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Complex patterns of male alliance formation in a dolphin social network

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The formation and maintenance of alliances is regarded as one of the most socially complex male mating strategies in mammals. The prevalence and complexity of these cooperative relationships, however, varies considerably among species as well as within and between populations living in different ecological and social environments. We assessed patterns of alliance formation for Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in Port Stephens, New South Wales, Australia, to investigate the stability of these alliances, the structure of associations, as well as variation in schooling patterns among males. Our results showed that association patterns among males within this population showed considerable variability. Males either formed strong and enduring alliances that lasted for at least 8 years with minimal partner switching, or less stable partnerships within a much larger male social network. Male alliances with the strongest levels of association within a given time period were significantly more likely to maintain their relationships over the long term compared with alliances with lower levels of association. Males in stable alliances also associated in significantly smaller schools than males who formed less stable alliance partnerships. Finally, we found that alliances consisting of more related males did not persist longer than alliances between unrelated individuals. Our study suggests that intrapopulation variation in male alliance formation in dolphins likely reflects different mating strategies adopted as individual responses to their complex fission–fusion social environment.

Key words: alliance stability, bottlenose dolphin, coalition, cooperation, relatedness, social behavior, *Tursiops*

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The formation of coalitions and alliances is regarded as one of the most socially complex male mating strategies in mammals. Coalitions are generally defined as individuals opportunistically cooperating with others during competitive or aggressive interactions, whereas alliances refer to groups of individuals that maintain long-term cooperative relationships with each other (De Waal and Harcourt 1992). The formation of male coalitions and alliances for the purpose of reproduction has been an intriguing area of research given that in some cases, males cooperate to obtain a nondivisible resource (i.e., successful fertilization; van Hooff and van Schaik 1994). The degree of complexity of coalitionary behavior has been related to the presence of 3 traits: mutual tolerance, cooperation, and preference for particular partners on the basis of factors such as age, competitive ability, familiarity, and relatedness (Olson and Blumstein 2009). Only a few primate and delphinid species have been shown to possess all 3 traits, whereas several other species display less complexity with only 1 or 2 typical coalitionary behaviors (reviewed in Olson and Blumstein 2009). Cooperative partnerships among males

may evolve through 3 possible interdependent pathways: kin selection, where individuals obtain indirect fitness benefits by cooperating with kin (Hamilton 1964); mutualism, where individuals gain immediate benefits from cooperation (Dugatkin 1997); or reciprocal altruism, in which the reciprocation of altruistic acts over time results in overall net benefits to all cooperating individuals (Trivers 1971).

Mutual tolerance and collaboration among males can increase an individual's reproductive success through a variety of mechanisms, including increased success in mate guarding (bottlenose dolphins, *Tursiops*—Connor et al. 1992a; lions, *Panthera leo*—Packer et al. 1991; chimpanzees, *Pan troglodytes*—Watts 1998), increased success in aggressive contests with other males (baboons, *Papio cynocephalus*—Noë 1994; lions—Grinnell et al. 1995), larger home ranges, which may increase their encounter rates with females (bottlenose



dolphins—Owen et al. 2002), greater ability to defend or acquire territories (cheetahs, *Acinonyx jubatus*—Caro 1994), increase in social rank (chimpanzees—Goodall 1986), greater foraging efficiency (river otters, *Lontra canadensis*—Blundell et al. 2004; prairie dogs, *Cynomys gunnisoni*—Verdolin 2007), and reduced predation risk (squirrels, *Xerus inauris*—Waterman 1997).

Theory predicts that alliances form only under a restricted range of social conditions, many of which are dependent on environmental variables. For example, alliances may be expected to form in populations when male competition is high due to limited availability of receptive females, when the benefits of group living (e.g., increased mating opportunities) outweigh the costs (e.g., increased feeding competition), or when alliances are effective in outcompeting single roving males (Whitehead and Connor 2005). Consequently, the prevalence and complexity of alliance formation is expected to vary considerably among species as well as within and between populations living in different ecological and social environments (Gehrt et al. 2008; Kappeler 2000; Whitehead and Connor 2005). Intrapopulation differences in social tactics among males (i.e., alternative reproductive behaviors) may result from 2 different pathways. First, individuals may adopt fixed strategies that remain constant over time (e.g., horses, *Equus caballus*—Feh 1999). More commonly, however, variation reflects conditional strategies, where males switch between mating tactics depending on their physical condition, age, or social rank in an attempt to increase their chances of reproductive success (e.g., three-spined stickleback, *Gasterosteus aculeatus*—De Fraipoint et al. 1993; and lance-tailed manakins, *Chiroxiphia lanceolata*—DuVal 2007; chimpanzees, Nishida 1983; baboons—Noë 1994).

In bottlenose dolphins, genus *Tursiops*, patterns and complexity of alliance formation vary greatly among populations and appear to be correlated with population density and degree of sexual dimorphism. For instance, in 1 high-density embayment population, almost all males were found to associate in alliances and complex hierarchical patterns of alliance formation were also observed (Connor et al. 1992a, 2011). These higher-level alliances include second-order alliances, consisting of 2 or more 1st-order alliances, and 3rd-order alliances, which could consist of a combination of 1st- or 2nd-order (or both) alliances (Connor et al. 2011). Since males in this population are only slightly larger than females, cooperation in alliance partnerships may be required to successfully monopolize receptive females (Connor et al. 2000). In contrast, there has been no evidence of alliances in some low-density populations where either males are substantially larger than females and appear to use more solitary reproductive strategies (Wilson 1995) or where males associate in large, stable mixed-sex groups (Lusseau et al. 2003).

