



Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins

Joanna Wiszniewski^{a,b,*}, Simon J. Allen^{b,1}, Luciana M. Möller^{a,b}

^a Molecular Ecology Laboratory, Department of Biological Sciences, Macquarie University

^b Marine Mammal Research Group, Graduate School of the Environment, Macquarie University

ARTICLE INFO

Article history:

Received 19 October 2008

Initial acceptance 28 November 2008

Final acceptance 10 March 2009

Published online 23 April 2009

MS. number: 08-00673

Keywords:

association pattern
bottlenose dolphin
community structure
ecological constraint
kinship
social network
Tursiops aduncus

We investigated community structure and association patterns for a small population of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, inhabiting the Port Stephens embayment in southeastern Australia. Association data for 120 regularly sighted individuals were obtained from seasonal photo-identification surveys collected over 7 years (1998–2007). Using a combined cluster and social network analysis approach, we found association patterns between dolphins were hierarchically structured, where two mixed-sex communities were subdivided into smaller, temporarily dynamic social groups. Community membership corresponded to differences in individual ranging patterns and habitat occupation. The larger eastern community inhabits a typically marine environment, while individuals of the western community range over a larger area that is dominated by estuarine processes. Both communities were composed of long-term preferred companions; however, the degree of social cohesion differed considerably between the two communities. Associations between individuals were considerably stronger and temporally more stable in the western community. Western individuals also had significantly fewer preferred associates despite living in similar-sized schools. Finally, in direct contrast to associations within each community, intercommunity associations were highly variable and resulted primarily from aggregative behaviour. We propose the segregation of communities resulted from individual adaptation to local environmental conditions, facilitated by individual variability in association preferences. The disparity in association patterns between communities may have resulted from a combination of ecological, population density, kinship and anthropogenic factors.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

High rates of group composition changes in fission–fusion societies are generally an adaptive response to the dynamic interaction of ecological variables such as prey resource availability and predation risk (Wrangham 1982). The stability of social relationships in a population, however, increases when net benefits of stable, cooperative relationships with relatives or familiar individuals outweigh costs, such as increased resource competition (Krause & Ruxton 2002). Long-term social bonds can increase the reproductive fitness of individuals through a variety of mechanisms such as enhanced breeding success (e.g. in red howler monkeys, *Alouatta seniculus*: Pope 2000) and information exchange (e.g. in African elephants, *Elephas Maximus*: McComb et al. 2001), or reduced predation risk (e.g. in delphinids, Gowans et al. 2008), aggression (e.g. in spider monkeys, *Ateles geoffroyi*: Asensio et al.

2008) and risk of infanticide (e.g. in bottlenose dolphins, *Tursiops* spp. Dunn et al. 2002). In fission–fusion societies, such as those of African elephants, bottlenose dolphins and some primates, a multitiered hierarchical structure of social relationships provides the flexibility for individuals to aggregate for a period of time when fitness benefits of sociality are high (Takahata et al. 1994; van Schaik 1999; Connor et al. 2000; Wittemyer et al. 2005), while maintaining minimal group size governed by local ecological and social pressures (Dunbar 2002). For instance, Wittemyer et al. (2005) demonstrated that social cohesion in a hierarchically structured African elephant population decreased disproportionately at higher social tiers when food resources were significantly scarcer, and the number of interacting units was not fixed, but changed over time with the growth of the population. A hierarchical organization has been clearly demonstrated for male bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*), where the size and presence of male alliances in a population are correlated with predation risk and population density factors (Connor et al. 2000). Second-order alliances, which consist of two or more first-order alliances, have been observed in one bottlenose dolphin population and appear to form temporarily as a consequence of

* Correspondence: J. Wiszniewski, Department of Biological Sciences, Macquarie University, NSW 2109, Australia.

E-mail address: jwisznie@bio.mq.edu.au (J. Wiszniewski).

¹ S. J. Allen is now at the Murdoch University Cetacean Research Unit, Centre for Fish and Fisheries Research, Faculty of Sustainability, Environmental and Life Sciences, Murdoch University, South Street, Murdoch, WA 1650, Australia.

high competition between males for access to a limited number of oestrous females (Connor et al. 2000).

Social network analysis, developed in the physical sciences and extensively applied to human social systems, is a powerful analytical tool that describes relationship patterns, individual-levels of connectivity and group structure within a population (reviewed in Boccaletti et al. 2006). The recent application of network theory to the study of nonhuman social behaviour has greatly facilitated our understanding of how ecological, social and population-level factors influence association patterns (e.g. Croft et al. 2005; Flack et al. 2006; Sundaresan et al. 2007; Wolf et al. 2007), and how individual behaviour and network structure subsequently influence the reproductive success of individuals (e.g. McDonald 2007). Studies on bottlenose dolphins are routinely based on community-level differences in social behaviour (Lusseau et al. 2006), foraging specializations (Chilvers & Corkeron 2001; Sargeant et al. 2007), habitat utilization (Rossobach & Herzing 1999) and dispersal levels (Krützen et al. 2004; Sellas et al. 2005; Möller et al. 2007), especially to examine the effect of various sociological factors on populations resident in particular areas. Where communities are not discretely structured, however (e.g. Chilvers & Corkeron 2001; Lusseau & Newman 2004; Lusseau et al. 2006), recent statistical developments in network techniques (Newman 2004, 2006a; Lusseau et al. 2008) can help detect statistically significant divisions in the population, thereby providing novel insights into the selective forces driving sociality. In one population of common bottlenose dolphins, *T. truncatus*, Lusseau & Newman (2004) demonstrated that community division probably arose from preferential assortment of individuals by sex and age class, while an absence of assortative mixing by degree (number of associates an individual has) promoted resilience of the network to fragmentation. These network techniques provide a means to understand the complex interaction of various selective socioecological pressures responsible for the diverse range of patterns in the social

organization observed between (Gowans et al. 2008), as well as within (Connor et al. 1999), bottlenose dolphin populations.

The *T. aduncus* population in Port Stephens is relatively small (around 90 individuals considered residents based on photo-identification between 1998 and 2000; Möller et al. 2002) and genetically distinct from communities ranging on the adjacent coastline (Möller et al. 2007). Female bottlenose dolphins show high site fidelity to the area, with most falling into one of four social clusters (Möller et al. 2006). Closely associating females tend to be more genetically related; however, the presence of nonrelated females in these clusters indicates that other factors, such as female reproductive state (Möller & Harcourt 2008), play a role in determining association levels. Typical of other bottlenose dolphin populations (Connor et al. 2000), males are often found in alliance partnerships (Möller et al. 2001). The alliances in Port Stephens consist of randomly related individuals and facilitate low to moderate levels of genetic exchange with coastal communities (Möller et al. 2007). From these Port Stephens studies, different social groups appear to use two ecologically different regions in the port. The eastern basin is typically a marine environment, with a strong tidal influx of coastal waters, sandy substrate and large areas of sea grass, while the deeper western port is dominated by estuarine processes, including turbid, freshwater outflow from rivers and a muddy benthic habitat (Fig. 1). This study aimed to determine whether significant community structure was present in the population using recently developed network techniques. We define a community here as a set of individuals that are behaviourally discrete from neighbouring dolphins and where most associations occur between community members (Whitehead 2008b). Since ecological constraints appear to drive sociality in gregarious animals, we predicted differences in spatial and temporal patterns of associations would occur between communities inhabiting different environments. We anticipate these results will add to the current socioecological framework that attempts to identify and understand the complex interaction of factors driving fission–fusion dynamics in general.

