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Kinship influences social bonds among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*)

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Abstract
Male mammals employ a wide variety of mating strategies in order to increase their reproductive success, which in turn influence their social behavior. In some populations of bottlenose dolphins (*Tursiops* spp.), males cooperate in small groups or alliances to gain access to females for mating. However, the occurrence of these male cooperative groups has been predicted to occur only under certain social and ecological conditions, driven by factors such as differences in population density, operational sex ratio, and sexual size dimorphism. Here, we used generalized affiliation indices, social network techniques, and maternally and bi-parentally inherited genetic markers to investigate the affiliation patterns and genetic relatedness among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in a small embayment in South Australia. Photo-identification data and biopsy samples were collected in Coffin Bay from 2013 to 2015 through systematic boat-based surveys. We found that highly sighted male dolphins formed 12 social clusters composed of two to five individuals. Genetic analyses revealed that general male affiliation patterns were significantly correlated with mtDNA haplotype sharing. In addition, preferred affiliates showed significantly higher levels of genetic relatedness compared to casual and avoided male pairs. Our results corroborate theoretical expectations for the formation of social bonds in small delphinids and suggest that a high density of dolphins, with an expected skewed operational sex ratio and no apparent sexual size dimorphism, is likely to have favored the formation of strong male affiliations. In addition, the availability of genetic relatives within the population may have favored male affiliations based on kinship relationships.

Significance statement
Male bottlenose dolphins use different strategies to gain access to females, from single roving individuals, pairs or trios in alliances, to stable mixed-sex groups. Moreover, the role of kinship in the formation of male social bonds also varies within and among populations. This variability has been attributed to differences in ecological and intrinsic factors. Here, we studied the affiliation patterns and genetic relatedness in southern Australian bottlenose dolphins and demonstrated that kinship plays an important role in the formation of close male social ties. Furthermore, the results corroborate previous findings about the factors that contribute to the formation of male social bonds in these animals.

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Introduction

Social relationships among male mammals are usually determined by the strategies they use to increase their reproductive success (Emlen and Oring 1977; Clutton-Brock 1989). Males employ a variety of mating strategies to maximize the number of receptive females with whom they mate, such as physical contest (e.g., red deer, *Cervus elaphus*; Clutton-Brock and Parker 1992), or female defense, where solitary males accompanies a group of females and prevents access to other conspecifics (e.g., Blainville's beaked whales, *Mesoplodon densirostris*; McSweeney et al. 2007). Alternatively, males

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can employ a roving strategy, ranging widely to search and copulate with females while competing against other males (e.g., African elephants, *Loxodonta Africana*; Barnes 1982; sperm whales, *Physeter macrocephalus*; Whitehead 1990, 1993), or they can coerce females individually or in groups (e.g., orangutans, *Pongo pygmaeus*; Mitani 1985; bottlenose dolphins, *Tursiops* spp.; Smuts and Smuts 1993; Connor et al. 2000b). Moreover, these mating strategies may vary within and between populations of the same species living in different social and ecological conditions (Clutton-Brock 1989; Krützen et al. 2004a; Gehrt et al. 2008). Male mammals usually provide no parental care to their offspring, and therefore, their ability to mate with multiple females is largely determined by the spatial and temporal distribution of females, which in turn depends on ecological factors such as food availability and protection from predators (Emlen and Oring 1977; Clutton-Brock 1989; Silk 2002; Whitehead and Connor 2005).

Male alliances and coalitions, characterized by long-term cooperative relationships (Harcourt and de Wall 1992), are among the most complex social strategies of mammals (Connor and Krützen 2015). Alliances and coalitions have been described in various species of mammals such as chimpanzees (*Pan troglodytes*; Watts 1998, 2002), lions (*Panthera leo*; Packer et al. 1991; Grinnell et al. 1995), raccoons (*Procyon lotor*, Gehrt et al. 2008), otters (*Lontra canadensis*; Blundell 2002), cheetahs (*Acinonyx jubatus*; Caro and Collins 1987; Caro 1994), and bottlenose dolphins (Connor et al. 1992a; Möller et al. 2001; Parsons et al. 2003). These cooperative male relationships generally function to defend or gain access to females for mating (Packer et al. 1991; Connor et al. 1996; Möller et al. 2001; Wiszniewski et al. 2012b), increase rank (Goodall 1986), compete for territory (Caro 1994), improve foraging efficiency (Blundell et al. 2004), or reduce predation risk (Waterman 1997). The formation of alliances, however, is only expected to occur under certain social and ecological conditions (Packer et al. 1991; Caro 1994; Grinnell et al. 1995; Connor and Whitehead 2005; Whitehead and Connor 2005; Möller 2012). For example, using individual-based models, Whitehead and Connor (2005), suggested that alliances in mammals should be formed when male competition for receptive females is high and the benefits of group living (e.g., increased mating opportunities) offset the costs (e.g., feeding competition) or if by forming an alliance they are able to outcompete single males.

Kinship relationships have often been proposed as an important factor in the formation and maintenance of social bonds across several taxa (e.g., Packer et al. 1991; Parker et al. 1995; Parsons et al. 2003; Krützen et al. 2003; Chiyo et al. 2011; Holekamp et al. 2012; Carter et al. 2013). Hamilton's (1964) kin selection theory suggests that individuals can obtain indirect fitness benefits when associating with kin, such as those related to cooperative foraging, reduced aggression, protection from predators, increased growth rates, enhanced reproductive success, and shared social and ecological knowledge (e.g., Olsén and Järvi 1997; Silk 2002; Krützen et al. 2004a; Gerlach et al. 2007; Smith 2014). However, the influence of kinship in establishing and maintaining male cooperative associations vary in different species and populations, and it does not seem to be a prerequisite for the formation of alliances or coalitions (Packer et al. 1991; Mitani et al. 2000; Möller et al. 2001; Krützen et al. 2003; Parsons et al. 2003; Whitehead and Connor 2005; Wiszniewski et al. 2012b). For example, in some but not all bottlenose dolphin populations, kinship is an important factor for the establishment of male alliances (Möller et al. 2001; Krützen et al. 2003; Parsons et al. 2003). In male chimpanzees, closest associates are also not chosen on the basis of kinship (Mitani et al. 2000). Nonetheless, both strategies appear to provide fitness advantages to the members of an alliance (e.g., Möller et al. 2001; Krützen et al. 2004b; Wiszniewski et al. 2012b). In kinship-based alliances, the less successful individual may achieve inclusive fitness gains through kin selection if the other members of the alliance are successful (e.g., Packer et al. 1991; Krützen et al. 2004a). In non-related alliances, cooperation and assistance in the form of reciprocal altruism or mutualism at defending females or territories could also increase mating success of all alliance members (e.g., Feh 1999; Kays et al. 2000; Möller et al. 2001; Wiszniewski et al. 2012b).