In populations where male alliances are common, the range of alliance sizes and the stability of these alliances can vary considerably (Connor et al. 1992a; Möller et al. 2001; Parsons et al. 2003; Wells 1991). Explanations for such intrapopulation

variability appear to differ among populations. For instance, Owen et al. (2002) showed that males displaying solitary behavior in 1 population were in a transitional phase rather than using alternative mating strategies. In contrast, the males adopting different types of alliance strategies in another population (Connor et al. 1992a, 2011) have been successful in obtaining paternities (Krützen et al. 2004a). Similarly, the influence of relatedness in alliance partner choice and mating patterns also appears to differ among populations. For example, in populations where stable alliances are formed among closely related males (Krützen et al. 2003; Parsons et al. 2003), individuals that increase the reproductive output of their partners can obtain inclusive fitness benefits even if they are not successful at siring offspring themselves. Consequently, male reproductive success is often highly skewed within these types of alliances (Krützen et al. 2004a). In other populations, however, patterns of alliance formation cannot be explained by kin selection (Möller et al. 2001; Owen 2003) and several lines of evidences suggest that preferences for non-kin partners are genuine. First, bottlenose dolphins are capable of recognizing maternal kin by their unique signature whistles (Sayigh et al. 1999). Second, Owen (2003) showed that although close relatives were generally available at the time when a male was forming an alliance partnership, males more often chose nonrelatives as alliance partners. Finally, levels of kinship among partners can vary depending on alliance strategy (Krützen et al. 2003). Similar intraspecific differences in kinship structure have been observed in lions, where alliances of 2 to 3 males were generally not related, but larger alliances were (Packer et al. 1991). Thus, in the absence of kin selection, cooperation among males can be explained by either mutualism or reciprocal altruism (Grinnell et al. 1995; Möller et al. 2001; van Hooff and van Schaik 1994; Watts 2002).

Our study aimed to assess the long-term stability of male alliances in an embayment population of bottlenose dolphins (*T. aduncus*) in Port Stephens, Australia. The population displayed characteristics of a “fission–fusion” society and was socially and spatially segregated into 2 distinct communities (Wiszniewski et al. 2009). The core areas of the eastern and western communities coincide with a distinct change in habitat type (marine and estuarine, respectively; Fig. 1) and differences in social behavior have been observed between these 2 dolphin communities (Wiszniewski et al. 2009). School sizes were similar between the 2 communities (6 and 5.6 for the eastern and western communities, respectively); however, the average size of schools containing both eastern and western dolphins was more than double the size found for each community (Wiszniewski et al. 2009). Although the population was not strongly assorted by sex (Wiszniewski et al. 2010b), social relationships between males and females appear to be highly distinctive on the basis of short-term association patterns. Males often formed strong bonds with 1 to 3 other males (Möller et al. 2001), whereas females generally associated in a loose social network with a larger number of females (Möller et al. 2006). During the breeding season, male alliances were frequently observed cooperatively

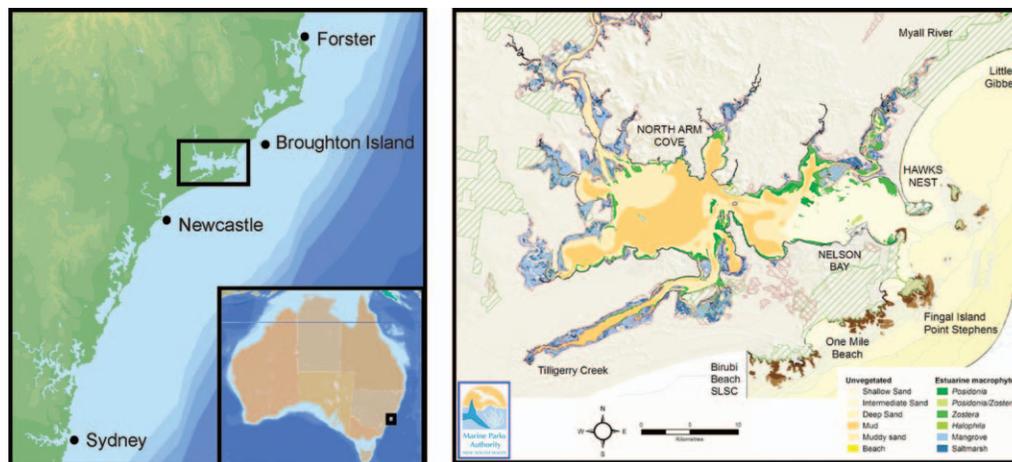


FIG. 1.—Habitat map of the Port Stephens embayment in New South Wales, Australia.

herding individual females for up to weeks at a time (Möller et al. 2001). We defined alliances using both association criteria and behavioral observations of 2 or more males herding a single female. Since the strength of association can vary among alliances (Möller et al. 2001) we investigated whether association strength is a good predictor of alliance stability. We also assessed whether strong associations existed between different alliances (2nd-order alliances, in sensu Connor et al. 1992a). We investigated potential differences in social patterns among males and compared alliance structure and complexity with other well-studied dolphin populations (e.g., Sarasota Bay, Florida and Shark Bay, Western Australia) to help increase our understanding of the social and ecological factors driving the evolution of complex male behaviors in dolphins and other social species (Connor et al. 2006; Olson and Blumstein 2009). Finally, we used a long-term behavioral and genetic data set to assess whether the longevity of alliances was significantly affected by the level of kinship among males.

MATERIALS AND METHODS

Data collection and restrictions.—The study was conducted within the Port Stephens embayment of approximately 166 km² in surface area, located 200 km north of Sydney on the New South Wales coast of Australia (32°42'S, 152°06'E). The eastern basin of Port Stephens is typically a marine environment, with a strong tidal influx of coastal waters, sandy substrate, and large areas of sea grass, whereas the deeper western port is predominated by estuarine processes, including turbid, freshwater outflow from rivers and a muddy benthic habitat (Fig. 1). The bottlenose dolphin population is relatively small, consisting of around 90 individuals that were considered residents on the basis of photoidentification between 1998 and 2000 (Möller et al. 2002). The population is also genetically distinct from communities ranging on the adjacent coastline, with male-biased dispersal and a directional bias in migration from Port Stephens (Möller et al. 2007; Wiszniewski et al. 2010a). Data on dolphin school

membership was obtained from transect surveys conducted between 1998 and 2008 using standard photoidentification techniques (Möller et al. 2006; for further details see Wiszniewski et al. 2009). A school was defined as all individuals within a 100-m radius (Irvine et al. 1981), and if traveling, the animals were heading in the same direction (Möller et al. 2006; Shane 1990). For each sighting, the latitude and longitude from a global positioning system, time, school size, number of calves, and predominant behavior were recorded. Sizes of schools were estimated by at least 2 trained observers. Estimates were later adjusted if the number of uniquely recognized dolphins exceeded the number of adults estimated in the field. To ensure reliability and independence of data, schools were excluded from the analysis if a minimum of 75% of the estimated school size was not reliably photographed; a fusion event occurred during photoidentification; or, if an individual was re-encountered during the survey, the second school was removed from the analysis. From a total of 945 schools, 113 did not meet the restriction criteria and were removed from the data set. Analyses were then conducted on data from the remaining 832 schools.

