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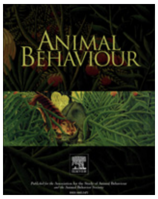

Female bisexual kinship ties maintain social cohesion in a dolphin network

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Social assortativity, where individuals preferentially mix with certain conspecifics, is widespread among a diverse range of taxa. Animals may assort by a variety of characteristics and receive substantial benefits from these interactions, such as a reduction in predation risk, increased foraging efficiency or greater access to resources. We investigated the social network structure of an embayment population of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, using a long-term photoidentification data set, and examined the impact of sex and kinship in maintaining the cohesion of the social network. We applied recently developed social network techniques that incorporate uncertainty into statistical measures to delineate four smaller social groups within two previously defined communities. Temporal stability of associations within social groups was substantially greater than among individuals from different groups. We also found that the dolphin population was not strongly segregated by sex and both males and females had similar degrees of social connectivity in the network. Moreover, genetic analyses showed that relatedness had a greater influence on female than on male social relationships, as association strength was positively correlated with genetic relatedness between females and between female and male pairs, but not between males. These results suggest that females and males may target kin interactions with females and that kinship appears to be important for maintaining the cohesiveness of this dolphin social network.

Social assortativity, where individuals preferentially mix with conspecifics sharing similar traits, is widespread among a diverse range of taxa. Animal populations assort by a variety of characteristics including sex (reviewed in Ruckstuhl 2007), age (Smith et al. 2002; Silk et al. 2006a; Wolf et al. 2007; Manno 2008), kinship (reviewed in Silk 2002), reproductive status (Sundaresan et al. 2007; Manno 2008; Möller & Harcourt 2008), morphological traits (Croft et al. 2005), sociability (Lusseau et al. 2006; Manno 2008), behaviour (Pike et al. 2008) and familiarity (Pinter-Wollman et al. 2009). The prevalence of assortative mixing may relate to benefits that individuals obtain by associating with others that have similar capabilities or share similar resource requirements. This includes a potential reduction in predation risk, increased foraging efficiency and greater access to resources (Krause & Ruxton 2002). Social assortativity combined with individual variation in connectivity can substantially affect a population's social network structure and have significant consequences for population-level processes (Krause et al. 2007; Wey et al. 2008). For instance, shorter path lengths between individuals increase the rate of information exchange and disease transfer through the population, while tighter clustering and assortative mixing of individuals restricts diffusion to smaller subgroups in the network (e.g. Guimarães et al. 2007; Naug 2008).

Large variability in centrality measures is also a common feature of many animal social networks. Individuals with high centrality are either connected to many others or have associates from different social clusters. These individuals are often few, but can have a disproportionate effect on the social cohesion of the population (Lusseau & Newman 2004; Williams & Lusseau 2006), quality and duration of individual and social group interactions (Flack et al. 2006; Manno et al. 2007), group-level decisions (Lusseau 2007) and reproductive success of close associates (McComb et al. 2001). As a result, the consequences of losing individuals from a population, through either death or emigration, vary not only with population size but also with the individual's functional role and the structural properties of the network (Lusseau & Newman 2004; Williams & Lusseau 2006; Manno 2008; but see Flack et al. 2006).

Bottlenose dolphins (genus *Tursiops*) commonly live in fission–fusion societies, where individuals have been shown to assort preferentially by sex (Wells et al. 1987; Smolker et al.

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1992; Lusseau & Newman 2004); females by their reproductive state (Möller & Harcourt 2008) and kinship (Duffield & Wells 1991; Möller et al. 2006), and males by kinship in some populations (Krützen et al. 2003; Parsons et al. 2003), but not in others (Möller et al. 2001; Owen 2003). Associations between females and males in bottlenose dolphin societies appear to be primarily driven by the reproductive state of females and mating season (Connor et al. 2000; Owen et al. 2002). However, the influence of genetic relatedness on associations between females and males and the potential role of sex and kinship in maintaining the cohesiveness of dolphin social networks have not been examined.

Kin selection theory predicts that individuals can obtain indirect fitness benefits by cooperating with kin (Hamilton 1964). Females across several mammalian taxa have been found to direct their affiliative behaviour towards maternal relatives. These preferential associations may be displayed in various ways including spatial proximity (Gero et al. 2008; Wolf & Trillmich 2008), physical contact (e.g. grooming, Silk et al. 2006a; Perry et al. 2008), coalitionary support during agonistic interactions (Smith et al. 2010) and allomaternal care (O'Brien & Robinson 1991; Jesseau et al. 2009). Furthermore, it appears that females may receive substantial fitness benefits from these targeted kin interactions (reviewed in Silk 2007). Males, on the other hand, associate closely and cooperate with male relatives more rarely, but do so in some populations of highly social species such as lions, *Panthera leo* (Packer et al. 1991) and chimpanzees, *Pan troglodytes* (Mitani 2009). In only very few societies are female and male relatives known to form strong, long-term social bonds (e.g. pilot whales, *Globicephala melas*: Amos et al. 1993; bonobos: *Pan paniscus*, Hohmann et al. 1999; killer whales, *Orcinus orca*: Baird & Dill 2000; baboons, *Papio cynocephalus ursinus*: Palombit et al. 2001; humans, *Homo sapiens*: Neyer & Lang 2003). Embayment populations of bottlenose dolphins generally show a high degree of site fidelity; females are highly philopatric (Duffield & Wells 1991; Connor et al. 2000; Möller & Beheregaray 2004) and males also show some degree of philopatry (Krützen et al. 2004; Möller & Beheregaray 2004; Sellas et al. 2005). Bottlenose dolphins also appear capable of identifying maternal kin by their unique acoustic signature whistles (Sayigh et al. 1990; Janik et al. 2006). Together, these observations suggest that opportunities for kin selection to act on the social behaviour of both females and males are present within these populations.