In cetaceans, defense of receptive females by roving males is a common mating strategy; however, much variation is present in whether females are defended or coerced by individual males or alliances (Connor et al. 2000b). In bottlenose dolphins, male association patterns appear to vary widely between, as well as within, populations (Connor et al. 2000a; Möller 2012; Connor and Krützen 2015). In some populations, males may search for potential mates alone (Wilson 1995) or form stable mixed-sex groups (Lusseau 2003, 2007), while in others they can form alliances for gaining access to females (e.g., Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012a; Connor and Krützen 2015). The variability in male association patterns in dolphins has been mainly attributed to differences in population density, operational sex ratio, and sexual size dimorphism (Whitehead and Connor 2005; Möller 2012). In populations with small male-biased sexual size dimorphism, high population densities, and male-biased operational sex ratio (OSR), male dolphins may favor to form alliances for successfully monopolizing receptive females (Whitehead and Connor 2005; Möller 2012). In contrast, when population densities are low, males are larger than females, and/or with an even OSR, search for potential mates alone may be more advantageous (Whitehead and Connor 2005; Möller 2012;

Wiszniewski et al. 2012b). Male alliance formation has been reported for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay and Port Stephens, Australia (Möller et al. 2001; Connor and Krützen 2015), and for common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, USA (Wells et al. 1987), and The Bahamas (Parsons et al. 2003). In Shark Bay, male dolphins form alliances at different levels of association in an open social network: stable first-order alliances of two–three males cooperate to form consortships with individual females, while second-order alliances, which are aggregations of two first-order alliances, attack or defend females from other alliances (Connor et al. 1992a, b; Connor and Krützen 2015). Second-order alliances can also show preferred associations and compete against other alliances forming third-order alliances (Connor et al. 2011; Connor and Krützen 2015). In addition, a super-alliance composed of four to 14 dolphins, which function as labile coalitions to attack and defend females from other alliances has also been reported in Shark Bay (Connor et al. 1999).

The importance of kinship in alliance formation and stability in bottlenose dolphins also appear to differ among populations. In the Bahamas and Shark Bay populations, stable alliances are formed among related males (Parsons et al. 2003; Krützen et al. 2003), while in Port Stephens and Sarasota Bay, alliance membership was not associated with genetic relatedness (Möller et al. 2001; Owen 2003), suggesting that kinship is not a prerequisite for cooperation and alliance formation among male bottlenose dolphins. Möller (2012) proposed that alliances in delphinids could be formed irrespective of kinship relationships, but if related individuals of similar sexual and social maturity are available within the population, kin associations could be favored through kin selection.

Here, we used generalized affiliation indices (Whitehead and James 2015), social networks, and maternally and bi-parentally inherited genetic markers to investigate the affiliation patterns and genetic relatedness among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*; Charlton-Robb et al. 2011) in Coffin Bay, South Australia. Coffin Bay is a small protected embayment with high density of dolphins (1.57–1.70 dolphins/km^2; Passadore et al. 2017), similar male to female ratio of genetically sexed individuals (males = 46–52; females = 52–60; Passadore et al. 2017), but likely male-biased OSR considering an inter-birth interval for females similar to that reported to other bottlenose dolphin populations (3–6 years: reviewed in Connor et al. 2000a; Möller 2012), and no apparent sexual size dimorphism (FD-A and CP pers. obs.). The population, estimated at approximately 200 individuals (Passadore et al. 2017), is socially structured into two communities with discrete home ranges, in which individuals of the same community are on average more bi-parentally related than individuals from opposite communities (FD-A et al. unpubl. data). We predict that male

southern Australian bottlenose dolphins in Coffin Bay may form social clusters similar to the alliances reported for other high-density populations, with male-biased OSR and no apparent sexual size dimorphism, such as Shark Bay and Port Stephens. In addition, we expect that the formation of male social affiliations may be influenced by kinship as observed for Shark Bay's first-order alliances, given the known availability of genetic relatives within the communities identified in Coffin Bay.

Materials and methods

Study site and data collection

From March 2013 to October 2015, we carried out regular boat surveys in the inner area of Coffin Bay, South Australia (Fig. 1). Coffin Bay is a 123-km^2 reverse estuary characterized by shallow waters (< 12 m) and numerous different habitats. Kellidie and Mt. Dutton Bay are primarily dominated by seagrass, whereas Pt. Douglas has a wider variety of environments such as tidal sandflats, temperate reefs, seagrass, and deep sandy bottoms (Saunders 2012). The boat surveys were planned to cover all seasons and performed in calm sea conditions (Beaufort scale < 3). We followed pre-determined zigzag line transects created to cover all the habitat types within the inner area. Further details about boat surveys and the study area are provided in Passadore et al. (2017).

We approached all groups of dolphins sighted and recorded their GPS location, group size, and composition. Group size was estimated as the total number of dolphins within a 100-m radius (within a particular group; see below for group definition). We also attempted to collect photographs from each dolphin in a group using digital SLR cameras equipped with 80–300 mm and 100–400 mm zoom lenses. It was not possible to record data blindly because of the nature of our research involving wild dolphins. Individuals were identified using long-lasting marks on the edges of their dorsal fins (Würsig and Jefferson 1990), and the best images of each individual within a group were selected and sorted using Discovery v. 1.2 (Gailey and Karczmarski 2012). We followed the protocols described in Passadore et al. (2017) for classifying photographs.