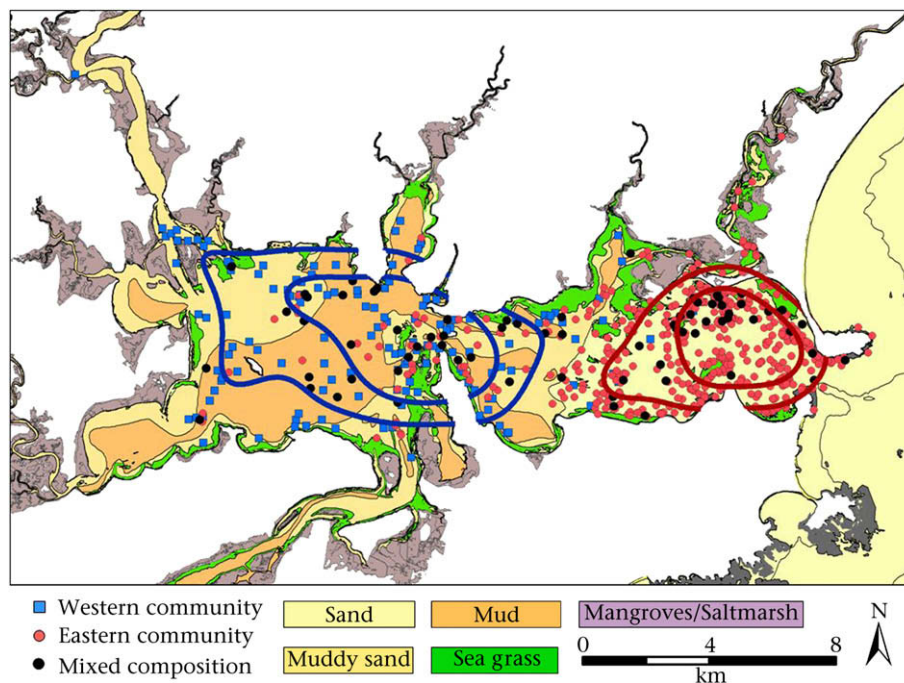


Figure 1. Habitat map of the Port Stephens embayment in New South Wales displaying dolphin school sightings between 1998 and 2007. Blue squares denote schools consisting of western dolphins, red circles represent eastern individuals and black circles represent schools with both eastern and western individuals. Fixed kernel density distributions are displayed for both west (blue) and east (red) communities, where inner and outer volume contour lines represent the 25% core area and 50% home range.

METHODS

Study Site and Data Collection

Port Stephens (PS) is a relatively enclosed embayment of approximately 166 km² in surface area and is located 200 km north of Sydney on the New South Wales coast of southeastern Australia (32°42'S, 152°06'E). Data on school membership were obtained from 180 systematic transect surveys that covered the main areas of the port during seven breeding (December–April) and three nonbreeding (June–August) seasons from the 1998/1999 summer to 2007. All surveys were conducted in calm waters (Beaufort scale ≤ 3) and good light conditions. A total of 241 adult dolphins in 1084 schools were encountered (breeding season: $N = 704$, mean \pm SE = 101 ± 8.7 ; nonbreeding season: $N = 365$, mean \pm SE = 121 ± 10.3). 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). For each sighting, the global positioning system (GPS) location, time, school size, number of calves and behaviour were recorded. Sizes of schools were estimated in the field by at least two trained individuals. Estimates were later adjusted if the number of uniquely recognized dolphins exceeded the number of adults estimated in the field. Dolphins were photographed and individually recognized using natural markings on their dorsal fins (Würsig & Würsig 1977; Würsig & Jefferson 1990). Schools were excluded from the analysis 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 re-encountered within 1 h of the first sighting with different associates (as in Smolker et al. 1992; Rossbach & Herzog 1999). Analysis of school size and home range was further restricted by excluding all schools resighted within a day.

The study was conducted under licences from the Department of Environment and Climate Change NSW (DECC) and the NSW Marine Parks Authority (MPA) and approved by Macquarie University Animal Ethics Committee.

Defining Associations

Associations were based on school membership, such that individuals present in the same school were assumed to be associated. Strength of association among dyads ($N = 7140$) was calculated using the half-weight index (HWI; Cairns & Schwager 1987) for distinctively recognized adults and juveniles sighted more than 10 times over the entire study period (greater than or equal to the median number of sightings per individual). The HWI was used to account for missed associates in a school (Cairns & Schwager 1987) along with facilitating comparisons with other bottlenose dolphin studies. A Monte Carlo permutation test was conducted following the methods of Bejder et al. (1998) and Whitehead et al. (2005) to determine whether associations in the Port Stephens population were significantly different from random. Daily sampling periods were used to remove demographic effects occurring during the study period, such as birth, death, immigration and emigration (Whitehead 1999). The original association matrix was randomized 40 000 times with 100 flips per permutation. A significantly higher coefficient of variation (CV) of real association indices compared to that of randomly permuted data indicates the presence of long-term preferred companions in the population (Whitehead 1999). All social and network structure analyses were run in SOCPROG, version 2.3 (Whitehead et al. 2005) in MatLab 7.0.4 (Mathworks Inc., Natick, MA, U.S.A.). The sex of individuals was determined through genetic methods (as described

in Möller et al. 2001) or the repeated presence of a dependent calf for females.

Social and Spatial Segregation of Communities

Dolphin community structure in Port Stephens was examined using Newman's (2006a, b) modularity technique implemented in SOCPROG (Lusseau et al. 2008; Whitehead 2008b). The eigenvector-based method finds statistically significant divisions in the network using the difference between total proportions of weights (association indices) within clusters of the real network and the expected weights if pairwise association coefficients were randomly distributed. Expected weights were determined by two methods: (1) controlling for gregariousness of individuals (Newman 2004); and (2) taking spatial clustering and preferred/avoided companionships into account by permuting associations within daily sampling periods using 1000 permutations and 100 flips per permutation (Whitehead & Dufault 1999; Lusseau et al. 2008; Whitehead 2008b). Group structure was subsequently defined by the association index at which modularity was maximized, and visualized using an average-linkage hierarchical cluster analysis (Newman 2006a; Lusseau 2007). Newman's assortativity coefficient, r (Newman 2003) was then calculated to determine whether preferred associations formed between individuals that had similar ranging patterns. The degree of geographical homophily in the population was quantified as in Lusseau et al. (2006), where individuals were split into two groups based on their individual ranging patterns. The coefficient ranges from zero to one, where higher values indicate greater assortativity. The standard deviation was calculated by the jackknife procedure (Newman 2003).

