solitary, but when and why females should invest in maintaining long-term affiliative relationships remains an open question. As kinship is a consistent predictor of female bond formation, in this study we explored whether a female's sociodemographic environment predicts how many affiliative relationships she forms as well as her position within the wider social network. As Shark Bay dolphins are heavily sex-segregated in their social relationships (Galezo et al., 2018; Smolker et al., 1992), we focused only on female–female associations throughout.

Adult females exhibit up to three orders of magnitude variation in their number of social connections (Gibson & Mann, 2008; Mann et al., 2012) and meet the criteria for high fission–fusion dynamics (Aureli et al., 2008), with temporary social groups changing composition on average over five times per hour (Galezo et al., 2018). Despite the fluid nature of groups, females do have highly differentiated relationships and demonstrate social partner choice through both long-term preferences and avoidances within their home ranges (Strickland et al., 2017). These persistent social associations likely fulfil the criteria for social bonds (Silk, 2002), correlating with measures of synchrony, petting and other affiliative behaviours (Foroughirad, 2019; Leu et al., 2020) as well as lasting up to 18 years or longer (Miketa, 2018). Shark Bay bottlenose dolphin females show strong kin preferences in their same-sex associates (Frère, Krützen, Mann, Watson-Capps et al., 2010) and have multiple lineages of kin available throughout their lifetimes, as both sexes are philopatric and inherit the ranging patterns and preferences of their mothers (Mann et al., 2021; Strickland et al., 2021; Tsai & Mann, 2013). To date, evidence suggests that female reproductive success is related to having other reproductively successful social associates (Frère, Krützen, Mann, Connor, et al., 2010) and consistent long-term social associations (Miketa, 2018). Females may pass some of these benefits to their offspring by shaping their social networks during the period of dependency (Stanton & Mann, 2012). This variation in degree of social connectedness can therefore be leveraged to better understand the adaptive nature of sociality.

In this study, we investigated (1) the extent to which female kin are preferred social partners, (2) under which demographic conditions individuals form bonds with unrelated females and (3) how availability of female kin, age and foraging-related behaviour together shape the gregariousness and social network position of individual female bottlenose dolphins. We first examined the extent to which kin preferences are affected by lineage (matrilineal or nonmatrilineal) and degree of relatedness. We sorted by matrilineal membership rather than maternal or paternal relationship in an attempt to most meaningfully pool the relationship categories present over multiple overlapping generations and degrees of relatedness. We expected strong matrilineal kin recognition and preference because of the long infancy period in which the relationship between the mother and offspring can be readily observed, and this mother-mediated familiarity likely persists across multiple overlapping generations (Karniski et al., 2018; Mann et al., 2000; Rendall, 2004). Mechanisms for nonmatrilineal kin recognition, if present, are unknown. Once we determined which types of kin are salient to social decisions, we then examined the relative propensity for individuals to also form bonds with nonkin and increase their measures of social connectivity or social integration. We investigated multiple measures of social connectivity, including the total number of affiliations as well as network centrality metrics with demonstrated fitness correlates for cetaceans (i.e. eigenvector centrality: Stanton & Mann, 2012; closeness centrality: Ellis et al., 2017; Rankin et al., 2022).

We considered several ways in which kin availability could influence connectivity, starting from the evidence that females typically affiliate with their available female kin (Frère, Krützen, Mann, Watson-Capps et al., 2010; Tsai & Mann, 2013) but will also affiliate with unrelated individuals under certain conditions. We characterize these potential patterns as (1) 'kin-proportioned', in which a female's social connectivity is predicted by her family size (i.e. number of kin), but those kin have no effect on her propensity to associate with unrelated individuals, (2) 'kin-compensated', in which there is an inverse relationship between a female's kin availability and her propensity to associate with unrelated individuals, driven by the female compensating for limited kin availability by bonding with nonrelatives (e.g. Carter et al., 2017; Silk, Alberts et al., 2006) and (3) 'kin-accelerated', in which there is a positive relationship between kin availability and an individual's propensity to associate with unrelated individuals as well, for example, because individuals may bond transitively (i.e. 'friends-of-friends') with both their kin and the associates of their kin (Wey et al., 2019), or possibly because there is positive feedback between social connectivity and overall matrilineal fitness (Holekamp & Sawdy, 2019).

To discriminate between these potential scenarios, we leveraged the longitudinal data set of demographic and ranging data along with recent high-quality relatedness estimates from high-throughput sequencing data (Foroughirad et al., 2019). We compared observations of social behaviour against predictions from a spatially explicit null model (SENM) to extract affiliations and residual network metrics from opportunistic survey data. SENMs can provide robust measures of social affiliations because they incorporate individually specific fine-scale home range utilization, population level gregariousness, and demographic turnover (Carter et al., 2009; Strickland et al., 2017). Controlling for spatial overlap is crucial to the study of kin preferences, especially in populations where some or all individuals exhibit natal philopatry. These populations are characterized by high encounter rates between kin, which are expected to produce correlations between relatedness and associations even in the absence of kin recognition. SENMs allow us to marginalize these expected rates of association to determine whether these relationships are driven by more than

just accessibility. Many studies have examined kin preferences in affiliative behaviours, and our study extends this work by accounting for kin availability and determining its relative impact on nonkin social bonds and social connectivity for females exhibiting high fission–fusion dynamics.

METHODS

Since 1984, a resident, coastal population of Indo-Pacific bottlenose dolphins, *T. aduncus*, in Shark Bay, Western Australia, has been systematically studied with demographic, behavioural and environmental data collected during boat-based surveys. Individuals are identified through photographs using markings on the fin and body (Bichell et al., 2018; Würsig & Würsig, 1977). Birth years are known for most individuals born since the 1980s determined from observation of individuals as calves. Alternatively, birth years for older individuals were estimated from body size and the degree of ventral-to-dorsal speckling, and are typically accurate to within ± 3 years (Krzyszczuk & Mann, 2012; Van Aswegen et al., 2019). For all individuals included in this study, 56% of birth years were known and 44% were estimated. Social associations were determined during the first 5 min of a sighting by grouping individuals using a 10 m chain rule, where any individual within 10 m of any other member was considered a member of the group (Smolker et al., 1992). GPS locations of the groups were recorded when the boat was within 50 m of the group. Between 2013 and 2019, skin and blubber samples were obtained during surveys using a remote biopsy system (Krützen et al., 2002) for genetic analyses.

Female social networks were generated from a subset of 13 years of data from May 2007 to December 2019, comprising 941 survey days and 4304 group observations. We restricted the analysis to this time period as these were the years in which we had genotype information available for the majority (range 51–82% each year) of individuals with 10 or more sighting records, excluding calves. Although this is a relatively long period over which to measure social relationships, we note that social bonds between these females have been shown to last up to 18 years (Miketa, 2018). Social network edges were based on association rates estimated from group memberships using the half-weight index (HWI, described below).

Identifying Kin and Assigning Lineage

Relationships between individuals were assigned through the observed maternal pedigree and/or through calculation of a genetic relatedness coefficient. Genetic relatedness was obtained using single nucleotide polymorphism (SNP) markers generated from DArT-sequencing (Jaccoud et al., 2001; Kilian et al., 2012) as described in Foroughirad et al. (2019). A quality-filtered panel of 4235 SNPs was used to calculate relatedness coefficients using the dyadic maximum likelihood estimator (Milligan, 2003) implemented in the 'COANCESTRY' software (Wang, 2011). Parentage assignments were conducted with the R package 'Sequoia' (Huisman, 2017) and used to help assign lineage. We defined close relatives as predicted first-, second- and third-degree relatives. When a pedigree was not available, close relatives were defined as a dyad with an expected relatedness coefficient of 0.125. Based on previous empirical work, we set the threshold for our observed genetic relatedness coefficient to 0.0935 to allow for some variation around our expected coefficient due to recombination and genotyping error in order to maximize our inclusion of close kin (Foroughirad et al., 2019). In this polygynandrous mating system, our definition of close relatives is expected to include primarily mother–daughter, grandmother–granddaughter, half-sisters and half-aunt–niece relationships, although other relationships, e.g.

full sisters, are present at low frequencies. We also examined the probability of affiliating with more distant (probable fourth-degree, $r \geq 0.0362$) relatives, although we kept these distant relations as a separate category from close relatives as our accuracy in assigning these relationships would be substantially lower than for close relatives (Foroughirad et al., 2019).