Biopsy samples from identified non-calf individuals (see below) were collected using the PAXARMS remote biopsy system for small cetaceans (Krützen et al. 2002), or a biopsy pole system for bow-riding dolphins (Bilgmann et al. 2007). When using the pole system, dolphins were sampled only if they were photographed before they started bow-riding. Samples were preserved in a 20% dimethyl sulfoxide solution saturated with sodium chloride and then frozen in a − 20° freezer (Amos and Hoelzel 1991). In this study, we
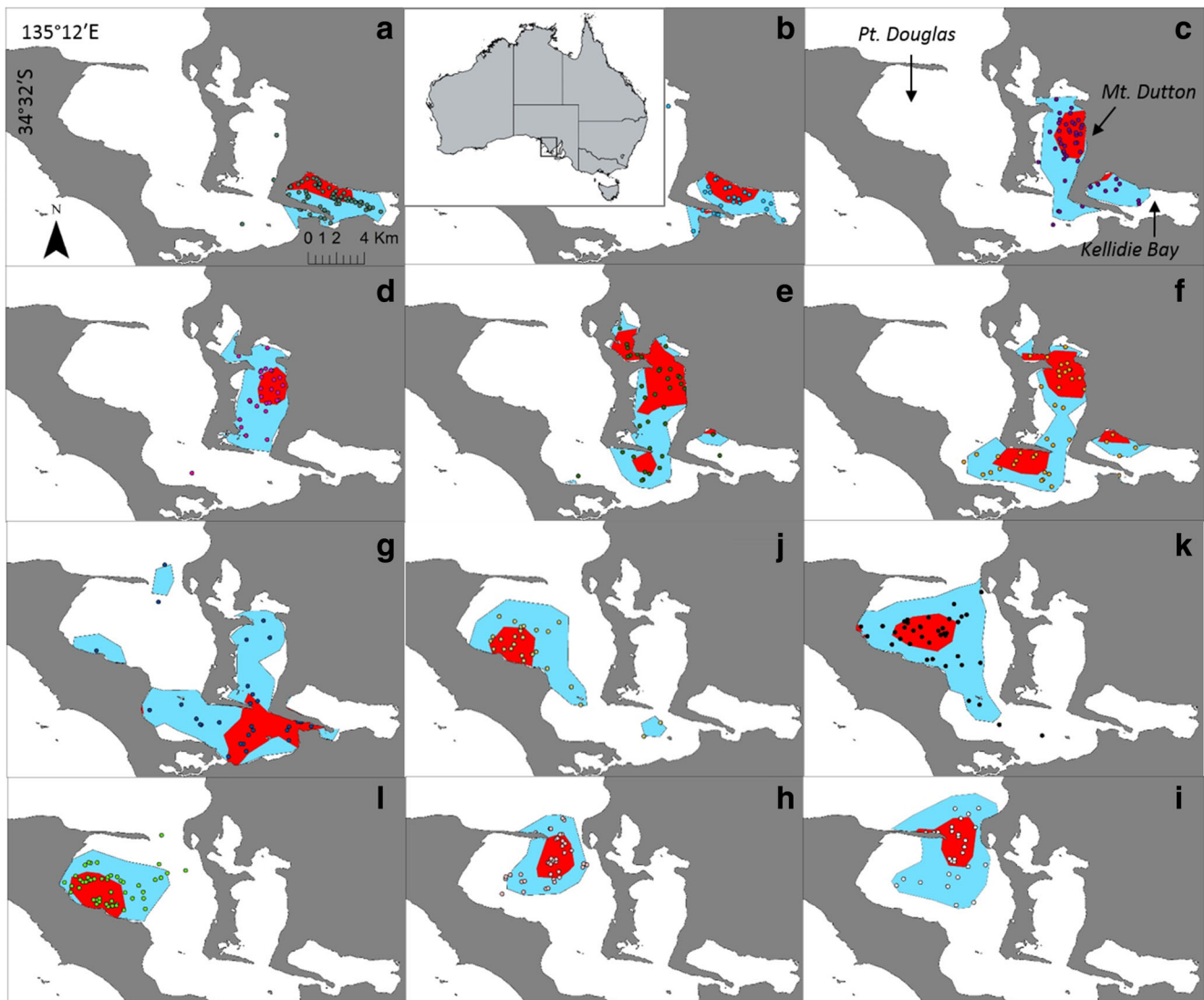
Fig. 1 Map of Coffin Bay, South Australia, showing kernel density estimates (KDE) for each of the 12 males social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified. The red shades represents core areas (50% KDE) and blue shades are the representative ranges (95% KDE) for each cluster, with lower case letters following those identified using Newman's modularity algorithm (Fig. 2). Colored dots represent the locations of distinct groups of males for each social cluster following the colors used in the social network (Fig. 2)

categorized all individuals > 1.5 m in length as non-calves and calves as all individuals ≤ 1.5 m in length and closely accompanied by a non-calf individual.

Genetic analyses

Total DNA was extracted from biopsy samples by proteinase K digestion followed by a salting-out protocol (Sunnucks and Hales 1996). A set of 11 polymorphic cetacean microsatellite loci were genotyped using the protocols described in Pratt et al. (2018). Samples were mixed with an internal size standard and run on an ABI 3130 Genetic Analyzer, with allele fragment sizes scored using GENEMAPPER v.4.1 (Applied Biosystems). MICRO-CHECKER v 2.2.3 (van Oosterhout et al. 2004) was used

to check for evidence of null alleles and allelic dropout, and deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium were assessed in GENEPOP v 4.2 (Raymond and Rousset 1995) based on the Markov chain method with 1000 iterations. Significance levels were adjusted using Bonferroni corrections (Holm 1979). There was no evidence of population genetic subdivision within the inner area of Coffin Bay (Pratt et al. 2018).