Recently, a hierarchical organization in association patterns was found for an embayment population of Indo-Pacific bottlenose dolphins, *T. aduncus*, inhabiting Port Stephens, southeastern Australia. In this area, two mixed-sex communities inhabiting ecologically different regions of the embayment were subdivided into several smaller groups (Wiszniewski et al. 2009). In the present study, we critically assessed the delineation of individuals into smaller social groups using recently developed network techniques and examined the temporal stability of associations within these groups. Using this information, we then examined the role of sex and kinship in maintaining the cohesion of the dolphin social network and tested whether individuals born locally in Port Stephens are more integrated in the social network than immigrants. To the best of our knowledge, this is the first study to assess the influence of kinship on long-term associations between male and female bottlenose dolphins.

METHODS

The study was conducted in the Port Stephens embayment, located 200 km north of Sydney on the New South Wales coast of southeastern Australia (32°42′S, 152°06′E). Indo-Pacific bottlenose dolphins inhabiting the embayment are genetically distinct from communities on the adjacent Hunter coast population, while the two socially segregated eastern and western communities within Port Stephens also show some genetic differences (Möller et al. 2007; Wiszniewski et al. 2010). The core areas of the two communities coincide directly with a change in habitat type: the larger eastern community consists of at least 90 dolphins and inhabits a typically marine environment with sandy bottom and sea grass beds, while about 30 western individuals range over a larger and more estuarine region of the port, characterized by a mud bottom and mangroves (Wiszniewski et al. 2009).

Data on school membership were obtained from 180 systematic transect surveys conducted during seven breeding seasons (December to April) and three nonbreeding seasons (June to August) between 1998 and 2007 using standard photoidentification techniques (for further details see Möller et al. 2006; Wiszniewski et al. 2009). No photoidentification surveys were conducted in 2003 and 2004. A school was defined as all individuals within a 100 m radius (Irvine et al. 1981), and if travelling, the animals were heading in the same direction (Shane 1990; Möller et al. 2006). Schools were excluded from analyses if a minimum of 75% of the estimated school size were not reliably photographed, a fusion event occurred during photoidentification, an identical school was resighted during the day, or individuals were reencountered within 1 h of the first sighting with different associates (Wiszniewski et al. 2009).

Sample Collection and Genetic Analyses

Skin samples for this study were collected from adults and juveniles during sampling surveys in the Port Stephens embayment between 1999 and 2008. We used the PAXARMS biopsy system (PAXARMS N.Z. Ltd, Timaru, New Zealand), which was specifically designed for sampling small cetaceans and has been shown to cause minimal short-term impacts to the dolphins (Krützen et al. 2002). Samples obtained were usually 5 mm in diameter and 1 cm in length and included both skin and blubber tissue. Individuals were recognized at the time of sampling using photoidentification techniques. Our targeted sampling scheme for known individuals and the short time allocation for sampling individuals within a school ensured minimal stress to the dolphins. Biopsy sampling and photoidentification surveys were conducted under licences from the Department of Environment and Climate Change and Marine Parks Authority and under approval by the Macquarie University Animal Ethics Committee.

Samples were preserved in 20% dimethyl sulphoxide saturated with sodium chloride (Amos & Hoelzel 1991) or 100% ethanol. The sex of individuals was determined by extracting DNA from skin samples of identified individuals using the salting-out procedure (Sunnucks & Hales 1996) and amplifying fragments of the *ZFX* and *SRY* genes using the polymerase chain reaction (PCR; as described in Möller et al. 2001). Females were alternatively identified by the repeated presence of a dependent calf (Möller et al. 2006).

Two sets of genetic markers were used to test for an association between genetic relatedness and association patterns among individuals: a 460-bp fragment of the mitochondrial DNA control region, which was amplified by PCR according to Möller & Beheregaray (2001) and a set of 10 nuclear DNA microsatellite loci markers (EV1, EV14: Valsecchi & Amos 1996; MK5, MK6, MK8, MK9: Krützen et al. 2001; TG20: Caldwell et al. 2002; KW2, KW9, KW12: Hoelzel et al. 2002). PCR conditions were as reported in Möller & Beheregaray (2004), except for EV14, KW9 and TG20, where each 10 µl radiolabelled reaction contained 0.6 mM $MgCl_2$ and was amplified using a 32-cycle 'touchdown' (59–51 °C for EV14 and KW9; and 63–55 °C for TG20). Tests for significant deviation