Original Article

Anthropogenic food patches and association patterns of *Tursiops truncatus* at Lampedusa island, Italy

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Anthropogenic food patches in the marine environment, such as aquaculture farms and active trawlers, may impact on the behavior of marine mammals through modification of habitats, changes in predation pressure, or alterations in food distribution, availability, and predictability, affecting related social interactions and population demographics. This study examined patterns of association of a population of common bottlenose dolphins (*Tursiops truncatus*) around Lampedusa Island (Italy) during 1996–2006 and tested the hypothesis that the trawl fishery and the presence of an aquaculture farm could affect such patterns. Here, we used measures of association between pairs of individuals to assess this impact on social unit composition/cohesion and some analytical techniques to describe the structure of dolphin social networks and temporal stability of associations. Association information for 71 regularly sighted individuals was obtained from photo-identification surveys within groups observed or not at "feeding stations." We found association patterns between dolphins were nonrandom. The Lampedusa population seems to be arranged into 6 clusters and organized in communities composed of animals that were either never seen in association with feeding stations (*N* individuals) or those that are (*Y* individuals), although mixed assemblages were also recorded. Both communities showed long-term preferred companions, with different degrees of social cohesion—as resulted by network measures and temporal analysis. Delineating community structure at Lampedusa Island has offered basic information for further investigations in the area, also providing novel evidences on how disparities in association patterns between bottlenose dolphin individuals may have resulted from a combination of ecological and anthropogenic factors. *Key words:* aquaculture, bottlenose dolphin, feeding, Mediterranean Sea, social structure, trawling fishery, *Tursiops truncatus*. *[Behav Ecol]*

INTRODUCTION

The social structure of many species is plastic; such intraspecific variation is thought to be adaptive (Lott 1991), but it raises the possibility that anthropogenic alteration can modify social structure and behavior, possibly changing the nature of social relationships (Blumstein 2010). Human activities can affect the behavior of mammals through the modification of habitats, changes in predation pressure, or alterations in food distribution, availability (Chilvers and Corkeron 2001), and predictability. This types of changes in food resources via human impact may modify feeding patterns, strategies, and behavior, by influencing also individuals' use of either personal information on resources derived from their own previous experience or social information obtained vicariously (Danchin et al. 2004; Dall et al. 2005), therefore affecting related social interactions as well as population demographics (see Bronikowski and Altmann 1996 for baboons, *Papio cynocephalus*).

Bottlenose dolphins (*Tursiops* spp.) are among the best-known cetaceans. Everywhere they have been studied, bottlenose dolphins live in fission–fusion contexts where animals, as a result of individual movements (van Schaik 1999), frequently join and split from parties (e.g., Smolker et al. 1992; Chapman et al. 1993), therefore forming unstable schools in

size and composition, often on a daily or hourly basis (Connor et al. 2000). Yet despite this fluidity, individuals form long-lasting, individually specific association preferences (Möller et al. 2006). Groups with this kind of highly flexible yet complex form of social relationship and degrees of "fission–fusion dynamics" (Aureli et al. 2008) possibly evolved in response to patchy and ephemeral food sources and perhaps to social and predator pressures too (e.g., van Schaik and van Hooff 1983). The association patterns of individuals can vary dramatically both among populations and within the same population over time (Aureli et al. 2008), being affected by a number of ecological factors and environmental variables that may have a role in shaping social structure, that is, resource acquisition, care of calves, etc (Wrangham and Rubenstein 1986) as well as population density (Connor et al. 2000; Wiszniewski et al. 2009). For example, anthropogenic food patches in the marine environment, such as aquaculture farms and trawlers, concentrate prey items and can be exploited by bottlenose dolphins presumably because it is energetically favorable to do so (Fertl and Leatherwood 1997; Karpouzli and Leaper 2004); thus, they can impact on their populations by causing changes in the spatial use of an area and by altering behavior or social structure and organization (Fertl and Leatherwood 1997; Chilvers and Corkeron 2001, 2003; Díaz López and Shirai 2008). Under this framework, the opportunity to look at patterns of association in nearshore bottlenose dolphin populations affected by human use of coastal waters, especially by fisheries activities and habitat modification (Fertl and Leatherwood 1997; Díaz López 2006a, 2006b), can

provide insight into the impact of such activities on fission–fusion dynamics.