The sex of each dolphin was genetically determined by using the polymerase chain reaction (PCR) to amplify a fragment of the ZFX and SRY genes, following the protocol developed by Gilson et al. (1998). A mitochondrial DNA (mtDNA) control region fragment of approximately 450 base pairs (bp) in length was amplified by PCR with primers Dlp-5 (5′-CCA TCG WGA TGT CTT ATT TAA GRG GAA-3′) and

Dlp-1.5 (5′-TCA CCC AAA GCT GRA RTT CTA-3′) (Baker et al. 1993), as per conditions detailed in Möller and Beheregaray (2001). PCR products were sequenced on an Applied Biosystems 3130xl Genetic Analyzer. MtDNA sequences were aligned and cleaned using SEQUENCHER v5.2.4 (Gene Codes Corporation, Ann Arbor, MI, USA) and resulted in a 437-bp fragment.

Defining associations and estimating male affiliation indices

Dolphin groups were defined as all individuals within a 100-m radius and participating in similar behavioral activities following Wells et al. (1987). Groups with at least 75% of the individuals photo-identified (based on the visually estimated group size) were used for analysis, with the exception of identical groups resighted within the same day. An individual was only included in the first group if it was sighted in a particular day and if different individuals joined a group during a sighting, they were considered part of that group. In addition, only dolphins observed on more than 11 times (median number of sightings for the population) were included in social analyses to minimize the potential for false null associations due to the low number of sightings. We also controlled for the number of cumulative sightings of a given pair of dolphins during estimation of the generalized affiliation indices (GAIs) (see below). In the subsequent analyses, we only considered individuals genetically identified as males through the sexing analysis (above).

The strength of the associations between pairs of males was estimated using GAIs (Whitehead and James 2015). This method takes into account the effects of confounding structural factors that could influence the true pattern of associations between individuals. A matrix of association was constructed based on the half-weight index (HWI) because it prevents biases related to missing individuals in a group (Cairns and Schwager 1987), which is generally the case in cetacean studies.

Subsequently, we use multiple regression quadratic assignment procedures (MRQAP) for testing the partial correlations between the association indices and three predictor variables (while controlling for the other variables): spatial home range overlap, gregariousness (typical number of associates of an individual, Godde et al. 2013), and cumulative number of sightings for each dolphin pair.

We estimated individual home ranges as 95% utilization distributions using the AdehabitatHR (Calenge 2006) package in R v 3.2.3 (R Development Core Team 2014). We estimated the smoothing parameter (h) using the href function and then adjusted that value by visually examining individual ranges. A value of $h = 550$ was chosen as this provided the best representation of the data. Areas of home range overlap between male dolphins were then calculated in AdehabitatHR

(Calenge 2006) using the utilization distribution overlap index method (Fieberg and Kochanny 2005). Gregariousness, correlation analyses, and GAIs were estimated using SOCPROG 2.7 (Whitehead 2009).

Analysis of male affiliation patterns

To test for the presence of preferred and avoided associations among males, we used two different approaches. First, we randomly permuted the association data using the Bejder et al. (1998) test, with Whitehead's (2009) modifications, considering daily sampling periods to avoid demographic effects (Whitehead 1999). In this test, the association data was randomly permuted until p values stabilized using the standard deviations of the mean association indices as test statistics. Second, we converted raw residuals of the GAIs into deviance residuals for identifying pairs of preferred, causal, and avoided companionships (Whitehead and James 2015). Following the recommendations of Whitehead and James (2015), values above 2.5 were considered preferred companionships, between 2.5 and −2.5 casual pairs, and below −2.5 avoided affiliates.

We used Newman's modularity matrix clustering technique (Newman 2004, 2006; Newman and Girvan 2004) implemented in SOCPROG 2.7 (Whitehead 2009) to examine male social divisions and social network diagrams to display male clusters and affiliations (using NETDRAW 2.1.5.5; Borgatti 2002) Modularity values above 0.3 are considered to represent a meaningful description of the data (Newman 2004). Furthermore, to examine the spatial distribution of males, we estimated core (50%) and representative ranges (95%) for the social clusters identified using the utilization distribution method explained above considering group locations.

Genetic relatedness and kinship relationships

To assess the role that kinship plays on male affiliations, we examined maternal kinship and genetic relatedness between pairs of males included in the social analysis using maternally inherited mtDNA control region sequences and bi-parentally inherited microsatellites, respectively. With the mtDNA sequences, a matrix of pairwise haplotypes was constructed, with values of 1 or 0 for pairs with identical or different haplotypes, respectively. We assumed that males with the same mtDNA control region fragment, or haplotype, were from the same maternal lineage. With the microsatellite genotype data, we used the simulation method (with known allele frequencies) in COANCESTRY v 1.0.1.5 (Wang 2011) to determine that the triadic likelihood estimator (TrioML; Wang 2007) was the best estimator for our population data set. This estimator was subsequently used for estimating relatedness between male pairs using the same software. For evaluating the

correlation between the strength of affiliations and either mtDNA haplotype sharing or microsatellite bi-parental relatedness, we used Mantel tests with 10,000 permutations implemented in SOCPROG 2.7 (Whitehead 2009).

We also compared the frequencies of shared mtDNA haplotypes between pairs of preferred, casual, and avoided affiliates and tested for differences among classes using a randomization chi-square test with 10,000 Monte Carlo permutations. Average pairwise relatedness was also compared with random expectations among the three affiliation classes using the permutation method implemented in PERM (Duchesne et al. 2006). Further, we inferred sib-ship relationships using the likelihood method in COLONY v 2.0 (Jones and Wang 2010). We then compared the frequencies of estimated full-sibs, half-sibs, and non-sibs among preferred, casual, and avoided affiliates using a randomization chi-square test with 10,000 Monte Carlo permutations.

In addition, we examined whether individuals belonging to the same social cluster (identified by the modularity clustering technique) had higher average pairwise relatedness than those belonging to different clusters. We also estimated the frequencies of shared haplotypes within and between clusters and tested for differences using a randomization chi-square test (with 10,000 Monte Carlo permutations). For the microsatellite data, we compared average pairwise relatedness within and between clusters in COANCESTRY v 1.0.1.5 (Wang 2011) using 10,000 permutations. Finally, we compared frequencies of sib-ship relationships (full-sibs, half-sibs, and non-sibs) within and between male clusters using a randomization chi-square test (with 10,000 Monte Carlo permutations).