Dolphin sightings meeting the restriction criteria were classified as either 'eastern' or 'western' schools based on the network assignment of each individual. Sightings were then visualized on a Port Stephens map created using GIS habitat type zoning data (provided by the NSW Department of Environment and Climate Change and NSW Marine Parks Authority). Differences in the core distribution between communities were described using the fixed kernel density estimate in Hawth's Tools extension (Beyer 2004) in ArcGIS version 9.2 (ESRI, Redlands, CA, U.S.A.). The 25 and 50% kernel isopleths were calculated to estimate core areas of each community using a smoothing factor selected with reference to the h_{ref} estimate (Silverman 1986; Worton 1995).

Social Organization at the Community Level

We used three analytical approaches to examine potential differences in association patterns between the two communities identified in the previous analysis: (1) association levels; (2) network metrics; and (3) temporal stability of associations. First, mean and maximum levels of association were compared by sex class (male–male, female–female, male–female) and for all associations including those of unknown sex. Differences in the number of preferred associates each individual possessed (as defined by the modularity cutoff technique, where $HWI > 0.092$) was also tested between communities using a Mann–Whitney U test. Second, three individual-based network statistics calculated from the weighted (association matrix) network were averaged over and within communities. These included the strength, which is a measure of gregariousness and is the sum of the association indices for each individual (Barthélemy et al. 2005), the clustering coefficient, which is the proportion of an individual's neighbours who are themselves neighbours (a measure of 'cliquishness' as calculated by Holme et al. 2007), and affinity, which determines whether individuals strongly connect to individuals who also have strong connections (Barthélemy et al. 2005). Network metrics calculated

for each community were compared to those of an expected network based on 1000 permutations to test whether network structure is influenced by individual association preferences and whether association patterns differed significantly between communities (Lusseau et al. 2008). Finally, changes in association rates over time were calculated within and between communities using the lagged association rate (LAR; Whitehead 1995). Each LAR was compared to the null association rate initially to determine whether nonrandom patterns of associations occurred over the entire study period. Models of temporal stability were then fitted to the observed data to characterize the social components of the society. The components constituting the eight models tested included constant companions (CC), casual acquaintances (CA; nonpermanent relationships, which decay over various time lags) and rapid disassociations (RD). The model best describing the temporal dynamics of association patterns was indicated by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007). Standard errors for the LAR and parameter estimates were obtained by jackknifing (displayed as a ± 1 standard error interval around the mean). This procedure estimated the precision of the parameters by sequentially omitting 30-day sampling periods in which association data were collected (Whitehead 1995).

RESULTS

During the 10 field seasons conducted in Port Stephens between December 1998 and August 2007, 747 schools (breeding season: $N = 498$, mean = 71 ± 6.3 ; nonbreeding season: $N = 249$, mean = 83 ± 7.7) and 120 individuals met sighting criteria for this analysis. This included 54 females, 30 males and 36 individuals of unknown sex. The CV of true association indices using maximum likelihood was 0.93, indicating a very well-differentiated population. With a mean of 1.9 associations per dyad, the correlation between true and estimated association indices was moderate at 0.68, showing the data set has reasonable power to detect the correct social system (Whitehead 2008a). Significantly higher mean levels of association (mean = 0.066, random = 0.0655; $P < 0.001$) and CV of association indices (CV = 1.405; random CV = 0.99; $P < 0.001$) indicates that long-term preferred and avoided companions are present in the population (Whitehead et al. 2005).

Social and Spatial Segregation of Communities

The average-linkage cluster analysis divided the Port Stephens population into two mixed-sex communities. This division specifically corresponds to differences in the observed ranging patterns of the individuals: those predominately found in the eastern area of the port and those using mainly the western area (Fig. 1; geographical assortativity coefficient: $r = 0.80 \pm 0.026$). Community membership was consistent for both eigenvector-modularity techniques and between the breeding and nonbreeding seasons (results not shown). There were 89 individuals clustered in the eastern community (40 females, 21 males and 28 of unknown sex) and 31 dolphins assigned to the western community (14 females, nine males and eight of unknown sex). The number and composition of subgroups within communities changed slightly, however, depending on the technique chosen to calculate expected association index values. When accounting for the gregariousness of individuals, five clusters were delineated when modularity was maximized at 0.288. Here, modularity was close to the suggested 0.3 value which represents a good division (Newman 2004). Using the permutation method which clusters individuals based on preferred or avoided companions, maximum modularity was slightly lower at 0.118, separating eight clusters in the dendrogram

at an association index of 0.092 (Fig. 2). Relatively low modularity and change in subgroup clustering is consistent with a fission–fusion social structure within communities. Nevertheless, subgroups were generally correlated with the four female social clusters (K, S, N, W) previously identified (Möller et al. 2006). For both approaches, female social clusters were grouped together with several adult males; an additional mixed-sex subgroup was detected comprising mostly young adults; and a potential western male alliance (consisting of individuals with different ranging patterns prior to 2005; unpublished data) also clustered separately. Using the permutation technique, a male alliance (Möller et al. 2001) and a set of three individuals split from the main groups, while the N and W female social clusters that both use the north-eastern area of the port also separated. The segregation of these two clusters is in accord with sighting location data, such that only W individuals are seen in a river that enters the eastern port.

The core area of the two communities, defined by the 25 and 50% kernel density distributions, were restricted to separate geographical regions of the port that differ significantly in benthic substrate and habitat types (Fig. 1). For example, the eastern community clustered tightly in the far eastern side of the port where sandy substrate, sea grass beds and marine processes dominate. Conversely, individuals of the western community had a larger core area where estuarine conditions prevail (muddy benthic substrate, mangroves and salt marshes). Furthermore, the spatial segregation of communities was consistent between the breeding and nonbreeding seasons (results by season not displayed). While core areas were discrete, the 95% home ranges overlapped considerably (isopleths not shown) indicating that community structure did not result solely from spatial segregation of individuals.