Close relatives were split into two lineage categories, matrilineal and nonmatrilineal. Matrilineal kin were defined as females from the same maternal lineage that were connected through only female relatives. Nonmatrilineal kin included both paternal kin and maternal kin related through a shared male relative, e.g. the mother's paternal sister (see Fig. 1). Kin were segregated into lineages using a combination of the reconstructed pedigree and mitochondrial haplotypes obtained as in Krützen et al. (2004). Five mitochondrial haplotypes were present in the sample at frequencies from 5% to 40%, and kin with different haplotypes were coded as nonmatrilineal. Those with the same haplotype were coded as matrilineal only if this relationship could be confirmed through the pedigree. Pairs with shared inheritance from both lineages (such as full siblings) were rare, and in those cases assigned to the matrilineal category. Since we could not separate most distant kin unambiguously by lineage due to the shallowness of our pedigree, we retained them as a separate kin category in regression analyses. Pedigree information was available for about 70% of close relative pairs, while virtually all distant relatives (99%) were classified using genetic relatedness coefficients only.

Classifying Affiliations with a Spatially Explicit Null Model

We selected pairs of individuals whose relationship could be categorized as affiliative by comparing their observed association rate against expected results obtained from a spatially explicit null model. Spatially explicit null models are simulation-based networks that provide expectations of individual behaviour based on demography, sampling effort and other population level parameters (e.g. average group size), allowing for the robust quantification of interindividual variation (Carter et al., 2009; Strickland et al., 2017). The null model we used is multifaceted in that it includes both our process of observing the groups of animals as well as the movement of the animals themselves, but we note that a careful accounting of space use is necessary when examining kin preferences under bisexual philopatry where kin are expected to have high encounter rates (Tsai & Mann, 2013).

All females that had 10 or more sightings postweaning (average weaning age 3.98 years, range 2.56–8.59; Karniski et al., 2018) were included in the network ($N_{\text{females}} = 177$; median number of observations = 27; interquartile range 17–47). This minimum sighting threshold was set based on stabilization for rank-based metrics of social connectivity (Stanton, 2011). While 10 sightings represented the minimum threshold for inclusion as a node in the real and simulated networks, for specific models we used higher minimum sightings thresholds for focal pairs and individuals as described below. Juvenile females (those between weaning and sexual maturity at around age 10 years) were included as social associates in all models since females in our population show little evidence of age-biased association (Foroughirad et al., 2019), but we restricted our analysis of individual social metrics to only adult females.

Home ranges were estimated for all females as in Strickland et al. (2017) using the R package 'adehabitatHR' (Calenge, 2006) to create kernel utilization distributions (UDs) using the 'kernelUD' function across 250×250 m grid cells, a relatively fine scale compared to the typical 50–100 km² home range size. Land was removed by implementing the barrier method of the 'kernelUD' function using a simplified version of the coastline, and then

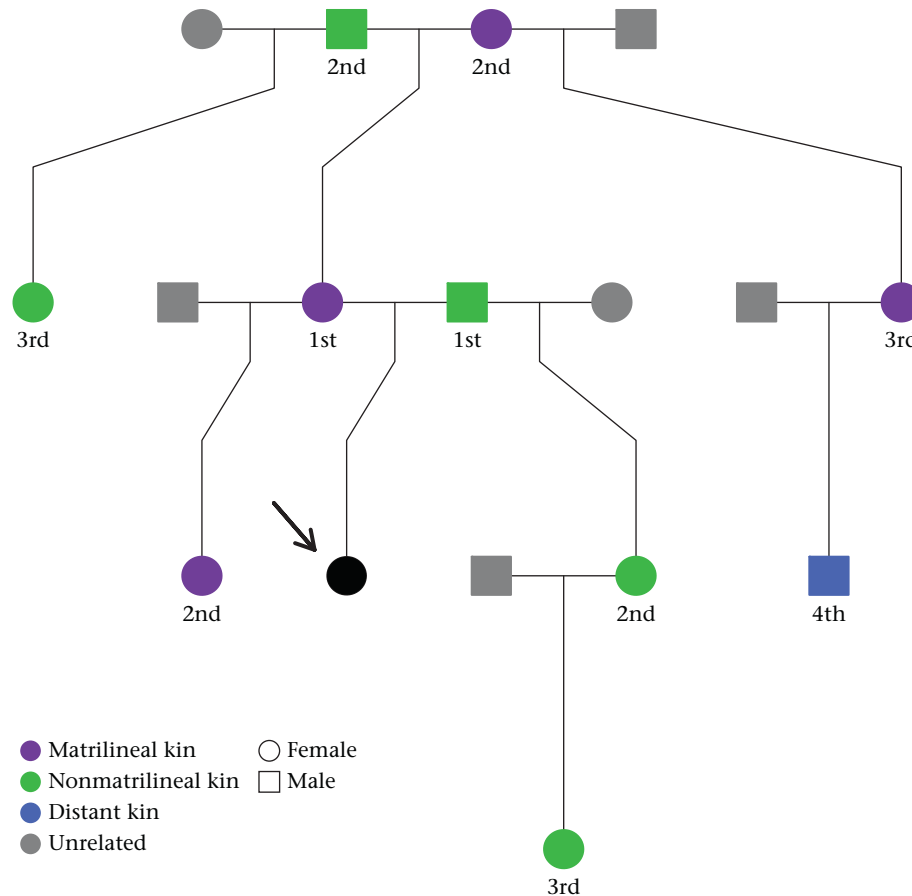


Figure 1. An example pedigree demonstrating assignment of kin categories by lineage (i.e. matrilineal, nonmatrilineal, distant, unrelated) and degree (first, second, third, fourth) from the perspective of an individual female (ID044 in study, indicated by arrow). Note that some maternal kin, such as the mother's paternal half siblings, are classified as nonmatrilineal with respect to the subject. Vertical lines represent parent–offspring relationships, while horizontal lines represent matings. Created in R with the 'kinship2' package (Sinnwell & Therneau, 2020).

further setting the use probability of any intersecting grid cells with the land polygon to NA and restandardizing the summed probabilities to 1. While social data were restricted to survey records between 2007 and 2019, we used all location data available for females from the long-term data set (1988–2019) based on evidence that home ranges remain relatively consistent throughout a female's adult life (Mann et al., 2021; Strickland et al., 2021; Tsai & Mann, 2013). Locations were filtered to include only the last point per day per individual to increase independence between points to achieve the best home range estimates.

To create the null model, we simulated the 13 years of survey effort on a day-by-day basis. For each sampling day, we created a search area polygon based on the portion of the study site covered by boat in that day's survey effort. We then intersected the boundaries of that search area with the set of calculated UD for all individuals, selecting all UD grid cells that fell completely or partially within the search area. A set number of dolphins was then randomly drawn from that area based on the observed number, and the identity of these dolphins was selected using a probability equal to the proportion of their UD that overlapped with the search area and in accordance with their temporal availability. Each sampled dolphin was then assigned to a random grid cell within the search area, chosen with a probability equal to the proportion of their UD on that cell, and their location within the cell was randomized.