Results

We conducted 152 boat surveys in Coffin Bay and encountered 967 dolphin groups during the study period. Of these, 657 groups were retained after excluding identical groups resighted on the same day and groups with less than 75% of dolphins photo-identified. A total of 227 non-calf individual dolphins were cataloged during the study period. The estimated adult population size of marked males in Coffin Bay is 46–52 and 52–60 marked females (Passadore et al. 2017). In the subsequent social analyses, we included 42 adult males with more than 11 sightings represented in 376 groups.

Male affiliation patterns

MRQAP tests showed a significant correlation between the three structural predictor variables and the association indices, and therefore, they were all retained for calculating male GAIs (Table 1). Affiliation indices using deviance residuals ranged from −3.11 to 8.93 (mean = −0.47; SD = 1.83; n = 779). Preferred/avoided affiliates were detected among male

Table 1 Effectiveness of predictor structural variables in explaining association indices among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. Partial correlation coefficients and results of MRQAP tests were obtained using 10,000 permutations in SOCPROG 2.7 (Whitehead 2009)

Predictor variable	Partial correlation	MRQAP
Home range overlap	0.50	$p < 0.01$
Gregariousness	0.13	$p < 0.01$
Cumulative sightings per pair	0.16	$p < 0.01$

dolphins using the permutation method (observed SD = 0.13, random SD = 0.10, p = 0.003), and after transforming GAIs to deviance residuals we identified 55 preferred, 707 casual, and 17 avoided pairs of affiliates (Table 2).

Social network analysis based on Newman's modularity technique identified 12 social clusters (Q max = 0.47; Fig. 2; Table 3) that ranged in size from two to five individuals (median = 4; SE = 0.29). No single males were identified according to the modularity analysis. Social clusters showed a mixture of discrete and overlapping areas of space usage within Coffin Bay, with two to four clusters sharing any particular general area (Fig. 1). As expected, closer affiliates in the social network also showed similar areas of spatial usage.

Affiliation patterns and kinship

We obtained mtDNA haplotype and microsatellite data for 38 of the 42 male dolphins considered in the social analysis (Table S1). There was a significant correlation between pairwise haplotype sharing and affiliations (GAIs) between males (r = 0.1; n = 703; p = 0.03); however, there was no significant correlation between pairwise genetic relatedness and affiliations (r = 0.02; n = 703; p = 0.48).

We found significant differences for both mtDNA haplotype frequencies and mean pairwise genetic relatedness in respect to the type of affiliations that individuals formed. There was a higher frequency of shared mtDNA haplotypes (Fig. 3; $x^2 = 11.32$; df = 2; p = 0.003) among preferred than casual or avoided affiliates (Table 2). Similarly, mean pairwise

Table 2 Mean GAIs and genetic relatedness and count of haplotype sharing pairs for each affiliation category of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia

Affiliation category	N of pairs (N with genetic data)	Mean GAI deviance (SD)	Pairs sharing haplotype (%)	Mean genetic relatedness
Preferred	55 (49)	4.62 (1.36)	33 (67.3)	0.09[a]
Casual	707(639)	−0.83 (1.12)	317 (49.6)	0.07
Avoided	17(15)	−2.75 (0.19)	3 (20)	0.03[a]

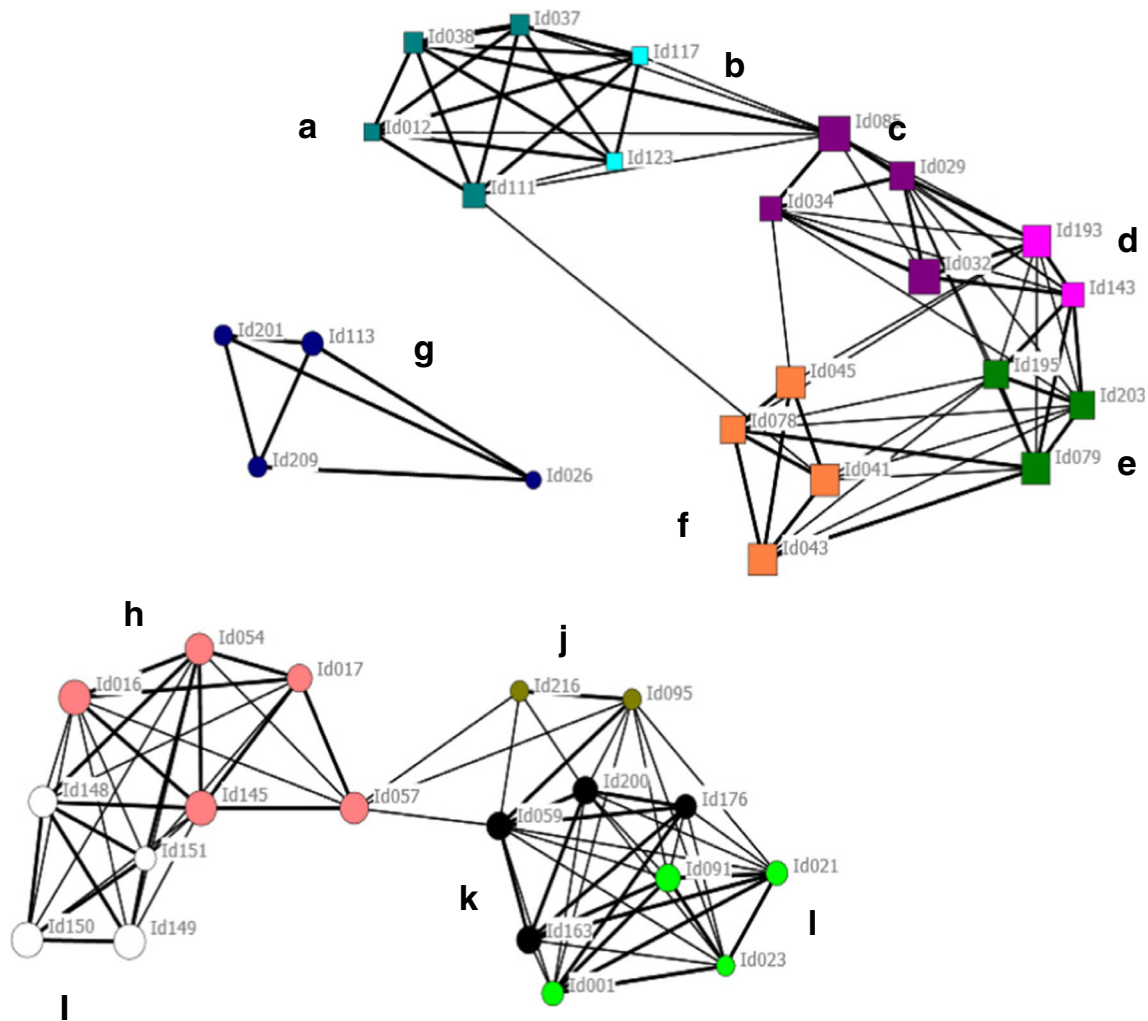[a] Mean genetic relatedness values that differed from random expectations