Social Organization at the Community Level

As expected based on network structure analysis, association levels were significantly higher within than between communities (Mantel test with 1000 permutations: $P < 0.001$), where the mean association level between communities was only 0.02 ± 0.01 and a maximum of 0.12 ± 0.04 . Within communities, mean and maximum levels of association were higher in the western community (0.15 ± 0.05 ; 0.56 ± 0.21) than in the east

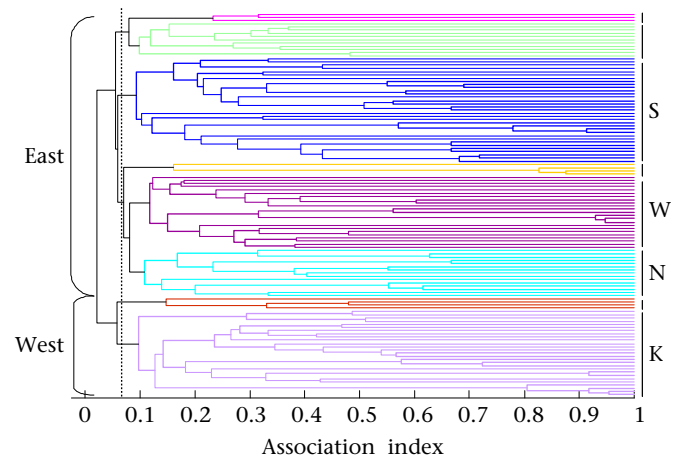


Figure 2. Cluster diagram of half-weight index (HWI) measures of association between Port Stephens dolphins using the average-linkage model. Applying Newman's modularity matrix algorithm based on permutation methods, modularity was maximized at the HWI of 0.092, resulting in eight clusters. Taking account only of the gregariousness of individuals resulted in five clusters (delineated by the dotted line). Groups labelled S, W, N, K correspond to the female social clusters previously identified (Möller et al. 2006).

(0.09 ± 0.02 ; 0.50 ± 0.20) and were consistent for all sex-class comparisons (Fig. 3). However, these differences may also be explained by differences in community size. Nevertheless, eastern individuals had more preferred associates (28 ± 0.96 , $N = 83$) than western dolphins (20 ± 1.21 , $N = 31$; Mann-Whitney U test: $U = 694$, $P < 0.001$, two tailed) and this occurred despite school sizes of the two communities being relatively similar (eastern mean = 6.0 ± 0.26 , range 1–36, $N = 462$; western mean = 5.6 ± 0.36 , range 1–21, $N = 149$; Mann-Whitney U test: $U = 34277$, $P = 0.09$, two tailed). Average size of schools containing both east and west individuals was more than double the size found for each community (13.4 ± 1.42 , range 2–65, $N = 69$, $P < 0.001$). Furthermore, differences in social behaviour between the two communities and from random expectations were strongly supported by three network measures (Table 1). Eastern individuals had higher measures of strength and affinity, although an individual's direct associates were less likely to be connected than expected in a random network (measured by the clustering coefficient). Comparatively, a denser network structure was evident in the west where individuals (who generally had fewer associates) showed tighter clustering. Within-community comparisons to random expectations showed distinctly different patterns between the two communities (Table 1) indicating the reported differences were not an artefact of community size. For instance, the eastern community had a significantly lower clustering coefficient and higher affinity than expected by chance, whereas no significant departure from random was detected in either measure in the western community.

Lagged association rate analysis first indicated that nonrandom associations persisted over the entire study within the eastern and western communities (Fig. 4a, b). Associations in the western community, however, were temporally more stable, where the best fitting model consisted of constant (long-term) companions, casual (short-term) acquaintances and rapid disassociations (Fig. 4a, Table 2). The length of time that associations persisted within the eastern community was notably shorter (Fig. 4b, Table 2). The lowest QAIC value indicated that the eastern community was driven by two levels of casual acquaintances, where the proportion of longer-term acquaintances was considerably lower than the frequency of constant companions in the western community. There was also some support for another model consisting of constant companions, casual acquaintances and rapid disassociations based on the small difference in QAIC values ($\Delta\text{QAIC} = 0.5$; Burnham & Anderson 2002); however, the proportion of long-term associations for both models remained smaller than in the west. In direct contrast to the patterns observed within the two

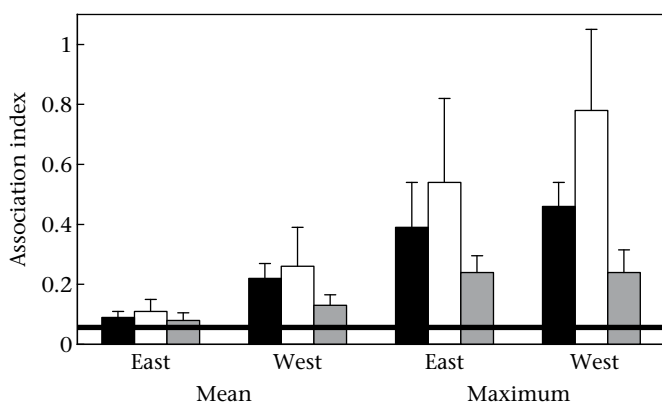


Figure 3. Mean and maximum levels of association (half-weight index) among males (black bars), among females (white bars) and between sexes (grey bars) for eastern and western dolphin communities. The horizontal black line indicates the level of association for two individuals associating at random. Error bars indicate SDs.

Table 1

Strength, clustering coefficients and affinity of individuals averaged over and within communities

	Strength	Clustering coefficient	Affinity
Class means			
Eastern	8.34 (2.20)	0.11 (0.02)	8.69 (0.42)
Random	8.28 (2.19)	0.15 (0.02)	8.56 (0.35)
	$P < 0.001$	$P < 0.001$	$P < 0.001$
Western	6.42 (1.54)	0.14 (0.04)	7.40 (0.40)
Random	6.44 (1.60)	0.14 (0.01)	7.72 (0.37)
	$P = 0.04$	$P = 0.45$	$P < 0.001$
Within classes			
Eastern	7.69 (2.01)	0.13 (0.02)	8.15 (0.38)
Random	7.65 (1.98)	0.18 (0.01)	8.12 (0.41)
	$P < 0.001$	$P < 0.001$	$P < 0.001$
Western	4.54 (1.43)	0.21 (0.04)	4.90 (0.38)
Random	4.53 (1.45)	0.22 (0.03)	4.91 (0.36)
	$P < 0.001$	$P = 0.06$	$P = 0.30$

Significant differences from a random network were assessed using 1000 permutations. SDs are given in parentheses.

communities, the intercommunity lagged association rate was almost identical to the null association rate over the entire study period (Fig. 4c). The majority of interacting dyads here disassociated rapidly, with only 7% identified as casual acquaintances (Table 2).

DISCUSSION

This study applied a recently developed network algorithm to a long-term photoidentification data set of bottlenose dolphins inhabiting the Port Stephens embayment and identified two distinct, mixed-sex communities. The hierarchical organization of this population, structured by communities and smaller subgroups, is comparable to those of other highly social species such as African elephants (Wittemyer et al. 2005), hamadryas baboons, *Papio hamadryas hamadryas* (reviewed in Hill et al. 2008), killer whales, *Orcinus orca* (Ford et al. 2000) and Galapagos sealions *Zalophus wollebaeki* (Wolf et al. 2007), where social tiers assist individuals to cope with variable ecological and social pressures. The observed dolphin hierarchical tiers are supported by previous short-term studies on association patterns, which showed social segregation of both male and female groups ranging in the two areas of the port (Möller et al. 2001, 2006), and a recent genetic study that found low, but significant, genetic differentiation between the two communities in nuclear DNA (J. Wiszniewski, L.B. Beheregaray, S.J. Allen & L.M. Möller, unpublished data). Here, we also show that male dolphins form long-term associations with specific female bands. Furthermore, delineation of an eastern subgroup consisting of mostly young adults suggests that age may have a significant influence on association patterns in Port Stephens. Assortative mixing by age may be favoured in bottlenose dolphin populations since the resources required by individuals (for food and defence) will change substantially over time (Wells 1991; Connor et al. 2000; Lusseau & Newman 2004; Lusseau 2007). Furthermore, mating within age cohorts could be a mechanism used by young females to avoid breeding with older male relatives (e.g. Höner et al. 2007).