The purpose of this study is to examine patterns of association for common bottlenose dolphins (*Tursiops truncatus*) around the island of Lampedusa (Italy) during the period 1996–2006 and test the hypothesis that the trawl fishery and the presence of a fish farm could affect such patterns, considering that some individuals are already known to interact with these human "feeding stations" in order to exploit them as opportunistic food sources (Pace et al. 1999, 2003). We expected that the social structure of groups seen with or without trawls/fish farm would reflect nonrandom associations occurring within them. Here, we used measures of association between pairs of individuals (i.e., half-weight association index; Cairns and Schwager 1987) to assess this impact on social unit composition and cohesion and analytical techniques to describe the structure of dolphin social networks (Lusseau et al. 2006) as well as temporal and spatial stability of associations (e.g., lagged association rates [LARs]; Whitehead 1995; Owen et al. 2002; Karczmarski et al. 2005). As many species with complex social lives are threatened by human influence, understanding the social behavior of these species, and how anthropogenic modifications of the environment impact social organizations, may prove critical for future conservation efforts (Couzin 2006).

MATERIALS AND METHODS

Study site

Bottlenose dolphins were observed around Lampedusa, a small Italian island included in the Pelagian Archipelago (lat 35°29′–35°52′N, long 012°20′–012°53′E) and located on the African continental shelf, at about 130 km from the Tunisian coast, in the Sicily Channel (Western Mediterranean basin) (Figure 1). Lampedusa is a geographically isolated low populated island, without great coastal impacts and human pressure. However, its waters are exploited by different kind of fisheries, with a significant impact of trawlers ($n = 27$ during the study period, with an additional undefined number of other trawling boats coming from the Sicilian coasts) operating principally in the South-Eastern and Western part of the Island (Pace et al. 1999, 2003). Moreover, an aquaculture inshore cage (containing greater amberjacks *Seriola dumerilii*) was placed at about 35 m depth off the eastern part of the island, between 1997 and 1999, causing a local temporary ecological change around the island (these structures are known to produce considerable amounts of nutrient waste in dissolved form—i.e., ammonia and urea—and in particulate form—i.e., uneaten food and feces, therefore triggering trophic enrichment; see Bergheim and Asgard 1996; Karakassis et al. 2000). The fish farm was destroyed by a storm in 1999 and never reestablished.

The coast and sea bottom of Lampedusa vary from south to north. The southern coast consists of a series of canyons forming a succession of high promontories and small sandy beaches in deep inlets. The bottom slopes softly reaching a maximum depth of 120 m down to the western coast of Tunisia and of 300 m on the eastern coast of Lampedusa. The northern coast consists of high steep cliffs; there are no beaches and the bottom drops off, reaching 300 m depth approximately 1 km off the coast.

Field techniques

Dedicated daily photo-identification surveys were conducted between 1996 and 2006 summer seasons (July–September each year) during daylight hours in calm seas (Beaufort sea state ≤ 3). The distribution of effort varied only according to

weather conditions, trying to equally cover the study area (about 500 km², within 6 nautical miles from the coast) each year, without specific effort at trawls/fish farm. The research platform changed over time: in 1996–1997, it was carried out with a 4 m inflatable boat; in 1998–2001, with two 4.5 and 5.2 m rigid hull inflatable boats and a 12 m sailing vessel (2001 only); and in 2002–2006 with a 4.7 m rigid hull inflatable boat and a 12 m sailing vessel. A code of conduct was established for the observing vessels to minimize their effects on the focal schools (Lusseau 2003a). Observations ended when the weather deteriorated, the focal school was lost or the day ended. During each encounter with dolphins, Beaufort sea state, location (by estimating initial position obtained through triangulation with landmarks in the earlier years and by GPS in later years), behavior, and the total number as well as age class of dolphins in the group were estimated. Information on gender was collected whenever possible.

Once a school was detected, weather or not associated with trawls/fish farm, the identity of individuals in the group was determined using standard photo-identification techniques on the distinctive characteristics (e.g., size, shape, and markings) of their dorsal fins and body markings (Würsig and Jefferson 1990). Photographs were taken throughout the duration of each encounter in an attempt to photograph each individual in the group. During 1996–2001, slide film was used to obtain photographs of dolphin dorsal fins with a Nikon D50 and Canon EOS cameras equipped with 70–210 and 100–300 mm lenses. The slides were later digitized for analysis. During 2002–2006, digital images were obtained using a D70 Nikon camera with 80–300 mm lenses.