Fig. 2 Social network of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. The color of the nodes represents the clusters identified using Newman's modularity algorithm (denoted by a lower case letter). Node sizes represent the gregariousness of the individuals and the nodes shape the community: square and circles represents Mt. Dutton-Kellidie Bay and Pt. Douglas communities, respectively, according to results presented in FD-A et al. (unpubl. data). Edge width is proportional to the strength of the affiliations and for clarity are only displayed for affiliation indices greater than 0.94 (twice the mean affiliation index over all male individuals)

genetic relatedness was higher than expected between preferred affiliates and lower than expected between avoided affiliates ($p = 0.004$; Table 2). However, the sib-ship analysis did not detect significant differences in the proportion of kinship relationships among the three affiliation categories ($x^2 = 3.47$; df $= 4$; $p = 0.48$).

At social cluster level, we observed a higher frequency of mtDNA sharing within than between the identified social clusters (Fig. 4; Table 3; Table S1); however, this difference was non-significant ($x^2 = 2.97$; df $= 1$; $p = 0.08$). Similarly, there was a tendency for higher average pairwise genetic relatedness between individuals of the same cluster than between individuals of opposite clusters, but this difference was not statistically significant (Table 3; $p = 0.12$). Similarly, the sib-ship analysis did not reveal significant differences in the proportion of kinship relationships within and between clusters ($x^2 = 0.95$; df $= 2$; $p = 0.66$).

Discussion

In this study, we reveal that male bottlenose dolphins in Coffin Bay, South Australia, form non-random associations and social clusters. In addition, the strength of the associations, and the formation of preferred affiliations, was associated with bi-parental genetic relatedness and maternal kinship. The pattern of male associations in clusters resembles to that encountered in other bottlenose dolphin populations where males form alliances and higher-level alliances (e.g., Connor et al. 1992b; Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012a; Connor and Krützen 2015) and conforms to theoretical predictions for the formation of social bonds in male dolphins regarding density, OSR, and sexual size dimorphism (Whitehead and Connor 2005; Möller 2012).

Our analytical approach, which considered the effects of three structural variables when estimating affiliation indices, makes

Table 3 Mean GAIs and genetic relatedness and count of haplotype sharing pairs for each of the 12 male social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Social cluster IDs are represented as in Fig. 2

Cluster ID	N of individuals	Mean GAI deviance (SD)	Pairs sharing haplotype (%)	Mean genetic relatedness	Range of genetic relatedness
A	4	5.6 (1.23)	6 (100)	0.33	0–0.52
B	2	7.66 (0)	0 (0)	0	0
C	4	3.92 (0.60)	1 (100)[a]	0.4[a]	0.4–0.41
D	2	4.24 (0)	1 (100)	0.12	0.12
E	3	5.5 (0.39)	3 (100)	0.02	0–0.04
F	4	3.92 (0.67)	1 (33.3)[a]	0.01[a]	0–0.03
G	4	5.93 (0.67)	2 (33.3)	0.16	0–0.35
H	5	3.47 (0.41)	2 (20)	0.18	0–0.29
I	4	5.53 (0.71)	6 (100)	0.09	0–0.14
J	2	5.19 (0)	0 (0)	0	0
K	4	4.23 (0.14)	3 (100)[a]	0.05[a]	0–0.11
L	4	4.55 (0.29)	3 (50)	0.05	0–0.19
Within clusters		4.49 (1.71)	(62.2)	0.11	0–0.52
Between clusters		−0.79 (0.21)	(48.9)	0.09	0–0.64
All males		−0.47 (0.12)	(49.8)	0.08	0–0.64

[a] Clusters where genetic data are missing for some of the members

comparison with previous studies using association indices somewhat difficult. However, this method provides advantages when estimating the true social interactions experienced by animals (Whitehead and James 2015), in particular considering the strong correlation that has been reported between home range overlap and association indices in different taxa, including cetaceans (e.g., Frère et al. 2010; Carter et al. 2013; Best et al. 2014). For example, Whitehead and James (2015) found that in northern bottlenose whales (*Hyperoodon ampullatus*), the use of GAIs decreases the structuring of the population while revealing preferred affiliates that were not detected using only association indices. In our study, the use of this method seems to have produced a similar effect, generally decreasing the high-level

structuring. Thus, the results reported in other studies that considered only association indices may have overrepresented high-level and underrepresented low-level structuring due to the inclusion of structural noise in the social analyses. The use of GAIs into the study of animal societies represents a substantial improvement for overcoming these issues.