Samples for genetic analysis were collected between 1999 and 2008 using the PAXARMS biopsy system (Timaru, New Zealand; Krützen et al. 2002), as described in Möller and Beheregaray (2001) and Wiszniewski et al. (2010a). Photo-identification and biopsy sampling surveys were conducted under licenses from New South Wales (NSW) Department of Environment and Climate Change (DECC; license no. S10763) and the NSW Marine Parks Authority (MPA; permit no. PSGMLP 2008/003). The research was also under approval by Macquarie University Animal Ethics Committee (AEC reference no. 2007/013) and met guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Males were identified using either genetic methods as described in Möller et al. (2001) or in the absence of genetic data, an individual was considered a male if the following 3 criteria were met: the individual was sighted more than 12 times over the study period, which was the median number of sightings over all individuals ($\bar{X} = 17.4$, $SE = 1.1$, $max =$

65); the individual was considered an adult in 2002 or earlier (on the basis of size) and never seen with a dependent calf; and the individual's top associate was a genetically sexed male. We found 9 individuals that met all 3 criteria. Although there is some uncertainty in this classification, these restriction criteria indicate a high probability that these individuals were males (Santos and Rosso 2008; Shane 2004). For example, of the 64 females identified in the population, only 2 had a top associate that was a genetically sexed male. All calves and juveniles were excluded from the analysis on the basis of studies conducted in Sarasota Bay, Florida, where males only reach sexual maturity at approximately 8 years (Wells et al. 1987) and form alliances at an average age of 11 years (6 years minimum—Owen et al. 2002). Notwithstanding, the sex of a juvenile males' closest associate was also generally unknown.

Patterns of association among males.—Strengths of association among dyads were calculated using the half-weight index (HWI—Cairns and Schwager 1987) for all males present in each 2-year time period (December 1998, 1999–2000; 2001–2002, 2005–2006, and 2007–2008). The HWI index is calculated using the formula: $HWI = X/(X + 0.5[Y_A + Y_B])$, where X is the number of schools with individuals A and B seen together; Y_A is the number of schools with individual A sighted but not individual B; and Y_B is the number of schools with just individual B sighted. The HWI index ranges from 0 (2 dolphins never sighted together) to 1 (2 dolphins always sighted together). We used 2-year time periods to obtain sufficient number of sightings per individual. Long-term preferred associates in each of the 4 time periods were identified using a Monte Carlo permutation test (Bejder et al. 1998; Whitehead et al. 2005). The observed association matrix was randomized 100,000 times with 1,000 flips per permutation. Dyads were considered preferred associates if the observed HWI was greater than 95% of the random HWI for that pair. HWI calculations and identification of preferred associates were conducted using SOCPROG, version 2.4 (Whitehead 2009) in Matlab 7.6 (The Mathworks Inc. 2002). We assessed alliance composition within each of the 4 time periods. Males were considered allied (i.e., in an alliance) if they were sighted at least 3 times individually in the respective sampling period (Parsons et al. 2003), were observed jointly herding a female at least once (Möller et al. 2001), and met 2 of the 3 association criteria: identified as preferred associates; were reciprocal top associates, or when a male did not have a reciprocal closest associate, the male was the second closest associate of another male pair and had a coefficient of association (HWI) within 20% of that of both individuals; and the HWI of the male pair is greater than the average maximum HWI calculated over all males in the respective time period. These criteria were adapted from previous studies (Connor et al. 1992b; Möller et al. 2001; Owen et al. 2002; Parsons et al. 2003) to facilitate comparisons among different populations of bottlenose dolphins.

To further assess the dynamics of male association patterns, social network analysis was then conducted on the 8-year pooled data set. Here, we constructed a social network of the

38 males that were sighted 12 or more times over the study period and used the modularity matrix clustering technique described by Newman (2006) and Lusseau et al. (2008) to identify male group structure. In brief, the modularity matrix is the association index (i.e., weight) between 2 individuals minus the expected weight if associations were randomly distributed in the population. We calculated the expected weight by permuting associations within daily sampling periods using 10,000 permutations and 1,000 flips per permutation. This approach was used since it can account for the number of observations and associations of dolphins in each sampling period (Whitehead 2008). The eigenvector of the dominant eigenvalue of the modularity matrix is then used to successively split the matrix into 2 clusters. This divisive procedure is then iterated on all resulting clusters. The most parsimonious division in the network is subsequently determined by the division that maximizes the modularity coefficient, Q . Modularity is calculated by subtracting the expected proportion of total associations within groups from the observed proportion. Thus, Q ranges from 0, indicating randomly assigned groups, to 1, indicating no intergroup associations. The HWI matrix and resulting group structure determined by Q_{max} was visualized using the spring-embedding method (Kamada and Kawai 1989) in NETDRAW (Borgatti 2002). The spring-embedded algorithm is simply an iterative procedure that arranges nodes in such a way that those with the highest association levels are closer together (Gajer and Kobourov 2002). Thus, nodes with the greatest density of links are often more centrally located, whereas those with few links are placed on the periphery of the network.

Stability of male associations.—We used the male alliances defined in the four 2-year time periods to assign each individual a value between 1 and 4 on the basis of the number of 2-year time periods that the male had the same alliance partner (procedure adapted from Mitani 2009; Silk et al. 2006). Thus, males whose partner was the same in all 4 time periods had a stability index of 4. Males that were allied in 1 or no time periods were grouped together in category 1.