While the dolphin community division corresponds to differences in the ranging patterns of individuals (eastern versus western port), analysis of the spatial distribution of schools at the community level illustrated that core areas coincided directly with a change in benthic substrate and habitat types (Fig. 1). Since foraging specializations and diets of bottlenose dolphins are often linked to habitat type (Roszbach & Herzing 1999; Gannon & Waples 2004; Hastie et al. 2004; Sargeant et al. 2007), the correlation with

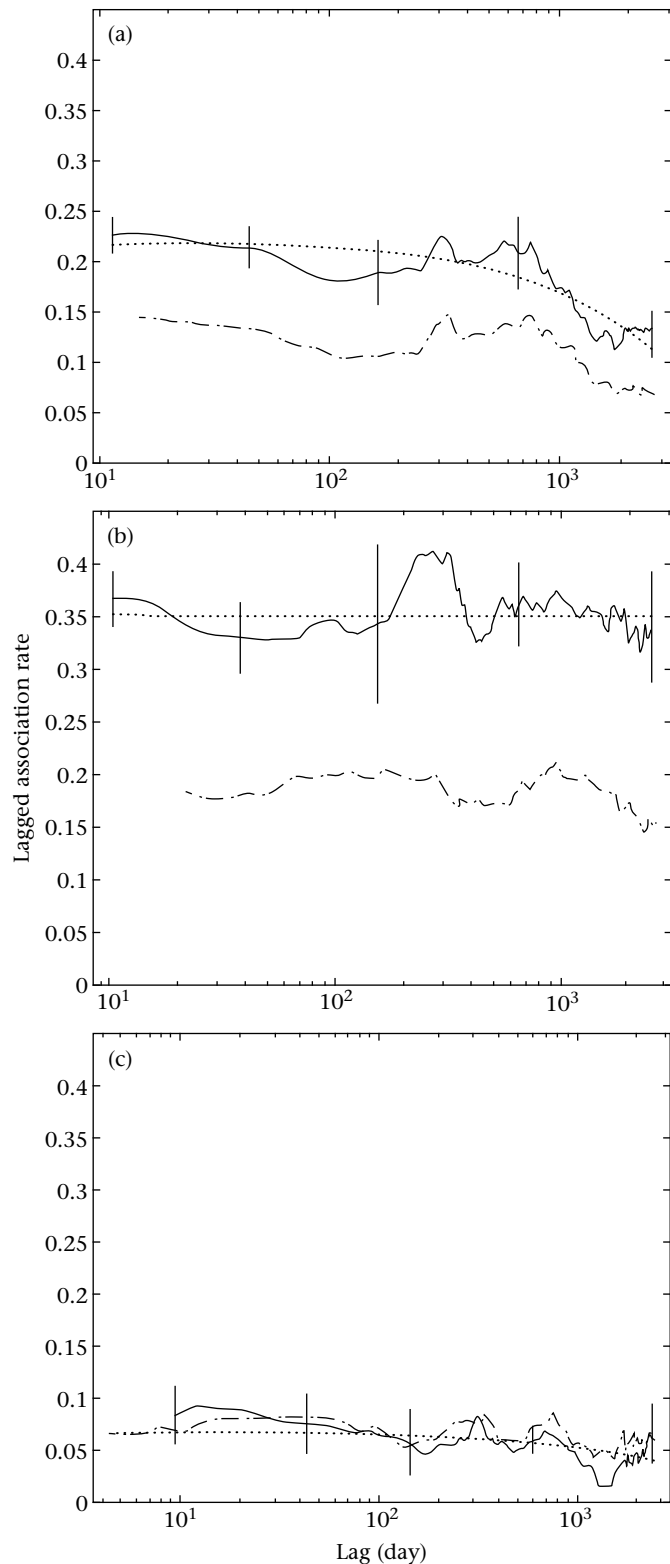


Figure 4. Lagged association rate (solid line) compared to the best fitting model (broken line) and null association rate (dotted line) for (a) eastern community, (b) western community, and (c) between communities. SEs (vertical lines) were computed by jackknifing over 30-day periods.

core area use and change in benthic substrate and habitats in the Port Stephens embayment suggest that the spatial segregation of communities may have arisen through individual adaptation to local environmental conditions. Dolphins may reside and

reproduce in their natal habitats as a result of resource and behavioural specializations, given that foraging specializations can be culturally transmitted and involve a significant learning component (Krützen et al. 2005; Sargeant et al. 2005). Furthermore, they may also attain substantial benefits by cooperating with individuals that have similar foraging preferences and experience (de Waal & Luttrell 1986; Díaz López & Bernal Shirai 2008).

Fine-scale site fidelity of gregarious animals that are capable of individual recognition creates an environment for social relationships to develop (Ramos-Fernandez et al. 2006; Wolf et al. 2007). The use of Newman's modularity matrix algorithm in this study demonstrated that the east–west dolphin segregation in the Port Stephens embayment resulted at least partly from genuine social preferences, rather than simply being an artefact of spatial separation and gregarious behaviour of the individuals. This is made possible by the ability of bottlenose dolphins to recognize and discriminate conspecifics by their unique signature whistles (Sayigh et al. 1999). Furthermore, while core areas of the two communities were distinguishable, overall home ranges of communities were not mutually exclusive and mixed-community schools were sighted 10% of the time. Thus, opportunities for social relationships to develop between eastern and western dolphins were present. Lusseau et al. (2006) used similar techniques to show that the long-term community division in the Moray Firth bottlenose dolphin population in Scotland was also driven by preferential associations that correlated with differential habitat use. The combination of resource and behavioural specializations shaping social group structure may alter the distribution of genetic variation in the population, resulting in significant genetic differentiation between communities. Although on much larger geographical scales, intraspecific affinity to specific habitat characteristics has been proposed as a mechanism promoting isolation of many bottlenose dolphin populations (Hoelzel et al. 1998; Natoli et al. 2005; Sellas et al. 2005; Möller et al. 2007).