Association analysis

Photographs of dorsal fins were sorted according to standard protocols, using nicks, notches, or scars (Würsig and Jefferson 1990). Good quality images of distinctive fins were compared with a photo-identification catalog of known individuals. Unidentified animals were not used in analyses.

For this study, associations were defined using the "gambit of the group," which assumes that animals that are clustered are interacting with one another (Whitehead and Dufault 1999). Therefore, association was defined by membership in the same group, that is, animals photographed in the same group and moving in the same general direction, interacting or engaged in similar activities were considered to be associated (Owen et al. 2002; Rogers et al. 2004; Möller et al. 2006). Focal group follows (Whitehead 2004) were used to collect associations and behavioral data.

A common problem in studies of social association is determining the minimum number of sightings required to include an individual in the analysis. There is no consensus in the literature on the appropriate threshold of sightings required, ranging from 2 (Slooten et al. 1993) or 3 (Rogers et al. 2004) sightings per individual to 10 (Quintana-Rizzo and Wells 2001) or 30 (Gero et al. 2005) sightings per individual. Chilvers and Corkeron (2002) discussed the trade-off between ensuring that data are representative (by including individual animals with low resighting frequencies) while also making sure that data are reliable (by having fewer individuals that were sighted more frequently). Many ($n = 50$) of the total identified animals ($n = 148$) in this study were present in Lampedusa area only during one survey season, compounding the problem of low sighting rates for individuals. Thus, in the absence of a consensus threshold, a commonly employed cutoff of 3 sightings was used. We chose 3 as our limit because it permitted enough individuals to be included in the analysis while allowing the results to be comparable with other studies. To ensure independence of sampling and avoid serial
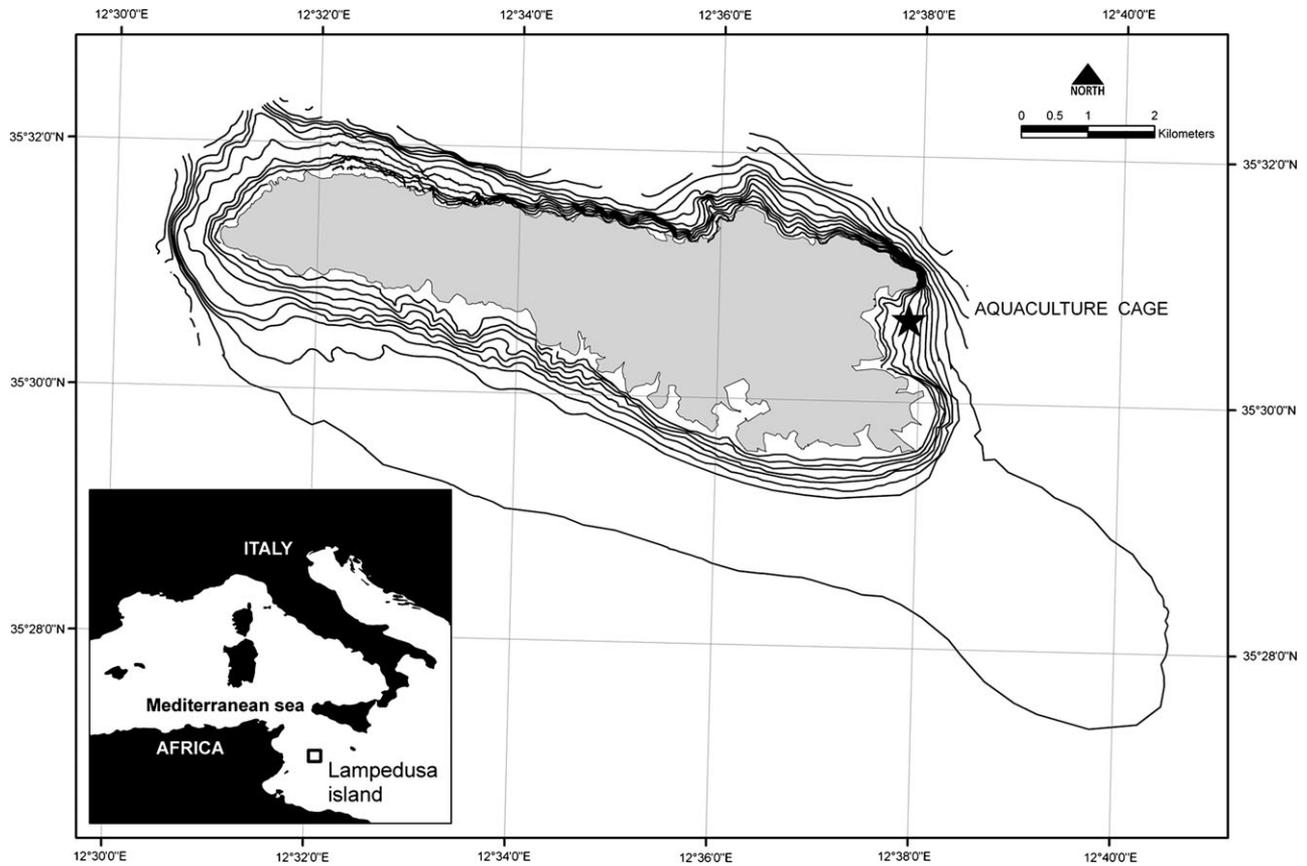
Figure 1
Map of the Mediterranean Sea showing the location of Lampedusa island and the main area in which the study was carried out.