To determine whether associations among males predicted their association levels in future years, we followed the procedure of Mitani (2009) and conducted a series of Mantel correlation tests (Hemelrijk 1990; Mantel 1967; Schnell et al. 1985) that compared pairwise HWI values calculated in 1 time period with values calculated in subsequent years. For each comparison, only males present in both time periods were included in the analysis. Significance for all correlations was assessed using 10,000 random permutations.

To assess whether alliance stability is related to strength of association, 2 statistical analyses were conducted. First, we correlated mean association strength within alliances with alliance duration using the Pearson's correlation coefficient. Second, we used lagged association rate (LAR) analysis (Whitehead 1995), where LAR is the probability of finding any given pair of individuals together after different time lags. The LAR was calculated for males within each category (i.e.,

TABLE 1.—Summary of male bottlenose dolphin (*Tursiops aduncus*) alliances in each 2-year time period.

Time period	Number of males categorized	Proportion of males allied	Average half-weight index within alliances (SE)	Average alliance size (SE)
1999–2000	35	0.79	0.83 (0.04)	2.5 (0.21)
2001–2002	36	0.77	0.78 (0.04)	2.7 (0.26)
2005–2006	30	0.69	0.81 (0.06)	2.9 (0.26)
2007–2008	35	0.80	0.79 (0.03)	2.5 (0.21)

males with the same alliance stability index) and compared with the null association rate, which is the association rate if individuals were interacting randomly over time. Standard errors for the LAR and parameter estimates were obtained by jackknifing (displayed as a ± 1 SE 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).

Influence of genetic relatedness on male associations.—Two sets of genetic markers were used to test for an association between genetic relatedness and association patterns for the 34 males that were biopsy sampled. First, a set of 10 nuclear deoxyribonucleic acid (DNA) microsatellite loci markers (TG20—Caldwell et al. 2002; KW2, KW9, KW12, Hoelzel et al. 2002; MK5, MK6, MK8, MK9—Krützen et al. 2001; EV1, EV14—Valsecchi and Amos 1996) were amplified by polymerase chain reaction (PCR). PCR conditions were as reported in Möller and Beheregaray (2004) and Wiszniewski et al. (2010b). No significant departures from Hardy–Weinberg equilibrium expectations and linkage disequilibrium among the 10 microsatellite loci have been detected (Wiszniewski et al. 2010b). There was also no evidence of null alleles at any of the loci. A 460-base pair fragment of the mitochondrial (mt)DNA control region was also amplified for each individual following the protocol described in Möller and Beheregaray (2001). Genotypes from the 10 microsatellite loci were then used to estimate pairwise relatedness between individuals using Queller and Goodnight's (1989) relatedness coefficient, r . The coefficient, ranging from -1.0 to 1.0 , was calculated by comparing the alleles shared by two individuals with the frequency of that allele in the Port Stephens population. The program KINSHIP 1.3.1 (K.F. Goodnight, Rice University) was used to calculate these relatedness coefficients.

We then assessed whether individuals from the same alliance in each of the 4 time periods were more closely related than individuals from different groups using permutation tests in the program PERM (Duchesne et al. 2006). This program first sums r values for all pairs of individuals belonging to the same group (i.e., alliance). The r values are then randomly permuted 40,000 times across groups while maintaining the original group structure. Significance was assessed by comparing the distribution of permuted intragroup sums with the observed sums. The stability of P values estimated over 10 iterations was used to determine the number of permutations required (i.e., the number of permutations was increased until the difference between P values across iterations was less than 0.01). Since statistical significance is dependent on the relatedness values of

all alliances included in the analysis, an alliance may be considered significantly related in 1 time period but not in another if group sizes and relatedness values are different. For mtDNA data, the proportion of males that are expected to match haplotypes was calculated using the formula $\sum_i (p_i)^2$, where p is the frequency of the i th haplotype in the data set (Ott and Longnecker 2001). This probability was then compared with the observed proportion of haplotypes matches among allied males. Furthermore, to determine whether alliance stability was influenced by kinship, we calculated the Pearson's correlation coefficient between alliance duration and genetic relatedness.

Variation in schooling patterns.—Variation in school size was compared among males in different alliance stability categories. On the basis of findings for Shark Bay, where males in a superalliance network interacted in larger groups of males (Connor et al. 1999), we tested the prediction that males in less stable partnerships are found in larger schools. This was assessed by determining the school sizes for each male and categorizing school sizes by the male's level of stability (categories: 1 to 4). Due to nonindependence of the data, we compared the mean school size among the 4 categories using 2-sample randomization tests with 10,000 iterations in the program RT (Manly 1997). The analysis was then repeated for schools without any females present.

RESULTS

Patterns of association among males.—Patterns of association and alliance formation were assessed for 43 adult individuals that were genetically sexed as males ($n = 34$) or identified as potential males through a set of strict association criteria ($n = 9$). Mean levels of association among males sighted at least 12 times over the 8-year study period was low ($n = 38$; $\bar{X} = 0.085$), whereas the coefficient of variation (CV) was significantly higher than for the random data ($CV_{\text{real}} = 1.85$; $CV_{\text{random}} = 1.19$; $P < 0.001$), indicating the presence of long-term preferred associations and avoidances among males. In each 2-year time period, the proportion of males considered allied was high, ranging from 69% to 80%, whereas the average size of alliances was 2.62 (Table 1). Further, 27% of males were always identified with the same alliance partner (stability index = 4), 9% of males had a stability index of 3 (i.e., sighted with the same partner in 3 time periods), 34% had a stability index of 2, and 30% of males had a stability index of 1 (allied in 1 or 0 time periods).