Delineation of community structure in a population and subsequent examination of group dynamics, distributions of association indices and network statistics can provide novel insights into the complex nature of social interactions found in bottlenose dolphins. First, association patterns between community members differed considerably to those found within the eastern and western communities. Association rates were low and highly variable over time, suggesting intercommunity associations resulted primarily from aggregative behaviour (i.e. nonsocial forces such as localized food resources, mating or predator avoidance, Whitehead 2008b). For example, the higher occurrence of mixed-community schools in the breeding than the nonbreeding seasons (58% and 42%, respectively) indicates that mating behaviour might be influencing association patterns. Nevertheless, our results are in direct contrast to the Moray Firth dolphin population, where temporal stability of associations was similar within and between communities (Lusseau et al. 2006). Furthermore, dolphin schools composed of individuals from both embayment communities were more than twice the size of schools that were composed solely of members of one community. This suggests intercommunity interactions occur during fusion events between small social groups more readily than they do at the individual level. Interactions between spatially segregated groups may be constrained to a minimum social unit size to reduce predation risk (Heithaus & Dill 2002), while inherent benefits from remaining with several close associates during intercommunity interactions may also minimize aggression (Wilson & Wrangham 2003).

Moreover, we found dolphins in the eastern community generally had more preferred associates, while school sizes were similar to those of the west. Combined with significantly lower levels of clustering, higher levels of gregariousness and the low

Table 2
Models of temporal stability within and between communities in Port Stephens

Community	Model of association	p_{cc}	p_{rd}	p_{ca}	τ_{ca}	p_{perm}	τ_{perm}
Eastern	Two levels of CAs $g(d) = p_{ca}e^{-d/\tau_{ca}} + p_{perm}e^{-d/\tau_{perm}}$			0.78 (0.03)	0.36 days (0.2–21.3)	0.28 (0.03)	11.64 years (8.5–18.7)
Eastern $\Delta QAIC = 0.5$	CC+CA+RD $g(d) = p_{cc} + p_{ca}e^{-d/\tau_{ca}}$	0.08 (0.13)		0.15 (0.13)	5.61 years (0.9–7.0)		
Western	CC+CA+RD $g(d) = p_{cc} + p_{ca}e^{-d/\tau_{ca}}$	0.35 (0.03)		0.17 (0.09)	2.30 days (1.8–3.2)		
Between communities	RD+CA $g(d) = p_{ca}e^{-d/\tau_{ca}}$		0.93 (0.03)	0.07 (0.03)	13.64 years (10.0–21.6)		

The best fitting model chosen by minimizing QAIC, and is described by the association rate between individuals, $S(d)$, after a time lag, d . The model for each type of association consists of a proportion of constant companions (p_{cc}), rapid disassociations (p_{rd}), short-term, casual acquaintances (p_{ca}) that last for a particular length of time (τ_{ca}) and/or a proportion of casual associations (p_{perm}) that last for a longer period (τ_{perm}). The SE of each parameter (give in parentheses) was estimated by the jackknifing procedure. Parameters for the second-ranked model are given for the eastern community since the small difference in quasi-Akaike information criterion (QAIC) values indicates some support for this model of structure.

mean association rates, it is likely that eastern individuals change associates more regularly. These dolphins may preferentially associate with different individuals during different behavioural states (Gero et al. 2005; López & Shirai 2007). In contrast, the choice of associates for western individuals may be more constrained as a result of socioecological and demographic factors.

Habitat productivity and predation risk are often the primary selection pressures proposed to account for fine-scale differences in the social organization of bottlenose dolphin populations (reviewed in Connor et al. 2000; Gowans et al. 2008), as well as within other species that have fission–fusion social systems (Boinski 1999; Wittemyer et al. 2005; Sundaesan et al. 2007). Although the abundance and distribution of different prey resources in Port Stephens are currently unknown, the substantially lower density of dolphins in the western area may indicate lower productivity in this region. Higher clustering and more stable associations between individuals may increase the rate of information transfer and reciprocation of cooperative acts, which are required to exploit spatially and temporally variable prey resources (Perrin & Lehman 2001; Lusseau et al. 2003). Alternatively, potential differences in prey composition and availability in the two distinct environments of Port Stephens could lead to within-community differences in foraging strategies (as in other bottlenose dolphin populations, e.g. Würsig 1986; Rossbach & Herzing 1999; Hastie et al. 2004; Sargeant et al. 2007) and, in consequence, affect patterns of association (e.g. Díaz López & Bernal Shirai 2008). Similarly, the risk of predation has been found to change according to habitat type in other bottlenose dolphin populations (Wells et al. 1987; Heithaus & Dill 2002). Given that shark species known to prey on dolphins are present in Port Stephens, variation in predation pressure in the two environments may also create differences in dolphin behaviour and group dynamics between communities. Indeed, it is hypothesized that predation risk is the main driver of sociality in odontocetes (Whitehead 2003) and a significant factor in primate social evolution (Hill & Lee 1998). While adults and calves of both Port Stephens communities bear scars from nonlethal shark attacks, without any data on the abundance and distribution of various shark species in eastern or western Port Stephens, the risk encountered by each community and its relative influence on group formation remain unknown.

While population density may be constrained by ecological conditions, demographic and density-related factors may also explain differences in sociotemporal rates of bottlenose dolphin associations (Connor et al. 2000). In this study, we observed lower social cohesion within the larger eastern community which ranges over a smaller core area. High encounter rates of individuals may facilitate social familiarity to a larger number of individuals, thus allowing individuals to change associates more regularly according to nutritional and defence requirements (Connor et al. 2000).

Females in some bottlenose dolphin populations tend to associate more closely with those in similar reproductive condition (Wells et al. 1987; Möller & Harcourt 2008). However, the strength of associations between females is likely to change over years as a result of variable interbirth intervals (Mann et al. 2000; Barrett & Henzi 2002). In Port Stephens, the three female social clusters in the eastern community constituted a large network of individuals within which mature females of similar reproductive state (i.e. pregnant females or those with similar-aged calves) could preferentially associate. For mature females in the single western band on the other hand, finding another individual in similar reproductive condition may require leaving preferred habitats, potentially incurring a greater cost than remaining with socially familiar and/or related individuals.

Independent of the demographic and ecological factors that resulted in higher levels of relatedness between western females, the influence of kinship offers an additional explanation for greater cohesiveness in this community through kin selection (Hamilton 1964). While male alliances in the Port Stephens dolphin population in general were found to be randomly related (Möller et al. 2001), maternal kinship and genetic relatedness were higher among closely associating females (Möller et al. 2006). The disparity in kinship patterns and their effect on association patterns at the community level, however, remain to be tested.

Finally, increasing levels of anthropogenic activities may also impact group dynamics to some degree in the eastern community. Short-term changes in fission–fusion rates and behaviour have been observed in direct response to dolphin-watching activities which are concentrated in the eastern area of Port Stephens (Allen 2005). This repeated disruption to group structure in one community may result in suboptimal school sizes, changing the association dynamics (e.g. Bejder et al. 2006), and, in turn, influencing the fitness of individuals in the long term. Furthermore, prawn-trawling activities in eastern Moreton Bay, Queensland, appear to have shaped community structure in a continuously distributed bottlenose dolphin population, where individuals of one community feed in association with trawlers, while members of the other preferentially forage in sea grass beds (Chilvers & Corkeron 2001). While differences in social behaviour between the two communities were not documented, Díaz López & Bernal Shirai (2008) found association strength among preferred associates was considerably lower when individuals were opportunistically feeding near fish farms. Observations of individuals in Port Stephens feeding on trawling by catch, as well as around oyster aquaculture areas, highlight the need for continual monitoring to discriminate human-induced effects from other mitigating factors.