Within each simulated day, the set of sampled dolphin locations was spatially clustered into groups using complete-linkage hierarchical clustering (Murtagh, 1985) and setting the number of

clusters to equal the number of groups encountered. Average group size \pm SD was 1.95 ± 1.74 females with 4.64 ± 2.89 groups encountered per day of survey effort.

Pairwise association rates were calculated between all individuals in the simulated groups and the real data using the half-weight index (HWI; Cairns & Schwager, 1987; Weko, 2018) restricted to the period in which both individuals were available to associate (from postweaning until either death or 6 months after the last sighting date). The half-weight index attempts to estimate the true association rate (between 0, 'never together', and 1, 'always together'), while correcting for potential bias resulting from the probability of observing a pair apart versus together when only a fraction of the study area is covered during each sampling period. The simulation was repeated for a total of 1000 iterations to create a distribution of expected association indices for all pairs.

A relationship between a pair of females was deemed a statistically significant affiliation if the observed half-weight index fell above the 97.5th percentile of their expected indices from the simulation, and the pair associated over multiple years. We further restricted scoring affiliations between only those pairs in which both individuals had at least 35 total sightings, the minimum number needed to reliably calculate home range overlap (Foroughirad et al., 2019), and at least 20 sightings postweaning for social analysis ($N = 103$), as 20 sightings reliably measures consistent interindividual differences in social metrics (Evans et al., 2021).

Pairwise Affiliative Behaviour and Relatedness

We examined how the three kinship categories (matrilineal, nonmatrilineal, distant) affected the probability of pairs of females being classified as affiliative (0/1) relative to unrelated pairs using a binomial generalized linear model (GLM). In this model we also controlled for similarity in space use (hereafter home range overlap) using Bhattacharyya's affinity index (Fieberg & Kochanny, 2005). Kinship and home range overlap are expected to be correlated under matrilineal home range inheritance (Strickland et al., 2021; Tsai & Mann, 2013), and we assessed variance inflation factors to ensure these variables were appropriate to include in the same model since we were interested in distinguishing the role of kinship from simple familiarity. Following the advice of Weiss et al. (2021), who recommend including factors related to observation biases as covariates when modelling social connections, we additionally included two predictor variables related to our observation biases: the number of years the pair had been observed during the study and the combined number of sightings for the pair. These could bias our data if pairs that are more frequently sighted are merely more likely to be captured associating and affiliating than less frequently sighted pairs. We assessed significance of the parameters in our logistic GLM using the multiple regression quadratic assignment procedure (Krackhardt, 1988) with the Dekker double semipartialling method (Dekker et al., 2007) implemented in the R package 'sna' (Butts, 2008). This method permutes the residuals of the network model in a way that preserves correlations among rows and columns of the adjacency matrix and is appropriate for nonindependent network data.

We then used the results of this analysis to select which kinship categories to retain for our analyses of individual gregariousness. We note that genetic assignments are approximations of kinship categories and may not always accurately reflect the true pedigree relatedness. Therefore, we used the resulting affiliation probabilities to determine whether these genetically determined categories appeared to be socially meaningful when compared to unrelated pairs (Table 1, Appendix, Fig. A1).

Individual Gregariousness and Kin Availability

For models of individual gregariousness, females were further filtered to adults (≥ 10 years of age, earliest age of conception) who had at least 70% of their associates genotyped ($N = 87$). The 70% cutoff was selected to ensure that there was no relationship between the proportion of an individual's network that had been genotyped and the number of kin detected in her network.

We modelled the effect of kin availability on the number of significant affiliations an individual formed, as well as the number of significant affiliations formed specifically with unrelated individuals. While our primary predictors of interest were the

number of kin of each lineage and degree, previous studies have indicated that foraging strategy (Mann et al., 2012) and food provisioning (i.e. fish handouts at a tourism programme in Monkey Mia, Western Australia: Foroughirad & Mann, 2013; Mann et al., 2021) can also have marked effects on behaviour, so we added additional covariates to our models to control for these effects. Females in our study engaged in 15 different foraging techniques (see Appendix, Table A1 for ethogram), with most females using multiple techniques to varying degrees. Proportion of time devoted to each technique was therefore used to cluster individuals into several composite strategies. Individuals were grouped into categories using partition around medoids (PAM) clustering (Kaufman & Rousseeuw, 2005) with the general distance measure (Walesiak & Dudek, 2020) and number of clusters selected using the pseudo- F statistic (Caliński & Harabasz, 1974). This resulted in four clusters, which were designated as (1) sea grass foraging, (2) tail-out dive peduncle foraging, (3) sponge tool foraging and (4) a mixed strategy (tail-out peduncle dive foraging and mill foraging/bird milling), according to the predominant foraging type in each cluster (Appendix, Fig. A2). Tail-out peduncle dive foraging was the most common category, so was therefore set as the reference level for all models. Six of the adult female dolphins in our study participated in the provisioning programme based at Monkey Mia in which they were given daily fish handouts by tourists under the supervision of park rangers from the West Australian Department of Biodiversity, Conservation and Attractions (Mann & Kemps, 2003). Accepting fish handouts, like other foraging tactics, can have significant effects on behaviour, but as the fish received only make up a small proportion ($<10\%$) of the total daily needs of the individuals, participation in the provisioning programme was coded as a separate variable from overall foraging strategy.

We modelled the counts of individual significant affiliations using log link negative binomial GLMs rather than Poisson as the response variable showed overdispersion. In these models, the response was either the total number of significant affiliations or the total number of unrelated significant affiliations, and predictors included age (taken as each female's average age at observation), foraging cluster, provisioning status, number of years observed and the logged total number of observations of the individual. We logged the total number of observations since the probability of detecting new connections with increasing sampling effort typically follows a logarithmic pattern (Leu et al., 2020). Each model also included the number of matrilineal close kin, nonmatrilineal close kin and distant kin belonging to each individual as predictors. To control for variation in the availability of observed females within each subject's home range, we additionally included an offset term with the number of females that shared a minimum amount of home range overlap with the subject. The minimum amount of home range overlap between an affiliated pair was approximately 0.25. We therefore considered only females with a

Table 1

Estimates from logistic regression on the probability of forming a significant affiliation based on kinship category (as compared to unrelated), home range overlap, years the pair was observed and the combined number of sightings

	Odds ratio	Estimate	SE	Z	Reference interval	P
Intercept	—	−11.071	0.568	−19.482	−6.676, 3.957	—
Kin: Matrilineal close	4.721	1.552	0.291	5.331	−1.707, 2.006	<0.001
Kin: Nonmatrilineal close	2.597	0.954	0.28	3.405	−1.885, 1.992	<0.001
Kin: Distant	1.463	0.38	0.184	2.067	−2.083, 1.95	0.049
Home Range overlap (BA)	9.22×10^4	11.432	0.611	18.695	−2.662, 2.931	<0.001
Years pair observed	0.972	−0.029	0.023	−1.267	−4.223, 4.21	0.569
Combined sightings	1.003	0.003	0.001	2.806	−3.964, 3.942	0.171

Significance was assessed against the 95% reference interval of the z value test statistic generated from a double semipartialling quadratic assignment procedure on 1000 permutations. Significant values shown in bold.

range overlap of at least 0.25 as having the ability to regularly encounter one another and choose whether to affiliate, and we set the number of females meeting this criterion as the offset term (mean $N_{\text{females}} = 78$, interquartile range 69–89). Models were fitted using 'glm.nb' from the 'MASS' R package (Venables & Ripley, 2002), and model diagnostics included simulating scaled residuals for visual inspection using the R package 'DHARMA' (Hartig, 2021). Parameter significance was assessed by estimating 95% profile likelihood confidence intervals via the 'confint' routine in the 'MASS' package (Venables & Ripley, 2002), and coefficients were interpreted as significant if the interval did not include zero.