Social network analysis on the basis of the combined 8-year data set illustrates the complex dynamics of male associations in Port Stephens (Fig. 2). The male population was divided

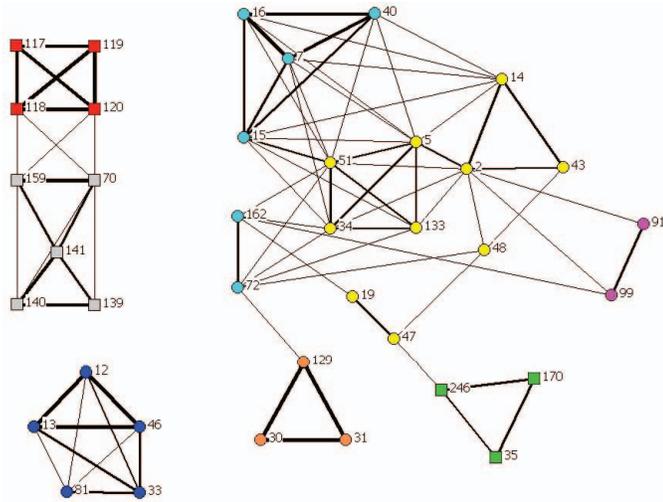


FIG. 2.—Social network of male bottlenose dolphins (*Tursiops aduncus*) in Port Stephens based on the association index (half-weight index [HWI]) for all years. Subgroup structure was identified using the modularity matrix technique that controls for data structure and gregariousness and is illustrated by different colors of the nodes. Community membership is represented by shape, where squares represent western males and circles represent eastern males. Line (edge) thickness running between 2 individuals is proportional to association strength and for clarity, lines are only displayed for association indices greater than 0.14 (twice the mean association index over all individuals).

into 8 groups ($Q_{max} = 0.153$) and of the 38 males that were connected to at least 1 other individual, 2 main types of association patterns were evident: males that were segregated into small groups with strong ties with only a few other individuals, and males that had some strong links but were loosely connected in a larger social network. Males in the former were in alliance stability categories between 2 and 4, whereas males in the larger social network (type 2) had alliance stability indices between 1 and 3.

Stability of male associations.—Since the strength of association among alliance partners varies considerably (ranging from 0.55 to 1.0; Table 2), we assessed whether the strength of association among allies is associated with temporal stability. The duration that alliances lasted in Port Stephens was significantly correlated with association strength ($n = 14, r = 0.615, P = 0.019$). Further, we found that association levels among male dyads in 1 year were positively correlated with association levels in later time periods (correlation between time periods 1999–2001 and 2001–2002: $n = 32, r = 0.791, P < 0.001$; 1999–2001 and 2005–2006: $n = 25, r = 0.798, P < 0.001$; 1999–2001 and 2007–2008: $n = 28, r = 0.698, P < 0.001$; 2001–2002 and 2005–2006: $n = 26, r = 0.778, P < 0.001$; 1999–2001 and 2007–2008: $n = 31, r = 0.708, P < 0.001$; 2005–2006 and 2007–2008: $n = 29, r = 0.828, P < 0.001$). The close relationship between association strength within alliances and the duration of alliances was supported by lagged association rate analysis (Fig. 3). Here, association levels of males who stayed with the same individuals over the entire 8-year study period (alliance category = 4) were consistently higher in a given time period than males in other alliance categories. Males in both categories 4 and 3 also formed the most temporally stable associations, whereas association rates for males in categories 1 and 2 were much less stable (Fig. 3).

For alliances that did not last over the whole study period, only 2 ended due to the disappearance of a partner (disappeared males: 81, 14, and 43) and 1 began after the appearance of 2 males (males 170 and 246). The remaining alliance switches occurred despite the fact that a male’s previous alliance partner was still present in the population after the change. These males were all in the larger social network shown in Fig. 2 in addition to western males 139, 140, and 141.

Influence of genetic relatedness on male associations.—We used microsatellite and mtDNA data available for 34 sampled

TABLE 2.—Male bottlenose dolphin (*Tursiops aduncus*) alliances identified in each 2-year time period. The average half-weight index and genetic relatedness estimate among males genetically sampled (in bold) are displayed in parentheses for each alliance identified. Alliances marked with an asterisk were significantly more related than expected by chance. Males not sighted at least 5 times in each period: ^a 3 and ^b 4 sightings, respectively.

1999–2000	2001–2002	2005–2006	2007–2008
12-13-46 (1.0, -0.26)	12-13-46 (0.88, -0.26)	12-13-46 (0.94, -0.26)	12-13-46 (0.80, -0.26)
117-118-119-120 (0.90, -0.01)	117-118-119-120 (0.90, -0.01)	117-118-119-120 (0.84, -0.01)	117-118-119-120 (0.81, -0.01)
30-31-129 (0.83, -0.24)	30-31-129 (0.71, -0.24)	30-31-129 (0.94, -0.24)	30-31-129 (1.00, -0.24)
139^a-140^b (0.86, 0.20)	139-140-141 (0.73, 0.20)	140-141 (0.6)	139-140 (0.75, 0.20)
70-159 (0.83, 0.39*)	70-159 (0.91, 0.39*)	70-159 (0.97, 0.39*)	70-159-141 (0.85, 0.39*)
34-51 (0.57)	34-51 (0.78)	5^b-34^a-51^b (0.82, 0.07)	5-34 (0.84)
33-81 (0.8, -0.18)	33-81 (0.69, -0.18)		91-99 (0.63)
	91-99 (0.56)		72-162 (0.88)
72^b-133^a (0.57, -0.18)			16^b-40^b (0.75)
7-16 (0.91)	7-15-16-40 (0.94, -0.06)		
15^a-40^a (1.00, 0.20)			
2-14-43 (0.83, 0.17)	2-14 (0.7)		19-47 (0.77)
		35-170-246 (0.55, -0.24)	35-170-246 (0.58, -0.24)