Overall, the use of a social network approach incorporating randomization techniques has provided strong evidence for two dolphin communities that inhabit different ecological

environments in the Port Stephens embayment. Community and social group structure have been previously identified as important evolutionary features maintaining the genetic health of populations of group-living species (Chesser et al. 1993; Dobson et al. 2004; Archie et al. 2008). Accordingly, these findings should be incorporated into population viability analysis and long-term trends in abundance so that conservation initiatives for this small population may be prioritized (as suggested for the isolated Moray Firth population, Lusseau et al. 2006). Here, delineating community structure has also provided a platform for future investigations into sex-specific relationship patterns, reproductive strategies and habitat use, and into the suite of interacting ecological, social and demographic parameters governing this social system.

Acknowledgments

We are grateful to Macquarie University staff for their logistical support, as well as the volunteers who assisted in field data collection. The manuscript was greatly improved by the comments of D. Lusseau and C. Brown and two anonymous referees. We also thank D. Lusseau for his advice on analyses and interpretation of results and H. Whitehead for his analytical and theoretical contribution to the study of social behaviour through SOCPROG. Funding was provided by Macquarie University, DEC and MPA.

References

- Allen, S. J. 2005. Management of bottlenose dolphins (*Tursiops aduncus*) exposed to tourism in Port Stephens, N.S.W., Australia. M.Sc. thesis, Macquarie University.
- Archie, E. A., Maldonado, J. E., Hollister-Smith, J. A., Poole, J. H., Moss, C. J., Fleischer, R. C. & Alberts, S. C. 2008. Fine-scale population genetic structure in a fission–fusion society. *Molecular Ecology*, **17**, 2666–2679.
- Asensio, N., Korstjens, A. H., Schaffner, C. M. & Aureli, F. 2008. Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. *Behaviour*, **145**, 833–1001.
- Barrett, L. & Henzi, S. P. 2002. Constraints on relationships formation among female primates. *Behaviour*, **139**, 263–289.
- Barthélemy, M., Barrat, A., Pastor-Satorras, R. & Vespignani, A. 2005. Characterization and modeling of weighted networks. *Physica A*, **346**, 34–43.
- Bejder, L., Fletcher, D. & Brager, S. 1998. A method of testing association patterns of social animals. *Animal Behaviour*, **56**, 719–725.
- Bejder, L., Samuels, A., Whitehead, H. & Gales, N. 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour*, **72**, 1149–1158.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatalecolology.com/htools>.
- Boccaletti, S., Latora, Y., Moreno, M., Chavez, M. & Huang, D. U. 2006. Complex networks: structure and dynamics. *Physics Reports*, **424**, 175–308.
- Boinski, S. 1999. The social organisations of squirrel monkeys: implications for ecological models of social organisation. *Evolutionary Anthropology*, **8**, 101–112.
- Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodal Inference: a Practical Information-theoretic Approach*. New York: Springer-Verlag.
- Cairns, S. J. & Schwager, S. J. 1987. A comparison of association indices. *Animal Behaviour*, **35**, 1454–1469.
- Chesser, R. K., Rhodes, O. E., Sugg, D. W. & Schabel, A. 1993. Effective sizes for subdivided populations. *Genetics*, **135**, 1221–1232.
- Chilvers, B. L. & Corkeron, P. J. 2001. Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society of London, Series B*, **268**, 1901–1905.
- Connor, R. C., Heithaus, M. R. & Barre, L. M. 1999. Superalliance of bottlenose dolphins. *Nature*, **397**, 571–572.
- Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 91–126. Chicago: University of Chicago Press.
- Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D. & Krause, J. 2005. Assortative interactions and social networks in fish. *Oecologia*, **143**, 211–219.
- Díaz López, B. & Bernal Shirai, J. A. 2008. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. *Behavioral Ecology and Sociobiology*, **62**, 887–894.
- Dobson, S. S., Chesser, R. K., Hooglang, J. L., Sugg, D. W. & Foltz, D. W. 2004. The influence of social breeding groups on effective population size in black-tailed prairie dogs. *Journal of Mammalogy*, **85**, 58–66.
- Dunbar, R. M. 2002. Time: a hidden constraint on the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, **31**, 35–49.
- Dunn, D. G., Barco, S. G., Pabst, D. A. & McLellan, W. A. 2002. Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. *Journal of Wildlife Diseases*, **38**, 505–510.
- Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. 2006. Policing stabilises construction of social niches in primates. *Nature*, **439**, 426–429.
- Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. 2000. *Killer Whales: The Natural History and Genealogy of Orcinus orca in British Columbia and Washington*. Vancouver: UBC Press.
- Gannon, D. P. & Waples, D. M. 2004. Diets of coastal bottlenose dolphins from the U.S. mid-Atlantic coast differ by habitat. *Marine Mammal Science*, **20**, 527–545.
- Gero, S., Bejder, L., Whitehead, H., Mann, J. & Connor, R. C. 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. *Canadian Journal of Zoology*, **83**, 1566–1573.
- Gowans, S., Würsig, B. & Karczmarski, L. 2008. The social structure and strategies of delphinids: predictions based on an ecological framework. *Advances in Marine Biology*, **53**, 195–294.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.
- Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M. & Thompson, P. M. 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, **144**, 397–403.
- Heithaus, M. R. & Dill, L. M. 2002. Food availability and tiger shark predation risk influences bottlenose dolphin habitat use. *Ecology*, **83**, 480–491.
- Hill, R. A. & Lee, P. C. 1998. Predation risk as an influence on group size in ceropithecoid primates: implications for social structure. *Journal of Zoology*, **245**, 447–456.
- Hill, R. A., Bentley, R. A. & Dunbar, R. I. M. 2008. Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. *Biology Letters*, **4**, 748–751.
- Hoelzel, A. R., Potter, C. W. & Best, P. B. 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proceedings of the Royal Society of London, Series B*, **265**, 1177–1183.
- Holme, P., Park, S. M., Kim, B. J. & Edling, C. R. 2007. Korean university life in a network perspective: dynamics of a large affiliation network. *Physica A*, **373**, 821–830.
- Höner, O. P., Wachter, B., East, M. L., Streich, W. J., Wilhelm, K., Burke, T. & Hofer, H. 2007. Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature*, **448**, 798–801.
- Irvine, A. B., Scott, M. D., Wells, R. S. & Kaufmann, J. H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, **79**, 671–678.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.
- Krützen, M., Sherwin, W. B., Berggren, P. & Gales, N. 2004. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Marine Mammal Science*, **20**, 28–47.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 8939–8943.
- López, B. D. & Shirai, J. A. B. 2007. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. *Behavioral Ecology and Sociobiology*, **62**, 887–894.
- Lusseau, D. 2007. Why are male social relationships complex in the Doubtful Sound bottlenose dolphin population? *PLoS ONE*, **2**, e348.
- Lusseau, D. & Newman, M. E. J. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London, Series B*, **270**, S186–S188.
- Lusseau, D., Schneider, K. & Boisseau, O. J. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology*, **54**, 396–405.
- Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., Barton, T. R. & Thompson, P. M. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, **75**, 14–24.
- Lusseau, D., Whitehead, H. & Gero, S. 2008. Incorporating uncertainty into the study of animal social networks. *Animal Behaviour*, **75**, 1809–1815.
- McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**, 491–494.
- McDonald, D. B. 2007. Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 10910–10914.
- Mann, J., Connor, R. C., Barre, L. M. & Heithaus, M. R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, **11**, 210–219.
- Möller, L. M. & Harcourt, R. G. 2008. Shared reproductive state enhances female associations in dolphins. article ID 498390. *Research Letters in Ecology*, doi:10.1155/2008/498390.
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G. & Krützen, M. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London, Series B*, **268**, 1941–1947.
- Möller, L. M., Allen, S. J. & Harcourt, R. G. 2002. Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins *Tursiops aduncus* in Jervis Bay and Port Stephens, south-eastern Australia. *Australian Mammalogy*, **24**, 11–21.
- Möller, L. M., Beheregaray, L. B., Allen, S. J. & Harcourt, R. G. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behavioral Ecology and Sociobiology*, **6**, 109–177.