Residual Centrality Metrics

Lastly, to test whether family size (number of female kin) influences an individual's position within the wider social network, we compared an individual's calculated centrality metrics against expected values obtained from our null model. As the null model contains no individually specific social parameters, the interindividual variation in the simulation results is expected to predominantly reflect sampling biases. Therefore, we used residual centrality metrics (observed – median simulated value) to marginalize the expected variation in centrality due to observational effort. For these metrics, each female's pairwise association indices were calculated only over the period in which she was alive and of adult age, and therefore dyadic metrics were not always symmetrical (e.g. in cases where juvenile females were counted as partners but were not focals).

The choice of which social network metrics to compare is a complicated one as there are multiple centrality measures to select from, of which many may be highly correlated, and indiscriminate selection of an increasing number of response variables increases risk of type I error (Webber et al., 2020). Therefore, we leveraged the results from previous studies to select the appropriate metrics with which to capture meaningful social variation with careful consideration of effect sizes. Two centrality metrics were modelled, closeness centrality and eigenvector centrality. An individual's closeness centrality is the number of steps required to access every other individual in the network, and eigenvector centrality is the eigenvalue of the first eigenvector from the matrix of associations and measures the influence of a node based both on its connections and the connections of its neighbours (Freeman, 1979). The indirect metrics were chosen as those were two ego level centrality metrics found to be correlated with juvenile (Stanton & Mann, 2012) and adult survival in dolphin networks (Rankin et al., 2022; see also Ellis et al., 2017 for a similar effect in killer whales, *Orcinus orca*). The same metrics were calculated both for the real observed network and for each of the simulated networks using the R package 'igraph' (Csardi & Nepusz, 2006), and then the residual metric was obtained by subtracting the individual's median simulated value from the observed value.

We tested the effect of kin availability on the residual centrality metrics using Gaussian linear models, with the residual centrality metrics scaled to have a mean of 0 and standard deviation of 1. In addition to the family size variables, the models included the average age of the female, provisioning status, foraging cluster, the number of years observed and the logged number of observations. Parameter significance was again assessed by estimating profiled 95% confidence intervals, and coefficients were interpreted as significant if the interval did not include zero. Variables in all models were checked for multicollinearity using variance inflation factors (VIF) in the R package 'car' (Fox & Weisberg, 2019), and all VIFs were <3, indicating no severe collinearity. All analyses were done in R version 4.1.0 (R Core Team, 2021).

Ethical Note

Ethics approval for all animal research was obtained from the University of the Sunshine Coast (AN/S/15/35) and Georgetown University Institutional Animal Care and Use Committee (13-069, 07-041, 10-023, 2016-1235). Field research was conducted under Western Australian Department of Biodiversity, Conservation and Attractions permits (SF-009876, SF-010347, SF-008076, SF009311, SF007457). Tissue sample collection was attempted via remote biopsy darting on each individual for up to 1 h. If the attempt was not successful within the hour, the animal was left alone to recover for a minimum of 24 h (if no physical contact was made) or a minimum of 1 year (in cases where contact was made but no sample obtained). These rest periods are designed to reduce distress and in the case of contact significantly exceed the average time for biopsy wound healing (23 days; Krützen et al., 2002).

RESULTS

Kin Identification and Lineage Assignment

We identified 198 pairs of close relatives between females that met the sighting threshold for classifying affiliations ($N_{\text{females}} = 103$). Of these pairs, 191 (96%) could be assigned to either a matrilineal ($N_{\text{pairs}} = 75$) or nonmatrilineal ($N_{\text{pairs}} = 116$) lineage and 395 pairs were classified as distant kin. Seven pairs of females were closely related but could not be assigned to either lineage, so these relationships were removed from the pairwise analysis.

Kin Discrimination in Forming Affiliations

For the 103 frequently sighted females, 403 affiliations out of 5253 possible pairwise relationships differed significantly from random (Fig. 2). Females had a mean \pm SD of 6.9 ± 4.8 significant affiliations, ranging from 0 to a maximum of 17, while the total number of other females a female was seen in association with at least once ranged from 7 to 72. Out of the 403 significant affiliations, 63% were between unrelated pairs, and of these 49% ($N_{\text{pairs}} = 125$) had different mitochondrial haplotypes (i.e. could not be matrilineal kin).

Both matrilineal and nonmatrilineal close female kin as well as distant kin were significantly more likely to affiliate than unrelated pairs (Fig. 3, Appendix, Fig. A1). Overall, matrilineal close kin were predicted to be 4.7 times more likely to affiliate than unrelated pairs, and nonmatrilineal close kin 2.6 times more likely to affiliate, compared with 1.5 times for distant kin (Table 1). For individuals with known pedigree kinship, we found the highest affiliation rates between maternal sisters (88%), followed by mother–daughter pairs (76%). Although these rates of affiliation with matrilineal close kin were very high, 22% of females had higher estimated association rates (HWI) with an unrelated individual than with any available matrilineal close kin. Overall, out of all female's top three associates, 56% were kin and 44% were unrelated individuals.

Effect of Kin Availability on Individual Gregariousness

There were 87 adult females for whom at least 70% of their associates were genotyped (mean \pm SD = 0.892 ± 0.057). A Pearson correlation test showed that there was no significant relationship between the proportion of the subject's network that was genotyped and the number of kin assigned to her ($r_{85} = 0.136$, $t = 1.266$, $P = 0.209$).

When modelling how the number of kin in each kin category predicted the total number of significant affiliates, we found that