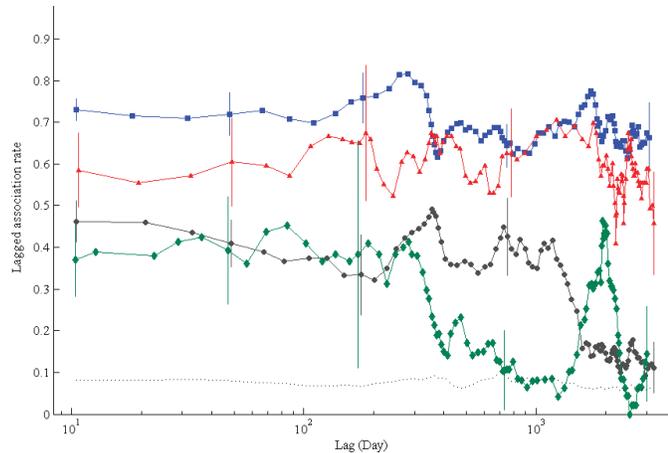


FIG. 3.—Lagged association rate (LAR) within each of the 4 alliance stability categories of bottlenose dolphins (*Tursiops aduncus*). Males in the most stable alliances (category 4) are represented in the blue squares, whereas males in less stable alliances are shown in red triangles (category 3), gray circles (category 2), and green diamonds (category 1). Vertical lines for each LAR are approximately ± 1 SE, which were calculated by jackknifing over 30-day sampling periods. The null association rate (black dotted line) was calculated for all individuals to represent the expected LAR if males were associating randomly.

males to assess the effect of relatedness on alliance partner choice. For mtDNA, 4 haplotypes were identified in Port Stephens (Genbank accession numbers: SEAust1: AF287951; SEAust2: AF287952; SEAust3: AF287953; SEAust5: AF287955). Within each 2-year time block, the sum of within-alliance relatedness values based on microsatellite data was not significantly higher than the expected sum if individuals were grouped randomly (Table 2). The only exception was a stable alliance (males 70 and 159) that was significantly more related than expected by chance in all time periods. For mtDNA, 40% of allied males shared the same haplotype, which is similar to the expected proportion of 38% if individuals were associating randomly. Finally, although some alliances displayed slightly higher levels of kinship, there was no correlation between genetic relatedness and alliance duration ($n = 11$, $r_9 = -0.202$, $P = 0.551$; Table 2, Appendix I).

Variation in schooling patterns.—Males in long-term alliances (i.e., category 4) were observed in smaller schools than males that formed weaker or less stable alliances (Table 3, randomization with category 3 males: $P = 0.0008$; category 2 males: $P = 0.0001$; category 1 males: $P = 0.0001$). Males in categories 3 and 2 were also found in significantly smaller schools than males in category 1 ($P = 0.012$, $P = 0.002$, respectively), although there was no significant difference among males in categories 3 and 2 ($P = 0.43$). Similar patterns were observed for category 4 males when schools containing females were excluded from the analysis (Table 3, randomization between categories 4 and 3: $P = 0.0002$; categories 4 and 1: $P = 0.0001$); however, there was no significant difference in school size between males in the most stable category (4) and category 2 ($P = 0.062$). For the less stable alliance categories,

TABLE 3.—Mean school size of bottlenose dolphins (*Tursiops aduncus*) and standard error for males with different degrees of alliance stability. Stability values range from 1 (males allied in 1 or 0 time periods) to 4 (male identified with the same alliance partner in all four 2-year time blocks).

Stability	All groups		Male-only groups	
	<i>n</i> (groups)	Mean (SE)	<i>n</i> (groups)	Mean (SE)
4	561	8.81 (0.31)	97	3.13 (0.10)
3	121	11.38 (0.86)	22	4.41 (0.55)
2	411	11.21 (0.47)	79	3.52 (0.25)
1	121	14.22 (0.94)	20	5.35 (0.63)

no significant differences in school size were found between males in categories 3 and 2 ($P = 0.121$) and between 3 and 1 ($P = 0.121$), but males in category 1 were sighted in significantly larger schools than category 2 males ($P = 0.002$). These results indicate that males in stable alliances do not associate regularly with males from other alliances.

DISCUSSION

Patterns of male alliance formation.—On the basis of long-term association patterns, our results suggest that alliance formation is the norm for males in the Port Stephens bottlenose dolphin population. However, considerable variation was also found, with males falling into one of three general behavioral categories: males that form strong and highly stable social alliances with 1–3 other males; males that form weaker and more labile alliances; and males that are solitary or allied for only a short period of time. Our findings mirror those of other long-term studies of bottlenose dolphins, in which association rates of long-term alliances match those seen for mother and calf pairs, whereas alliances of shorter duration are usually characterized by lower mean association rates (Connor et al. 2000; Owen 2003). Social network analysis on the basis of the pooled Port Stephens data set also revealed that males in stable alliances may be closely connected with 1 other alliance, but generally do not associate with many others (Fig. 2). In contrast, most males in the less stable alliance category were loosely connected within a much larger social network. These results were supported by school size analysis. In both mixed-sex and all-male schools, males in the most stable alliances were consistently observed in the smallest schools, whereas males in the more fluid social network were more often sighted in schools consisting of a larger number of males and females.

Through modeling, Whitehead and Connor (2005) showed that frequent alliance partner switching could greatly facilitate a male's expected reproductive success when there was low cost involved in switching allies (e.g., time spent finding a suitable partner and establishing a cooperative relationship). Frequent social interactions between males in different alliances may facilitate the development of social ties with prospective alliance partners through increased levels of tolerance and reduced rates of aggression (e.g., chimpanzees, Lehmann and Boesch 2009; Melis et al. 2006). This may be

particularly important in fission–fusion societies, where social conditions change frequently and males range beyond the general population boundary (Krützen et al. 2004b; Möller et al. 2002; Owen 2003). In Port Stephens, males in the more labile alliances were sighted more frequently in larger schools and several of these males had markedly lower sighting rates in some years. All males integrated in the larger social network were also found to concentrate their activities close the entrance of the embayment (Wiszniewski 2010; Wiszniewski et al. 2010b). These results suggest that males may be associating in a larger fission–fusion network, which consists of some males that appear to temporarily join the network from the coastal population or disappear from the study area. Moreover, it appears that the presence of male and female dolphins from the adjacent coastal population, which are frequently sighted near the Port Stephens border or occasionally within the embayment (Möller et al. 2002), may also be influencing male social behavior. This seems likely given that demographic factors, such as population density and social group structure, have been shown to influence male behavior in other group-living mammals (e.g., primates—Chapman and Rothman 2009; Mitani 2006). Similarly to Port Stephens, Connor et al. (1999) found that in the large, open Shark Bay population the highly dynamic 14-male superalliance interacted in larger schools of males compared with males in stable 1st-order alliances who were often sighted alone together. The overlapping home ranges of males in stable and unstable alliances in Port Stephens (Wiszniewski et al. 2009; Wiszniewski 2010) suggests that the differences observed in school size between males in stable and unstable alliances cannot be attributed to resource availability or predation risk (Connor et al. 1999). Instead, variation in school size preferences, especially regarding the number of females that males associate with, may relate to the adoption of different mating strategies. It is important to note that males in both stable and unstable alliance categories maintained long-term associations with some females (Wiszniewski et al. 2010b) and regularly changed their preferences for females, which is most likely a response to the changing reproductive states of females.