- Möller, L. M., Wiszniewski, J., Allen, S. J. & Beheregaray, L. B. 2007. Habitat type promotes rapid and extremely localized genetic differentiation in dolphins. *Marine and Freshwater Research*, **58**, 640–648.
- Natoli, A., Birkun, A., Aguilar, A., Lopez, A. & Hoelzel, A. R. 2005. Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London, Series B*, **272**, 1217–1226.
- Newman, M. E. J. 2003. Mixing patterns in networks. *Physical Review E*, **67** 026126.
- Newman, M. E. J. 2004. Analysis of weighted networks. *Physical Review E*, **70** 056131.
- Newman, M. E. J. 2006a. Modularity and community structure in networks. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 8577–8582.
- Newman, M. E. J. 2006b. Finding community structure in networks using the eigenvectors of matrices. *Physical Review E*, **74**, arXiv:physics/0605087v3.
- Perrin, N. & Lehman, N. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. *American Naturalist*, **158**, 471–483.
- Pope, T. R. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, **48**, 253–267.
- Ramos-Fernandez, G., Boyer, D. & Gomez, V. P. 2006. A complex social structure with fission–fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology*, **60**, 536–549.
- Rossbach, K. A. & Herzog, D. L. 1999. Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. *Canadian Journal of Zoology*, **77**, 581–592.
- Sargeant, B. L., Mann, J., Berggren, P. & Krützen, M. 2005. Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, **83**, 1400–1410.
- Sargeant, B., Wirsing, A., Heithaus, M. & Mann, J. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behavioral Ecology and Sociobiology*, **61**, 679–688.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D. & Irvine, A. B. 1999. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour*, **57**, 41–50.
- van Schaik, C. P. 1999. The socioecology of fission–fusion sociality in orangutans. *Primates*, **40**, 69–86.
- Sellas, A. B., Wells, R. S. & Rosel, P. E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conservation Genetics*, **6**, 715–728.
- Shane, S. H. 1990. Behavioral ecology of the bottlenose dolphin at Sanibel Island. In: *The Bottlenose Dolphin* (Ed. by S. Leatherwood & R. Reeves), pp. 245–265. San Diego: Academic Press.
- Silverman, B. W. 1986. *Density Estimation for Statistics and Data Analysis*. London: Chapman & Hall.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex-differences in patterns of association among Indian Ocean bottle-nosed dolphins. *Behaviour*, **123**, 38–69.
- Sundaresan, S. R., Fischhoff, I. R., Dushoff, J. & Rubenstein, D. I. 2007. Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Oecologia*, **151**, 140–149.
- Takahata, Y., Suzuki, S., Okayasu, N. & Hill, D. 1994. Troop extinction and fusion in wild Japanese macaques of Yukushima Island, Japan. *American Journal of Primatology*, **33**, 317–322.
- de Waal, F. B. M. & Luttrell, L. M. 1986. The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatologica*, **46**, 215–234.
- Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: *Dolphin Societies, Discoveries and Puzzles* (Ed. by K. Pryor & K. S. Norris), pp. 199–226. Berkeley: University of California Press.
- Wells, R. S., Scott, M. D. & Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy* (Ed. by H. H. Genoways), pp. 247–304. New York: Plenum.
- Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology*, **6**, 199–208.
- Whitehead, H. 1999. Testing association patterns of social animals. *Animal Behaviour*, **57**, F26–F29.
- Whitehead, H. 2003. *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.
- Whitehead, H. 2007. Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communications in Statistics: Simulation and Computation*, **36**, 1233–1246.
- Whitehead, H. 2008a. Precision and power in the analysis of social structure using associations. *Animal Behaviour*, **75**, 1093–1099.
- Whitehead, H. 2008b. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago: University of Chicago Press.
- Whitehead, H. & Dufault, S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior*, **53**, 1053–1067.
- Whitehead, H., Bejder, L. & Ottensmeyer, C. A. 2005. Testing association patterns: issues arising and extensions. *Animal Behaviour*, **69**, e1–e6.
- Wilson, M. L. & Wrangham, R. W. 2003. Intergroup relations in chimpanzees. *Annual Review of Anthropology*, **32**, 363–392.
- Wittemyer, G., Douglas-Hamilton, I. & Getz, M. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, **69**, 1357–1371.
- Wolf, J. B. W., Mawdsley, D., Trillmich, F. & James, R. 2007. Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour*, **74**, 1293–1302.
- Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, **59**, 794–800.
- Wrangham, R. W. 1982. Mutualism, kinship and social evolution. In: *Current Problems in Sociobiology* (Ed. by King's college Sociobiology Group), pp. 269–289. Cambridge: Cambridge University Press.
- Würsig, B. 1986. Delphinid foraging strategies. In: *Dolphin Cognition and Behavior: a Comparative Approach* (Ed. by R. J. Schusterman, J. A. Thomas & F. G. Wood), pp. 347–359. Hillsdale, New Jersey: L. Erlbaum.
- Würsig, B. & Jefferson, T. A. 1990. Methodology of photo-identification from small cetaceans. In: *Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters* (Ed. by P. S. Hammond, S. A. Mizroch & G. P. Donovan), pp. 43–52. Cambridge: International Whaling Commission.
- Würsig, B. & Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science*, **198**, 755–756.