autocorrelation of sightings, only the first sighting of an individual animal was used if an individual dolphin was sighted more than once in a day (Bëjder et al. 1998; Chilvers and Corkeron 2002).

It has become common in animal behavior studies to define an association index as a helpful tool that uses the frequency of specific interactions and behaviors to indicate the strength of a social relationship. An association matrix of all individuals may then be obtained from the group membership samples (Whitehead and Dufault 1999). Coefficients of association are estimates of the proportion of time that particular individuals spend together, and rates may range from 0, for animals that are never seen together, to 1, for animals that are always seen together. The half-weight index (HWI) (Cairns and Schwager 1987; Bräger et al. 1994) was used in this study to compute coefficients of association between the pairs of dolphins. HWI is calculated as: $HWI = 2N/(n_1 + n_2)$, where $2N$ is the total number of joint sightings counted once for every appearance of the 2 individuals together, n_1 is the total number of sightings for one individual and n_2 is the total for the other individual.

The HWI accounts for bias from pairs being more likely to be scored when separate than when together (Cairns and Schwager 1987). Therefore, the HWI was employed because it can be used in instances where not all individuals in a group are photographed and because it allows for comparison with many other studies on bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Bräger et al. 1994; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002; Lusseau 2003b; Möller et al. 2006; Wiszniewski et al. 2009).

HWI was calculated for 71 (of a total of 148) individuals in 1) all encountered groups (ALL; $n = 151$), 2) only groups not encountered at feeding stations (GHF; $n = 95$), and 3) only groups encountered at human feeding stations (GFS; $n = 56$). Individuals were divided into 2 classes: 1) those that were observed following trawls and/or near the fish farm at least once during the study (Y; $n = 55$) and 2) those that were never sighted following trawls and/or near the fish farm in any time during the study (N; $n = 16$). Understandably, GHF groups, that is those not encountered at feeding stations, may include Y individuals as these animals were not exclusively observed following trawls and/or near the fish farm. This was true for 54 of the 55 Y individuals.

We ran analyses on 3 levels to examine potential differences in association patterns of bottlenose dolphin at Lampedusa island: 1) association levels, 2) network metrics, and 3) temporal stability of associations. Given that these analysis are influenced by the number of times animals have been observed, the following aspects were evaluated to understand if sighted groups (and their memberships) were influenced by the higher possibility to encounter animals at human feeding stations: 1) relative abundance index (RAI, expressed in individuals per km; Laran and Drouot-Dulau 2007) in GHF and GFS calculated as $(n/L) \times s$, with n: the number of sighted groups, L: the effort in km (n/L represents the encounter rate), and s: the mean school size; 2) photographic capture rate by Y and N individuals in GHF and GFS groups; and 3) average time (in minutes) spent by Y and N individuals in GHF and GFS groups.

Association levels
The possibility that bottlenose dolphins at Lampedusa island could be divided into clusters, such that association indices are generally high among individuals in the same cluster

and low among individuals in different clusters, was assessed by modularity (Newman 2004). The difference between the proportion of the total association within clusters and the expected proportion if pairwise association coefficients were randomly distributed, given the summed associations of the different individuals (Whitehead 2008b). To find the best delineation, which could be defined as that with the highest modularity, the eigenvector-based method suggested by Newman (2006) was used.