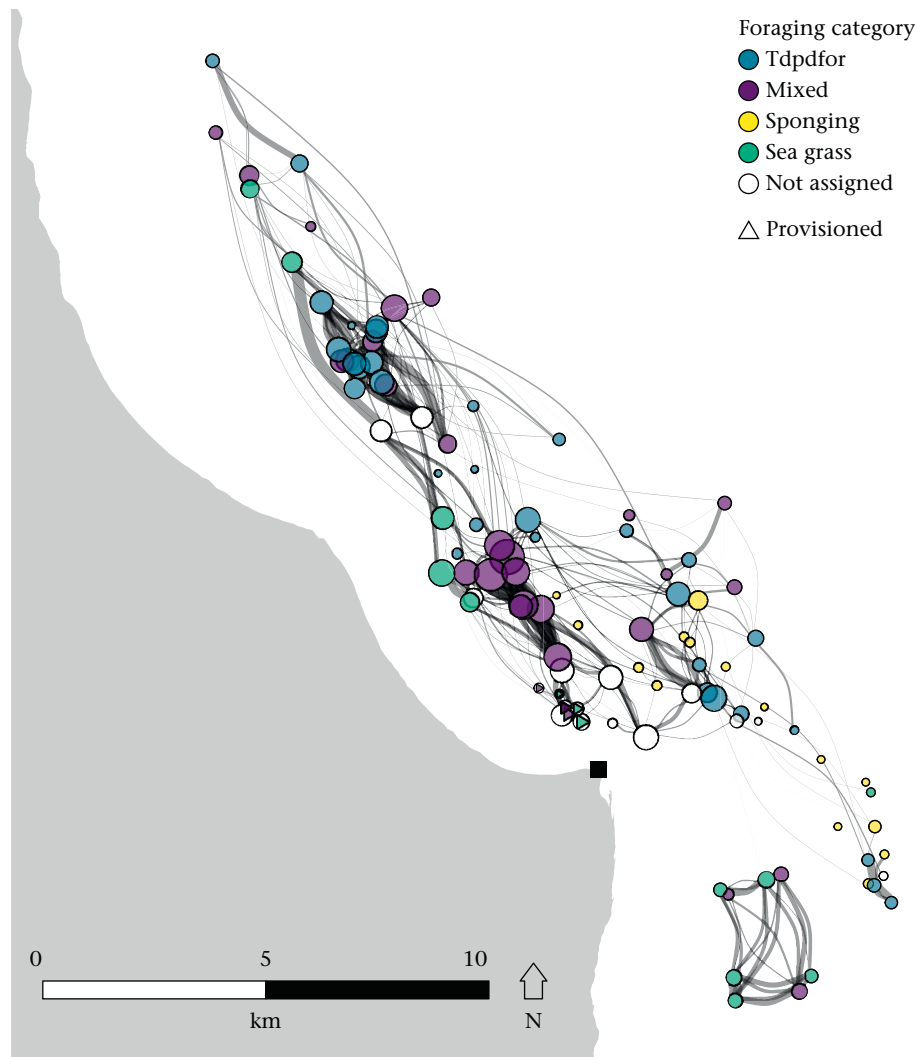


Figure 2. Affiliation network of the 103 females with adequate sighting data. Only associations between pairs that exceeded the 97.5th percentile of the expected association rates are shown as edges. Nodes are positioned on each individual's centroid; node size is proportional to the total number of significant affiliations; node colour represents the individual's foraging strategy (juvenile females were not assigned a foraging strategy; Tdpdfor = tail-out peduncle dive foraging). Edge widths are weighted by residual tie strength (observed – mean simulated association index). The boat launch site ($25^{\circ}47'52.4''\text{S}$, $113^{\circ}43'12.9''\text{E}$) was next to the provisioning site and is represented by the black square.

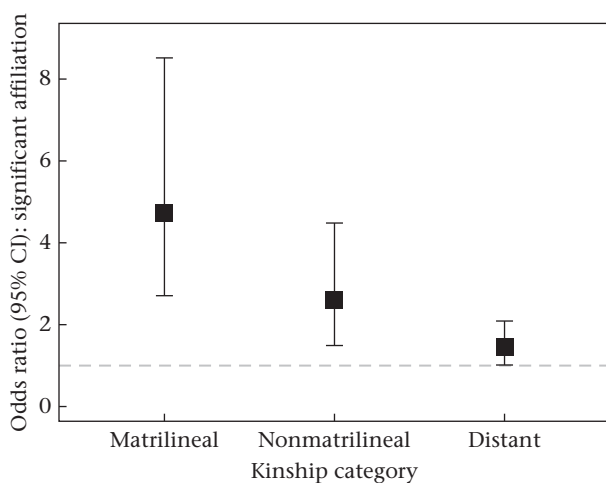


Figure 3. Odds ratios for the predicted probability of significant affiliation by kinship category for female pairs ($N_{\text{females}} = 103$), controlling for home range overlap, years observed and number of sightings. Point estimates and 95% confidence intervals generated using profile likelihood are shown.

the number of matrilineal close kin positively correlated with the total number of significant affiliations. However, there was no statistical relationship between the number of matrilineal close kin a female had and the number of significant affiliations she formed with unrelated individuals (Fig. 4, Table 2). The effect size of matrilineal close kin on total significant affiliations was such that females experienced a 14% increase in affiliations on an average of 6.9 affiliations, or approximately one additional affiliation per matrilineal close family member. The number of non-matrilineal close kin or distant kin that a female had was not correlated with either the total number of significant affiliations or the total number of significant unrelated affiliations she formed.

Older females also had fewer total significant affiliations, or about 17% less for every additional 10 years of age, but there was no significant effect between age and the number of significant affiliations with unrelated individuals (Table 2). Provisioned females had significantly fewer total and unrelated affiliations than expected compared to nonprovisioned females, as did sponge tool foragers when compared to the more common tail-out peduncle dive foragers.

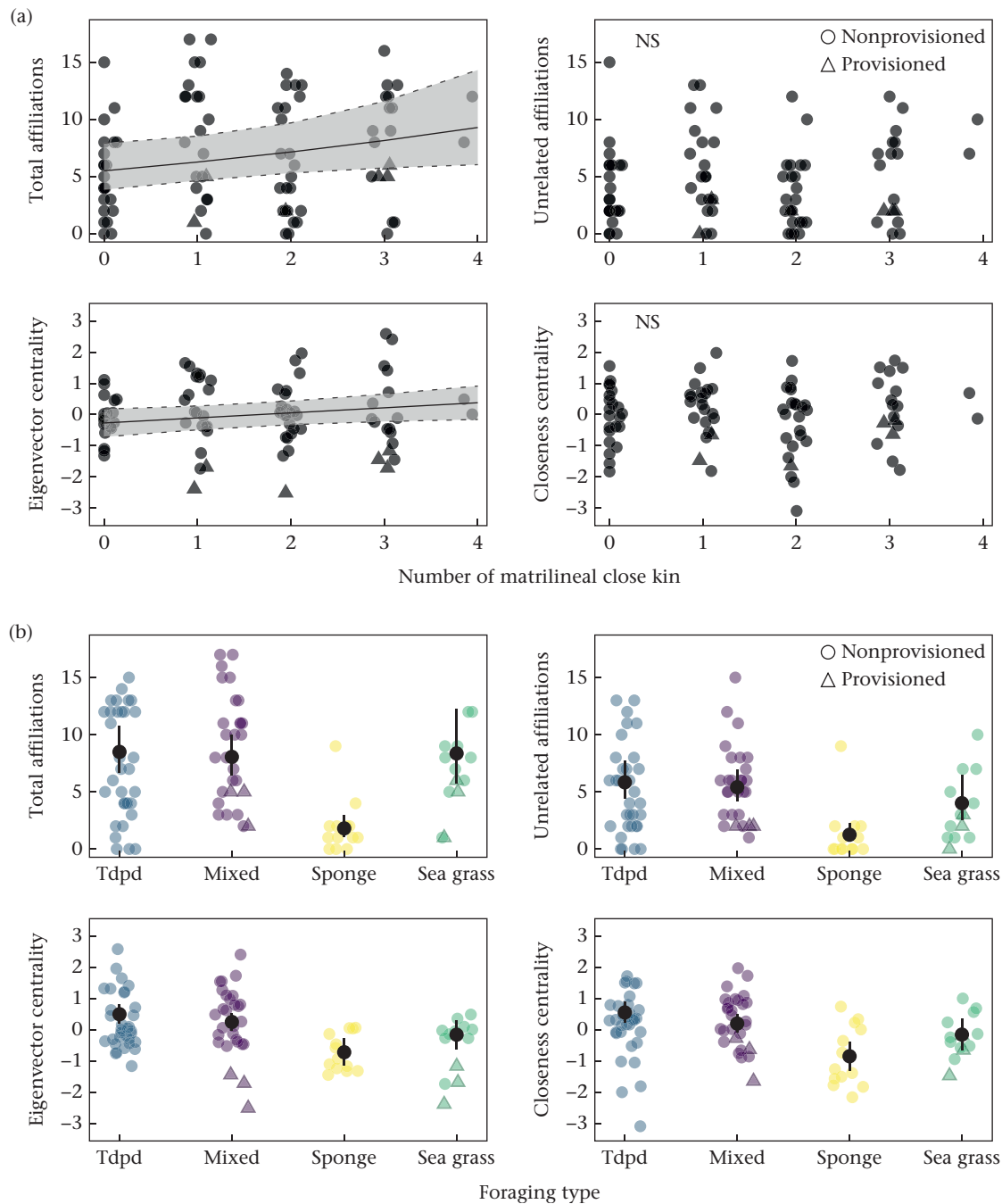


Figure 4. (a) Number of matrilineal close kin available to an adult female in relation to the female's total significant affiliations, residual eigenvector centrality, number of unrelated significant affiliations and residual closeness centrality. The partial effects and 95% confidence intervals from the negative binomial GLM (total significant affiliations) and Gaussian LM (residual eigenvector centrality) are shown. Kin categories that did not have any significant effects in these models are not shown. (b) Foraging type in relation to a female's total significant affiliations, residual eigenvector centrality, number of unrelated significant affiliations and residual closeness centrality. Partial effects and 95% confidence intervals for each foraging type are shown. Tdpd = tail-out peduncle dive foraging.