Male affiliation patterns in Coffin Bay

We identified preferred affiliates at pair level as well as 12 social clusters composed of two to five males in the Coffin Bay dolphin population. These preferred affiliations and social clusters are in general similar to the male alliances reported in other

Fig. 3 Proportion of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) with same and different mtDNA haplotypes with respect to affiliation categories identified in Coffin Bay, South Australia
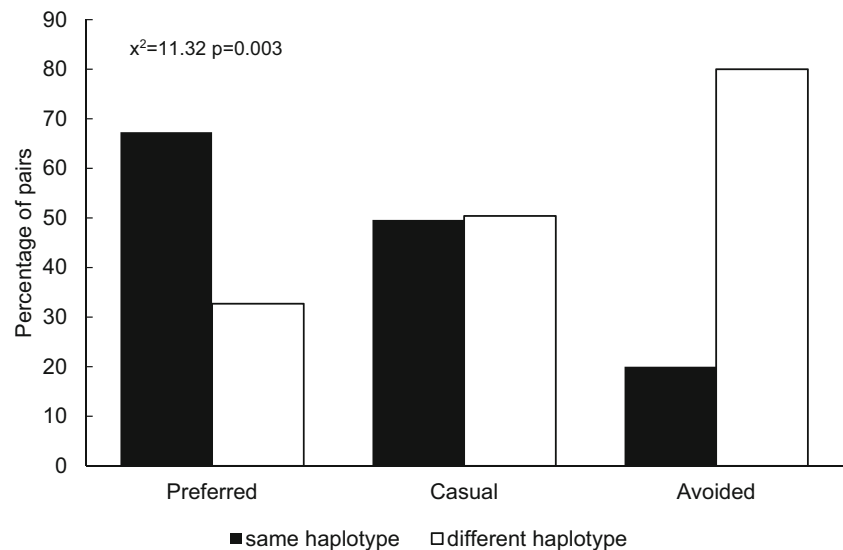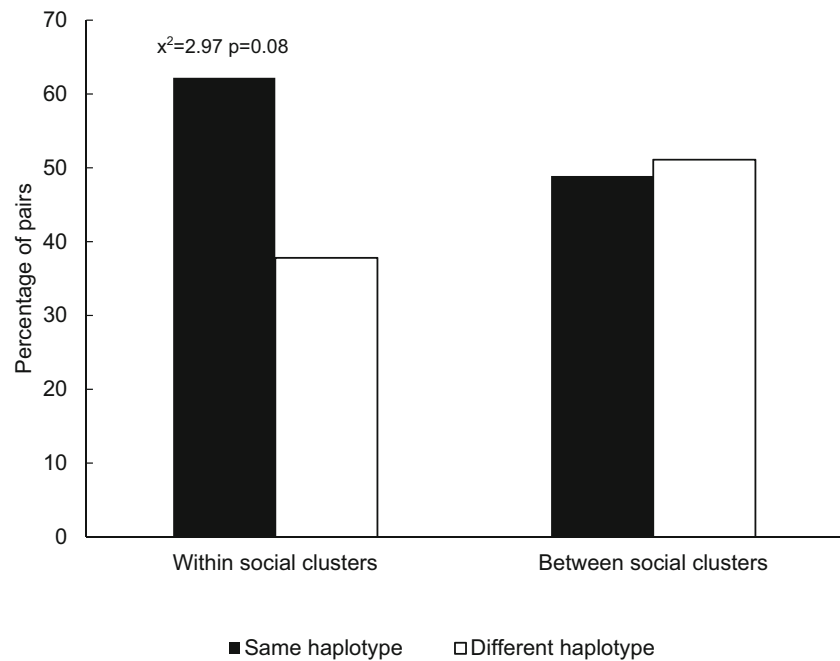

$x^2=11.32$ p=0.003

■ same haplotype □ different haplotype

Fig. 4 Proportion of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) with same and different mtDNA haplotypes within and between social clusters identified in Coffin Bay, South Australia

bottlenose dolphin populations, where pairs, trios, or larger aggregations of those (e.g., second-order, super-alliance) associate preferentially for gaining access to females for mating (Wells et al. 1987; Connor et al. 1992b; Möller et al. 2001; Parsons et al. 2003; Krützen et al. 2004a; Wiszniewski et al. 2012b). We observed a mixture of preferential areas of usage for males within Coffin Bay, with social clusters showing overlapping or discrete home ranges, similar to the mosaic of home ranges reported for male alliances in Shark Bay (Randic et al. 2012).

Six male social clusters are found within each dolphin community, suggesting a possible hierarchically organized social structure in Coffin Bay, which is characteristic of some bottlenose dolphin societies (e.g., Wiszniewski et al. 2009). We did not observe aggressive interactions among male dolphins or between members of different male social clusters, which suggest that similar to other dolphin populations (e.g., Connor et al. 2000a; Randic et al. 2012), defense of territory may be an unlikely explanation for the mosaic of spatial usage displayed by male social clusters. Alternatively, the social hierarchy among males of the population may be well established, and contests among male groups may therefore be rare. Considering that the distribution of male mammals is usually determined by that of females, which in turn largely depends on ecological factors (Emlen and Oring 1977; Clutton-Brock 1989; Silk 2002; Whitehead and Connor 2005), the pattern of spatial usage observed for male dolphins in Coffin Bay could be reflecting areas of high density of females within each community. Furthermore, differences in spatial ranges observed for males within the same communities could perhaps be explained by preferences for different ecological conditions (e.g., depth, benthic substrate, and productivity) between the different bays in the study area.