Intraspecific variation in alliance formation: evidence of alternative mating strategies?—Intrapopulation variability in male social behavior can represent either fixed alternative mating strategies (e.g., Feh 1999) or condition-dependent strategies, where changes in mating strategies over time may result from changes to the individual's age, dominance rank, competitive ability, or the availability of suitable partners (e.g., De Fraipoint et al. 1993; DuVal 2007; Nishida 1983; Noë 1994). Condition-dependent tactics have been observed in bottlenose dolphins. For instance, Owen et al. (2002) demonstrated that solitary males in the Sarasota Bay population were in a transitional phase rather than adopting an alternative mating strategy. However, discerning whether variation among males in Port Stephens relates to fixed or adaptive mating strategies requires relating individual characteristics such as age and competitive ability to changes in the

individual's social behavior. Obtaining this knowledge on individual characteristics and conducting a comprehensive paternity analysis would help to understand the effectiveness of both strategies at securing paternities in this population.

Differences in association patterns among males in Port Stephens do not appear related to age. For example, heavily scarred males identified at the beginning of the study were categorized in both alliance types. In addition, subadults that were identified on the basis of their smaller size either at the beginning or during the study period have been observed engaging in either typical 1st-order alliance behavior (e.g., synchronized swimming with same individuals, small average school size, and low association rates with other males) or associating with preferred partners within the larger male social network (data not shown). There were also some instances in this study where a male was allied in the first one-half of the study, but appeared to adopt a more solitary strategy in later years despite that fact that their previous alliance partner was still residing in the embayment.

Factors influencing alliance formation.—Analysis of relatedness between male alliance partners confirmed that alliances are generally not composed of relatives. We further showed that higher mean relatedness within some alliances does not lead to greater alliance stability. Cooperation (and stability among allied males) could also not be explained by kin selection in other bottlenose dolphin populations (Krützen et al. 2003; Owen 2003) and some populations of other highly social mammals (e.g., river otters—Blundell et al. 2004; raccoons, *Procyon lotor*—Gehrt et al. 2008; chimpanzees—Langergraber et al. 2007). Although we are currently unable to distinguish between the evolutionary mechanisms promoting cooperative alliance partnerships in Port Stephens in the absence of kin selection (i.e., byproduct mutualism or reciprocal altruism), recent theoretical reviews suggest that alliance or coalition formation generally results from the mutualistic benefits of cooperation (e.g., Clutton-Brock 2009). Moreover, it has been hypothesized that males may prefer alliance partners that are of similar age rather than close relatives as a result of greater familiarity, for example, through growing up in the same social environment and interacting in a more diverse range of social contexts (Mitani et al. 2002; Möller et al. 2001; Owen 2003). Concurrently, if a male's age is linked to his competitive ability, social rank, mating experience, or physical size, and considering that the interbirth interval between successive sons is relatively long (e.g., interbirth interval in the Shark Bay population: average = 4.55, range = 3–6.2; Mann et al. 2000), age difference between alliance partners may be actually negatively correlated with alliance stability (Mitani 2006; Mitani et al. 2002; Owen 2003). Although we are currently unable to test the influence of age-related factors in Port Stephens, there is some evidence to suggest that familiarity is an important factor in alliance partner choice as found in the Sarasota Bay dolphin population (Owen 2003). Importantly, given that one alliance was found to be significantly more related than expected by chance, we cannot completely exclude kinship as a potential

factor influencing alliance partner choice for some males. Alliance formation among kin has been observed for some other populations of bottlenose dolphins (e.g., Bahamas—Parsons et al. 2003) and at least 1 population of chimpanzees (Mitani 2009). In contrast to the Shark Bay dolphin population, however, the influence of kinship in Port Stephens does not appear to be related to different mating strategies among males (Krützen et al. 2003). For example, some stable alliances (i.e., category 4) were composed of kin, whereas other stable alliances contained unrelated males (Table 2, Appendix D). Future investigations are required with a larger and even longer data set to better understand the primary mechanisms involved during the development and maintenance of these cooperative relationships. Of particular interest is to determine how individual factors, such as age and dominance, affect alliance formation, in addition to the fitness benefits that males obtain by cooperating with other males over long periods of time.

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APPENDIX I

Pairwise relatedness between sampled male bottlenose dolphins that were sighted at least 3 times within one 2-year time period. *R* values within alliances are marked in bold.