For social connectivity metrics, residual eigenvector centrality and residual closeness centrality were moderately correlated with one another (Spearman's rank correlation: $r_s = 0.515$). Females with more matrilineal close kin had higher residual eigenvector centrality but not higher residual closeness centrality (Fig. 4, Table 3). The number of nonmatrilineal close kin or distant kin that a female had was not correlated with her network centrality. As with significant affiliations, provisioning was significantly negatively correlated with both residual eigenvector and closeness centrality, and sponge tool foragers had significantly lower centrality values than the more

common tail-out peduncle dive foragers. Females with more sightings and who were observed for more years in the data set had higher residual closeness centrality (Table 3).

DISCUSSION

Our results demonstrate that individual female sociality is influenced, but not dictated, by kin availability. Shark Bay dolphins are philopatric and prefer kin, but slow life histories and long interbirth intervals mean that average relatedness between

Table 2

Estimates from the negative binomial generalized linear models for family size on the total number of significant affiliations and the total number of unrelated significant affiliations

	Total significant affiliations		Unrelated significant affiliations	
	Odds ratio	β (95% CI)	Odds ratio	β (95% CI)
Intercept	0.049	−3.018 (−4.172, −1.875)	0.052	−2.955 (−4.266, −1.653)
Number of matrilineal close kin	1.14	0.131 (0.01, 0.253)	1.108	0.102 (−0.035, 0.241)
Number of nonmatrilineal close kin	0.999	−0.001 (−0.057, 0.056)	0.936	−0.066 (−0.133, 0.001)
Number of distant kin	1.007	0.007 (−0.026, 0.04)	1.004	0.004 (−0.032, 0.041)
Foraging: Mixed	1.054	0.053 (−0.271, 0.377)	1.079	0.076 (−0.291, 0.445)
Foraging: Sponging	0.224	−1.497 (−2.038, −0.982)	0.231	−1.464 (−2.101, −0.87)
Foraging: Sea grass	1.037	0.037 (−0.385, 0.462)	0.742	−0.299 (−0.806, 0.206)
Provisioned: Yes	0.36	−1.022 (−1.729, −0.327)	0.338	−1.086 (−1.983, −0.237)
Age (years)	0.979	−0.021 (−0.042, −0.001)	0.982	−0.018 (−0.042, 0.005)
Log (number observations)	1.235	0.211 (−0.063, 0.488)	1.193	0.177 (−0.136, 0.492)
Years observed	1.023	0.023 (−0.056, 0.102)	1.006	0.006 (−0.085, 0.096)

Parameter significance was assessed by estimating profiled 95% confidence intervals and coefficients were interpreted as significant if the interval did not include zero. The reference category for the foraging variable is tail-out peduncle dive (tdpd) foraging, and the model includes an additional offset variable for the total number of available females within the subject's home range. Significant values are shown in bold.

associates is not necessarily high. Low relatedness among group members is likely an important factor underlying social complexity (Silk, 2006), and the average (\pm SD) relatedness (r) between pairs of significant affiliates in this study was 0.08 ± 0.13 , near the 0.05 threshold proposed to foster relational social complexity in animal societies (Lukas & Clutton-Brock, 2018). Females affiliated with first-degree kin through distant kin (fourth-degree or greater), as well as kin from both their matrilineal and nonmatrilineal lineages, significantly more than with nonkin even when controlling for home range overlap. Only the number of matrilineal close kin, however, affected the social position of the individual, both when counting the total number of significant affiliations an adult female formed with other females and when measuring her residual eigenvector centrality within the female network. There was no relationship between a female's family size and her propensity to affiliate with unrelated individuals, or with her residual closeness centrality. While matrilineal relationships might be the foundation of bottlenose dolphin society, we found that other aspects of female behaviour, namely foraging strategies and human interaction (i.e. provisioning), played a role in shaping more metrics of social connectivity than an individual's family size.

The relationship between female sociality and kin availability can best be described by the kin-proportioned model with respect to matrilineal close kin. Females with more matrilineal close relatives had more total significant affiliations, but the size of this effect was approximately proportional at one additional affiliation per matrilineal close family member. As adult females typically had only a mean (\pm SD) of 1.5 ± 1.2 matrilineal close family members, the variation in these available kin explained only a small amount of the variation in total number of significant affiliative relationships (mean \pm SD = 7.7 ± 5.0) formed by each female during the course of the study. Fewer matrilineal kin did not predict an increase in the extent to which females formed bonds with unrelated individuals, suggesting that females did not compensate for lack of available female kin by seeking out more relationships with unrelated females, perhaps indicating that they lack a common optimal or minimum level of sociality. We found no evidence for kin acceleration either, as having more kin was not positively correlated with a female's number of significant affiliations with unrelated individuals.

Kin availability had a small or no effect on the social network metrics that have been linked to fitness in our study population. Eigenvector centrality of male, but not female, calves has been found to be correlated with the probability of survival to adulthood (Stanton & Mann, 2012), and calf social connectivity is partly dictated by the connectivity of their mothers (Evans et al., 2021;

Stanton et al., 2011). Therefore, the family size of the mother may affect the survival probability of her male calf, although even with perfect fidelity and the largest observed matrilineal, the size of this effect would be less than the effect of provisioning, or the difference between sponge tool use and other foraging strategies, for example. Closeness centrality, which may influence survival probability for adults (Rankin et al., 2022; see Ellis et al., 2017 for a similar effect in killer whales), was not predicted by family size. This suggests that the flexibility afforded by high fission–fusion dynamics means that family size is not a substantial determinant of social integration. This contrasts markedly with species that live in more stable social groups (e.g. rhesus macaques, *Macaca mulatta*: Brent et al., 2017; Asian elephants, *Elephas maximus*: Lynch et al., 2019; killer whales: Parsons et al., 2009). Although dolphin females show strong kin preferences, their fission–fusion social system may allow them to maintain a level of sociality that is only weakly correlated with kin availability and is instead more consistently impacted by characteristics related to foraging ecology (Mann et al., 2012; this study) and resource competition (Levensgood et al., 2022) or other factors. This flexibility in kin bonding mirrors that found primarily in male mammals forming cooperative reproductive coalitions, which often facultatively bond with close male kin when available but switch to nonkin otherwise (chimpanzees, *Pan troglodytes*: Mitani et al., 2002; Sandel et al., 2020; lions, *Panthera leo*: Chakrabarti et al., 2020; Assam macaques, *Macaca assamensis*: De Moor et al., 2020). Male Shark Bay bottlenose dolphins also affiliate with little attention to kinship, instead forming reproductive alliances from social relationships formed during the juvenile period primarily based on age similarity (Gerber et al., 2020) or shared foraging tactics (Bizzozzero et al., 2019) rather than relatedness. Integral to nonkin bonding in many of these instances is the idea of partner selectivity based on competence and compatibility for completing cooperative tasks such as resource defence (Chapais, 2006). However, to what degree female Shark Bay dolphin's social bonding is related to specific cooperative activities remains an open question, and unlike for males (Gerber et al., 2022) social bonds between females have not yet been shown to have any relationship with survival or reproductive success. Social bonding between females likely plays important roles in predator vigilance (Heithaus, 2001), buffering of male harassment (Connor et al., 2006) and opportunities for social learning (Mann et al., 2007), but the benefits are likely to vary across environmental niches (Strickland et al., 2021).