The presence of preferred associates and alliances in male dolphins has been proposed to occur in populations with small male-biased sexual size dimorphism and OSR, and in areas of high density of dolphins, where competition for receptive females is likely to be high (Whitehead and Connor 2005; Möller 2012). In Coffin Bay, there is a large density of dolphins, no apparent sexual size dimorphism, and similar male to female ratio of sexed individuals (Passadore et al. 2017) but likely male-biased OSR (below). Moreover, the pattern of spatial usage of the social clusters suggests that males do not rove over extensive areas in search of receptive females. Assuming an inter-birth interval similar to that reported for other bottlenose dolphin population (3–6 years: reviewed in Connor et al. 2000a; Möller 2012), the availability of receptive females at any given time may be low, and therefore, the OSR is likely to be male-biased, which in turn should promote competition among males for mating with females. Based on our results, we suggest that preferred male affiliates and the social clusters formed among male dolphins in Coffin Bay may function to facilitate access to, or for coercion of, receptive females, as has been previously observed in other populations where bottlenose dolphin alliances occur (e.g., Möller et al. 2001; Wiszniewski et al. 2012b; Connor and Krützen 2015). However, it is important to mention that our results point towards greater variation in the size of male social groups compared to other study populations where pairs and triplets have been reported as the norm for male bottlenose dolphin alliances (e.g., Connor et al. 1992b; Möller et al. 2001; Parsons et al. 2003). These differences may be attributed to how individuals were categorized within alliances in different studies. For example, individuals in one study were considered allied if they were preferred associates, reciprocal closest associates or, if

not, the second closest associate and also observed jointly herding females (Connor et al. 1992b). In our study, we based the social groupings on Newman's modularity algorithm (Newman and Girvan 2004; Newman 2004, 2006), which was developed to find the best partitioning of the data set into social clusters, thus allowing more flexibility in the aggrupation of male clusters compared to other studies. Further studies in Coffin Bay examining and comparing male behavior, access to females, and home range sizes, combined with paternity analyses could provide important insights into the mechanisms promoting and maintaining the association patterns observed among male dolphins in our study population.

The influence of kinship on male bonding

Maternal kinship was significantly correlated with the strength of affiliations between male pairs. Likewise, we found significant differences for both mtDNA haplotype frequencies and mean bi-parental genetic relatedness in respect to the type of affiliations that individuals formed. There was a higher frequency of shared mtDNA haplotypes among preferred than casual or avoided affiliates. Similarly, mean pairwise genetic relatedness was higher than expected among preferred affiliates and lower than expected among avoided affiliates. At social cluster level, maternal kinship and bi-parental relatedness while higher within than between groups, it was not statistically significant. The sib-ship analyses also suggested that preferred affiliates and members of the same clusters were not necessarily close relatives (i.e., full- or half-sibs).

Overall, pairs of males that spent more time together or that preferentially affiliate to each other were genetically more related. These results point towards kin selection (Hamilton 1964; Smith 2014) potentially playing a role in the formation of male social bonds in the Coffin Bay population, at least to some degree. This is similar to the patterns encountered in other male mammals such as elephants (*Loxodonta africana*; Chiyo et al. 2011) and lions (Packer et al. 1991), as well as in bottlenose dolphins inhabiting the Bahamas and Shark Bay. In these two populations, mean genetic relatedness was higher within than between male alliances (Krützen et al. 2003; Parsons et al. 2003). However, in Coffin Bay, some social clusters showed on average low genetic relatedness among their members, suggesting that kinship is not the only driving force underlying male social group formation. As has been reported in other mammals (e.g., chimpanzees; Mitani et al. 2000) and bottlenose dolphins (Möller et al. 2001; Owen 2003; Wiszniewski et al. 2012b), other mechanisms such as reciprocal altruism or mutualism could be operating in male groups, including in our study area. Alternatively, a dilution effect of relatedness values at cluster level may have affected the results due to some pairs exhibiting low genetic relatedness within social groups. In Shark Bay, bottlenose dolphins showed different patterns of relatedness in respect to the types of alliances they formed (Krützen et al.

2003). In first- and second-order alliances (2–6 individuals), males were more related than expected by chance, in contrast to males composing the larger super-alliance (14 individuals) which were not (Krützen et al. 2003). This suggests that different mechanisms for male affiliations can be operating on male social groups of the same population. Our results also suggest that male social groups or preferred affiliates were not necessarily formed among close kin or siblings. One explanation for this could be low power of the sib-ship analyses due to the number of genetic markers used to separate different sib-ship categories or the number of observations in each category estimated. Alternatively, the formation of preferred affiliates or social groups among siblings may not be viable option because of differences in age and sexual and social maturity (e.g., elephants; Chiyo et al. 2011).

The results of this study corroborates theoretical expectations proposed by Möller (2012), who suggested that if related individuals are available for associating, then kin selection may be an important factor promoting social bonds in dolphins. In Coffin Bay, female association patterns and cluster membership were found to be correlated with maternal kinship and bi-parental relatedness (Diaz-Aguirre 2017). In addition, females with dependent calves were more likely to associate with others in similar reproductive condition (Diaz-Aguirre 2017). Altogether, these results suggest that males during their young years may have numerous opportunities to develop and establish relationships with other males that belong to the same female social clusters, where relatives may occur, thus enhancing the chances for kin-based associations to form. However, as previously suggested in other studies (Möller et al. 2001; Krützen et al. 2003; Möller 2012; Wiszniewski et al. 2012b), kinship is not a prerequisite for the formation of male social bonds, and other mechanisms may co-exist within the same population.

Based on our results, we propose that kin selection may be an important factor influencing at least some of the strong male associations observed in Coffin Bay bottlenose dolphins. Further behavioral and genetic studies evaluating the reproductive success of males composing different social clusters may provide important information about the function and potential reproductive skew in these groups. This in turn could be valuable for testing the importance of kin selection as well as other evolutionary mechanisms, which may be operating in the formation and maintenance of male social bonds in this population. Our findings add to the growing evidence of complex male social behavior in bottlenose dolphins and highlight that social, genetic, intrinsic, demographic, and ecological factors are likely to contribute to the formation and maintenance of male bonding in dolphins.

Data availability The data sets used in this study are available from the corresponding author on request.

Compliance with ethical standards

Ethical approval All procedures performed in this study were in accordance with the ethical standards of Flinders University Animal Welfare Committee, approval number E310 and under permits to undertake scientific research: E26171-1, E26171-2, E26171-3, and MR00056-1 from the Department of Environment, Water and Natural Resources (DEWNR), South Australia, and under S115 ministerial exemptions (MEs: 9902601, 9902660, 9902714, and 9902779) from Primary Industries Resources South Australia (PIRSA).

Conflict of interest The authors declare that they have no conflict of interest.

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