ID	12	13	46	117	118	119	120	129	139	140	70	159	5	51	33	81	72	133	7	15	40	2	43	170	246	19	37	48	91	123	125	192	214				
12	1																																				
13	-0.41	1																																			
46	-0.12	-0.25	1																																		
117	0.50	-0.10	-0.03	1																																	
118	0.29	-0.07	0.36	0.53	1																																
119	0.45	-0.27	-0.56	0.19	-0.17	1																															
120	0.20	-0.21	0.18	-0.26	-0.19	-0.18	1																														
30	-0.17	-0.55	0.03	-0.24	-0.33	0.04	0.08	1																													
129	0.41	-0.09	-0.34	0.21	0.16	-0.02	-0.27	-0.24	1																												
139	0.02	-0.23	0.15	0.31	0.09	0.04	0.13	-0.18	-0.18	1																											
140	0.26	-0.05	-0.16	0.15	0.03	0.07	-0.52	-0.45	-0.08	0.20	1																										
70	-0.23	-0.62	0.24	0.24	0.27	-0.21	-0.09	0.03	-0.07	0.07	-0.02	1																									
159	-0.42	-0.05	0.10	0.51	0.62	0.18	-0.19	-0.37	0.25	0.06	0.09	0.39	1																								
5	-0.01	-0.28	-0.07	0.11	0.09	0.08	-0.17	-0.16	-0.06	0.23	0.08	-0.11	-0.02	1																							
51	0.19	-0.58	0.06	-0.14	-0.03	-0.03	-0.25	-0.05	-0.23	-0.01	-0.20	0.00	-0.25	0.07	1																						
33	0.23	-0.22	0.07	-0.17	-0.04	0.08	0.05	0.04	-0.28	0.49	0.12	0.00	-0.11	0.08	-0.17	1																					
81	-0.28	-0.11	-0.28	0.20	0.17	0.38	-0.16	-0.15	0.24	-0.10	-0.32	-0.10	0.32	-0.17	-0.07	-0.18	1																				
72	-0.32	-0.15	0.07	-0.11	-0.14	-0.12	-0.21	0.58	-0.10	-0.23	-0.26	-0.15	-0.06	-0.13	-0.19	-0.14	-0.12	1																			
133	-0.34	-0.32	-0.12	-0.05	0.14	-0.16	-0.32	-0.05	0.35	-0.22	-0.12	0.02	0.23	-0.09	0.13	-0.33	0.12	-0.04	1																		
7	0.07	-0.34	0.26	0.10	0.39	-0.19	-0.11	-0.10	-0.20	0.42	0.06	-0.05	0.05	0.22	0.06	0.38	0.05	-0.25	0.21	1																	
15	-0.06	-0.33	-0.06	0.07	-0.08	-0.17	-0.23	0.26	-0.11	-0.34	-0.39	0.03	-0.06	-0.14	-0.12	-0.43	-0.05	0.22	-0.25	-0.27	1																
40	-0.45	-0.35	0.26	0.21	0.24	0.32	0.33	0.30	0.24	-0.01	-0.21	0.09	0.24	-0.01	0.01	-0.08	0.31	0.26	0.02	-0.12	0.20	1															
2	-0.09	-0.11	-0.10	-0.15	0.21	-0.40	-0.40	-0.46	-0.03	-0.20	0.14	0.12	0.30	-0.18	-0.24	0.13	0.01	-0.29	0.05	0.08	-0.60	-0.34	1														
43	-0.41	0.10	0.69	0.18	0.57	-0.30	0.20	-0.09	0.01	0.04	-0.05	0.24	0.39	-0.04	-0.10	-0.03	-0.03	0.00	0.18	0.20	-0.33	0.37	0.17	1													
170	-0.12	-0.14	-0.58	-0.19	-0.22	-0.36	0.19	-0.42	-0.32	-0.24	-0.29	-0.25	-0.34	-0.41	-0.48	-0.11	-0.50	-0.53	-0.38	-0.38	-0.48	-0.39	-0.09	-0.35	1												
246	-0.30	0.43	0.01	-0.08	-0.06	-0.45	-0.29	-0.62	-0.36	-0.12	0.07	-0.40	-0.20	-0.03	-0.32	-0.39	-0.26	-0.29	-0.40	-0.14	-0.31	-0.41	-0.10	0.03	-0.22	1											
19	0.07	-0.07	0.01	0.20	0.08	0.03	-0.11	0.10	-0.09	0.43	-0.05	-0.15	0.05	0.22	-0.11	0.38	0.23	0.34	-0.13	0.32	0.01	0.06	0.09	-0.07	-0.26	-0.14	1										
37	-0.18	-0.28	0.49	-0.03	0.37	-0.12	0.19	-0.03	-0.02	0.01	-0.21	-0.08	0.02	-0.16	0.12	0.04	0.03	-0.19	0.06	0.20	-0.30	0.47	-0.05	0.54	-0.19	-0.35	-0.10	1									
48	-0.11	-0.45	0.14	0.46	0.51	-0.28	-0.37	-0.16	0.32	0.06	-0.03	0.26	0.15	0.14	0.30	-0.28	0.14	-0.13	0.20	0.30	0.27	0.15	0.00	0.04	-0.31	-0.11	0.13	0.19	1								
91	0.19	0.03	-0.04	-0.11	0.01	0.16	0.00	0.11	-0.10	0.16	0.08	-0.28	0.16	0.05	-0.39	0.31	0.25	0.19	-0.14	0.25	-0.19	0.06	0.21	0.03	-0.30	-0.15	0.57	0.00	-0.24	1							
123	-0.13	-0.58	-0.22	-0.38	-0.29	-0.21	0.12	0.01	-0.29	-0.14	-0.38	0.17	0.06	-0.20	-0.43	-0.02	-0.36	-0.07	-0.22	-0.25	0.02	-0.02	-0.41	-0.32	-0.13	-0.47	-0.34	-0.39	-0.46	-0.27	1						
125	-0.21	-0.22	-0.25	0.00	-0.13	0.42	-0.19	0.10	0.12	-0.04	-0.04	0.04	0.05	0.60	-0.02	-0.12	-0.18	0.08	0.09	-0.24	0.01	0.14	-0.47	-0.14	-0.33	-0.36	-0.06	-0.27	-0.12	-0.06	0.04	1					
192	0.04	-0.38	-0.01	-0.10	-0.28	-0.09	-0.21	0.15	-0.37	-0.14	-0.45	-0.06	-0.38	-0.20	0.19	0.04	-0.19	0.13	-0.13	-0.24	-0.09	0.04	-0.29	-0.07	-0.14	-0.52	0.17	0.06	-0.21	-0.26	-0.31	-0.14	1				
214	-0.11	-0.37	-0.02	0.10	-0.05	0.23	-0.28	0.11	-0.06	0.23	0.18	0.07	0.06	0.13	0.30	-0.10	-0.02	0.17	0.10	0.21	0.18	0.07	-0.45	-0.21	-0.72	-0.43	0.22	-0.17	0.21	0.05	-0.04	0.28	-0.06	1			