Females that engaged in certain foraging practices, specifically those who primarily foraged with sponge tools, formed fewer significant affiliations and had reduced residual eigenvector and

Table 3

Estimates from the Gaussian linear models for family size on residual eigenvector centrality and residual closeness centrality

	Model estimates β (95% CI)	
	Residual eigenvector centrality	Residual closeness centrality
Intercept	0.656 (−0.8198, 2.1319)	−2.9631 (−4.5629, −1.3632)
Number of matrilineal close kin	0.1623 (0.0046, 0.32)	0.1091 (−0.0619, 0.28)
Number of nonmatrilineal close kin	0.022 (−0.0525, 0.0964)	−0.0594 (−0.14, 0.0213)
Number of distant kin	−0.0073 (−0.0505, 0.0358)	0.0104 (−0.0364, 0.0572)
Foraging: Mixed	0.2479 (−0.1772, 0.673)	0.3543 (−0.1065, 0.8151)
Foraging: Sponging	−0.9707 (−1.4932, −0.4482)	−1.0491 (−1.6155, −0.4828)
Foraging: Sea grass	−0.4086 (−0.9612, 0.144)	−0.3542 (−0.9532, 0.2448)
Provisioned: Yes	−1.8266 (−2.6745, −0.9788)	−1.5441 (−2.4631, −0.625)
Age (years)	−0.0196 (−0.0452, 0.006)	−0.015 (−0.0427, 0.0128)
Log (number observations)	−0.1841 (−0.5386, 0.1703)	0.4223 (0.0381, 0.8066)
Years observed	0.0482 (−0.0492, 0.1457)	0.1604 (0.0548, 0.2661)

Parameter significance was assessed by estimating profiled 95% confidence intervals and coefficients were interpreted as significant if the interval did not include zero. The reference category for the foraging variable is tail-out peduncle dive (tdpd) foraging. Significant values are shown in bold.

closeness centrality when compared to individuals using more common foraging strategies. This is in accordance with prior research demonstrating that these individuals are part of a tool-using subculture (Krützen et al., 2005; Mann et al., 2012) defined by using marine basket sponges during benthic foraging (Smolker et al., 1997). These sponge users have been shown to be more cliquish (Mann et al., 2012) and spend more time alone than other dolphins, devoting most of their activity budgets to their solitary foraging specialization (Mann et al., 2008). While we did not find correlations between social metrics and other broad foraging categories, we likely cannot interpret this to mean that other foraging strategies do not affect sociality, only that we may not have accounted for specific behavioural differences within these broad categories.

Another pervasive effect on sociality was the participation by six animals in our study in Monkey Mia's provisioning programme. These six females scored consistently lower than expected on all social metrics, suggesting that provisioning significantly affects their social positions. During this study, the females in the provisioning programme belonged to three matrilineal and all had some close kin available to associate with. Out of all the significant affiliations formed by this group ($N = 28$), only three were to females outside of the provisioned matrilineal, and these were formed by the two youngest females. These two females were not provisioned until they reached adulthood and were born after the provisioning programme instituted tighter regulations to minimize time spent at the provisioning area to promote dolphin welfare (Foroughirad & Mann, 2013; Mann & Kemps, 2003). Overall, the provisioned females formed only 36% as many significant affiliations as expected when compared to nonprovisioned females (Table 2) and had residual eigenvector centrality values almost two standard deviations lower than expected (Table 3), as well as significantly lower residual closeness centrality. This suggests that their participation in the provisioning programme somewhat isolated them from the rest of the population. We propose two possible explanations for this. First, that the provisioned females may have been competitively excluding other females from the provisioning beach, as the fish handouts are a localized and potentially defensible resource (Boydston et al., 2001). Second, while the provisioned animals were highly habituated to human presence and interactions, other dolphins may have been avoiding such frequent close encounters, and therefore were unable to sustain strong social bonds with the provisioned animals that spent a significant proportion of their time in close proximity to humans (Marty et al., 2019). Social isolation between individuals that have high levels of interaction with humans and those that do not have been found in many other populations of dolphins (Ansman et al., 2012; Kovacs et al., 2017;

Methion and Díaz López, 2020) and may represent an additional cost of human interaction.

Our results suggest that for most measures of female social connectivity in our population, kin do not function as a limiting resource and females do not simply form bonds with unrelated individuals only when kin are lacking. Nevertheless, pairs of females do frequently form social connections that are much stronger than what would be expected merely from overlapping ranges. This provides further evidence that Shark Bay female dolphins may not have a single optimal social strategy but rather vary their social strategies in accordance with constraints such as foraging strategies to fill diverse social niches (Bergmüller & Taborsky, 2010). Uncovering which aspects of local ecology, such as resource competition (Levengood et al., 2022) and predation risk (Heithaus & Dill, 2002), shape variation in social behaviour and their fitness consequences will be a productive avenue for future research. While Shark Bay bottlenose dolphins maintain consistent habitat use, foraging behaviours and sociability throughout their life spans (Evans et al., 2021; Strickland et al., 2021), other temporally variable factors such as reproductive state (Möller et al., 2006) are likely also at play, and we could not examine the effect of shorter-term reproductive changes within the long-term framework of this study. Likewise ageing had a small negative effect on the total number of significant affiliations, which may reflect increasing social selectivity with age (Rosati et al., 2020) or may correspond to changes related to reproductive senescence as successful calving probability decreases with age (Karniski et al., 2018). Future studies designed to measure the impact of short-term social relationships and temporally variable attributes will likely contribute to explaining more of the variability in female sociality. This heterogeneity in social strategies for females reflects some of the variation reported in male social strategies (Connor & Krützen, 2015), which also vary along environmental gradients (Connor et al., 2017; Hamilton et al., 2019) and likely influence one another (Gowans et al., 2007). Multiple social strategies within the contiguous population likely contribute to the complexity of the Shark Bay social network. Such network properties have critical implications for how information (e.g. cultural transmission; Mann et al., 2012) and disease (e.g. Kurvers et al., 2014; Leu et al., 2020) spreads through communities and how they respond to natural and anthropogenic threats.

Author Contributions

V.F. conceived the study, analysed data and wrote the first draft of the manuscript. V.F., A.L.L., A.M.K. and E.K. collected samples for genetic analysis and A.L.L. and V.F. conducted laboratory work. J.M.,

V.F. and E.K. collected behavioural and demographic data. All authors edited and approved the final version.

Data Availability

Code and data to reproduce all analyses are available at https://github.com/vjf2/Family_Size_Effects (<https://doi.org/10.5281/zenodo.7242808>; Foroughirad et al., 2022).

Declaration of Interest

None.

Acknowledgments

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Appendix

Table A1

Descriptions of 15 unique dolphin foraging tactics used by individuals in this study

Foraging tactic	Description
Beaching	A dolphin near the shoreline chases a fish to the shore until its ventral side is on sand. Fish usually becomes trapped, and the dolphin becomes partially or fully exposed onshore. Occurs in shallow beach areas (Mann & Sargeant, 2003)
Begging	Dolphin approaches a slow-moving boat or people on the beach and lifts its head out of the water with an open jaw (Mann & Sargeant, 2003)
Bird milling	Dolphins surface around a tight group of feeding pelicans or cormorants in water depths <4 m (Mann & Sargeant, 2003)
Belly-up foraging	Dolphin chases a medium size fish (i.e. larger than fish found in snacking events) while in a belly-up posture. Chases are usually unidirectional and brief
Coastal foraging	Dolphin chases a fish (often a mullet) within 10 m of the shoreline. Characterized by fast swims and hydroplaning, but not beaching
Kerplunking	Dolphin lifts peduncle out of the water, moving at variable degrees. A small splash occurs at ~45° angle of the fluke, followed by a large splash at a ~90° angle of the fluke, with an audible 'kerplunk'. Occurs in shallow water (Connor et al., 2000)
Leap and porpoise feeding	Dolphins mill about and leap continuously in a relatively small group or in a dispersed group (>1 km apart). Occurs with abrupt starts, stops and changes in direction (Mann & Sargeant, 2003)
Mill foraging	Dolphins change directions with each surfacing event and breath while foraging, with irregular breathing intervals (Mann & Sargeant, 2003)
Rooster-tail foraging	Dolphin rapidly chases a fish near the surface, creating a sheet of water that trails off the dorsal fin. After the chase, the dolphin dives to the bottom, moving away in the opposite direction of the fast swim (Mann & Sargeant, 2003)
Shallow sand flat foraging	Dolphin forages in shallow sand banks with little to no sea grass and performs bottom-grubbing behaviour, in which the dolphin is positioned vertically as it sticks its rostrum into the sea grass beds to find hiding fish (Mann & Sargeant, 2003)
Sea grass foraging	Foraging in shallow sea grass beds, often accompanied by bottom-grubbing behaviour
Shelling	Dolphin carries shells of large dead molluscs in its beak from the seafloor to the surface. Dolphin waves shells around in the air to shake out prey hiding inside (Allen et al., 2011; Mann & Patterson, 2013)
Snacking	Dolphin chases a small fish while in the belly-up posture and changes direction inconsistently. Dolphin catches fish at the surface of the water (Mann & Sargeant, 2003)
Sponge foraging	Dolphin carries a sponge on its rostrum while performing tail-out dives (see below). Dolphin remains under water for 2–3 min. Occurs exclusively in deep water channels (8–12 m) (Mann & Sargeant, 2003; Smolker et al., 1997)
Tail-out peduncle dive (tdpd) foraging	Dolphin performs distinct tail-out dives (flukes raised out of the water) or peduncle dives (peduncle or tail stock arched at dive, flukes partially submerged) while remaining submerged for 1–3 min after. Dolphin takes 1–12 breaths before diving again (Mann & Sargeant, 2003)

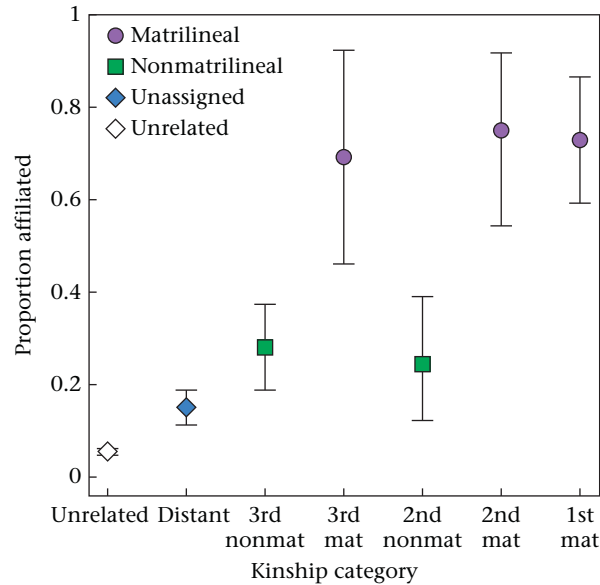


Figure A1. Proportion of significantly affiliated dyads in each potential kinship category analysed for this study. No first-degree nonmatrilineal pairs are present as only female–female relationships were included. Error bars are bootstrapped 95% confidence intervals. Kinship category was determined using a combination of pedigrees supplemented with genetic relatedness data (Pemberton, 2008). Genetic relatedness coefficients were determined using the dyadic maximum likelihood method (Milligan, 2003) implemented in the program COANCESTRY (Wang, 2011). Coefficients were used to assign pairs to kinship categories using the following thresholds: first-degree relatives ≥ 0.3925 ; second-degree relatives ≥ 0.1923 ; third-degree relatives ≥ 0.0935 ; distant relatives ≥ 0.0362 (see Foroughirad et al., 2019 for how thresholds were determined). We then combined all potential kinship categories into four categories for further analysis, based on similar affiliation probabilities: unrelated, distant, close matrilineal and close nonmatrilineal.

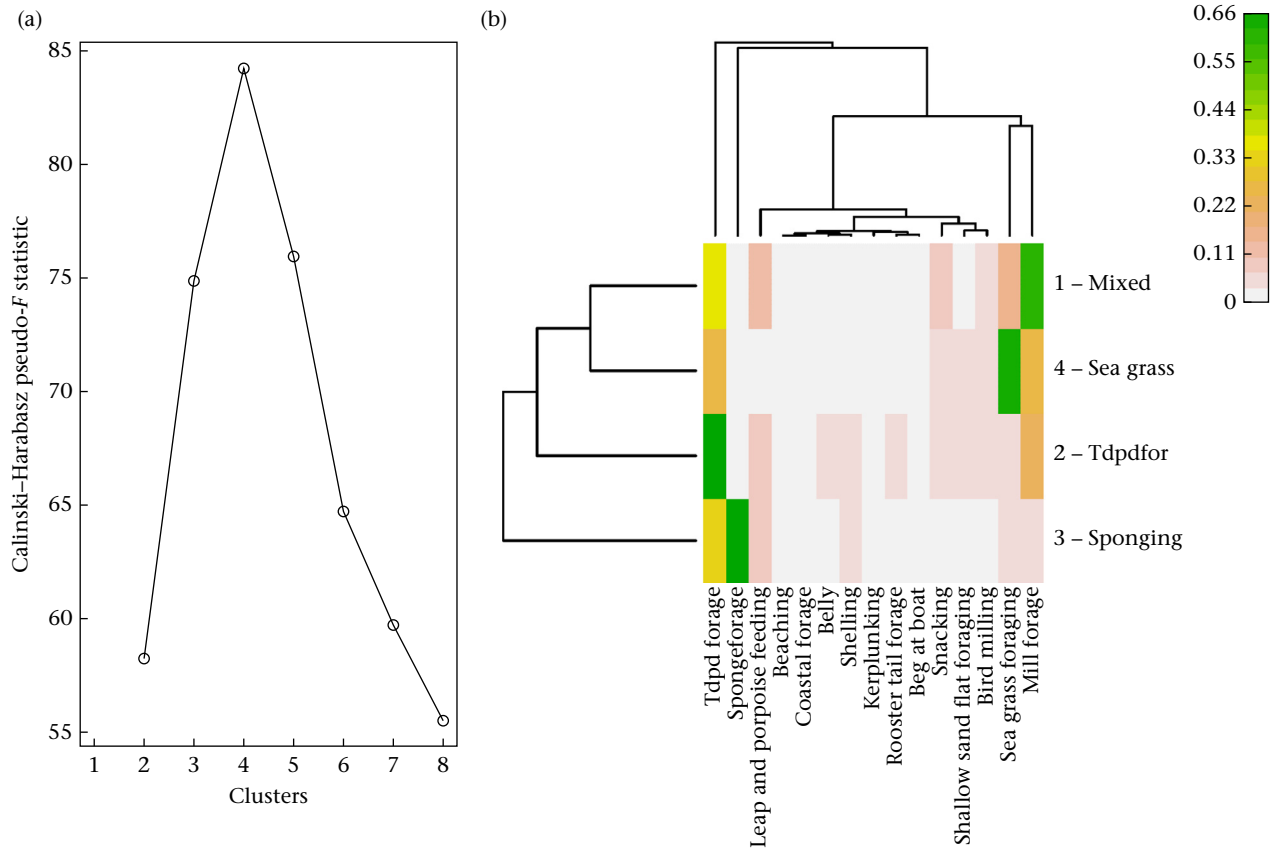


Figure A2. (a) The Calinski–Harabasz pseudo-*F* statistic was maximized for four clusters. (b) Mean proportion of each foraging activity attributed to each foraging cluster. Tdpdfor = tail-out peduncle dive foraging.