Then, mean (i.e., the mean proportion of time an individual is sighted with each individual in the sampled population) and maximum (i.e., how affiliative an individual is with its closest associate) levels of individual's associations were calculated. The mean association index, calculated as the mean association of all possible dyads in each group, is an estimate of the probability that a randomly chosen member of one class (Y or N) was associated with another randomly chosen individual of the same class or with a randomly chosen member of the opposite class during any sampling period (Whitehead 1997, 1999), and the estimates are insensitive to different numbers of Y and N. The maximum association index represents the mean of the association indices between maximum associates (individuals that shared the highest association rate) within and between classes.

Dyads occurring more often than expected by chance were defined using the Manly and Bejder permutation technique (Manly 1995; Bejder et al. 1998), with modifications introduced in Whitehead (1999, 2008a) and Whitehead et al. (2005), which sequentially inverts the intersection of 2 rows and 2 columns in a 1:0 data matrix, a "flip." This technique tests the significance of these associations by randomly permuting groups within sampling, keeping constant the group size and the number of times each individual was seen. We permuted groups within samples to test the null hypothesis that there are no preferred or avoided companions given the number of groups in which each individual was seen during each sampling period. We used 10 000 permutations until the P value stabilized (Bejder et al. 1998; Whitehead 2008b) with 1000 flips per permutation and a sampling period of 1 day to remove demographic effects occurring during the study period, such as birth, death, immigration, and emigration (Whitehead 1999). After each permutation, the HWI for each pair was calculated, and the observed HWI was compared with expected values of the HWI. If >95% of observed HWI estimates were higher than expected HWI, then it can be concluded that there are nonrandom associations. A dyad was identified as having a preferred association where its association index was ≥0.122: as suggested by Whitehead (2008a) and already used by Durrell et al. (2004) and Gero et al. (2005), this arbitrary value was chosen because it was approximately twice the mean association index, so that these are pairs of individuals that are associated at least twice as much as the expected value of a dyad chosen randomly in the community (Whitehead 2008a). Since it was reported (Whitehead et al. 2005) that low mean of HWIs, produced by short-term preferences, tended to lower the standard deviation (SD) of the HWIs and thus mask the presence of long-term preferences, to compensate for this effect, the coefficient of variation (CV) of the HWIs was used as a test for long-term preferences (Whitehead et al. 2005; Whitehead 2008a). A significantly higher (CV) of real association indices compared with that of randomly permuted data indicates the presence of long-term preferred companions in the population, whereas short-term preferred associations are indicated by a significantly smaller CV (Whitehead et al. 2005; Whitehead 2008b). Avoided companions are indicated by a significantly smaller proportion of nonzero HWIs in the observed versus random data (Whitehead 2008b).

Furthermore, because we have entered a class variable (Y and N), a Mantel permutation test (see Schnell et al. 1985) to investigate for correlations between 2 association matrices was carried out on the null hypothesis that "associations/interactions rates between and within classes were similar" (i.e., whether the dyadic values of one association measure are significantly correlated with those on another). Results were expressed as the t value (with infinite degrees of freedom), P value (for one-tailed test) for the analytical approximation, and matrix correlation coefficient. If within class associations/interactions were higher, t is positive, P large (>0.95), and the matrix correlation is positive (Whitehead 2008b).

The calculation of HWI, the modularity, the permutation test, and the Mantel test were carried out using SOCPROG 2.3 compiled version (Whitehead 2008b).

Network metrics

Three individual-based network statistics calculated from the weighted (association matrix) network were averaged over and within individuals. These included the strength, which represents a measure of individual's gregariousness and is the sum of the association indices for each individual (Barthélemy et al. 2005), the clustering coefficient, which represents a measure of individual sociality and is the proportion of an individual's neighbors who are themselves neighbors (a measure of "cliquishness" as calculated by Holme et al. 2007), and affinity, which represents weighted mean strength of neighbors, that is, determines whether individuals strongly connect to individuals who also have strong connections (Barthélemy et al. 2005). To test whether network structure was influenced by individual association preferences and whether association patterns differ significantly between classes of individuals within sightings, network metrics (Lusseau et al. 2008; Krause et al. 2009) calculated for each class of individual within different groups (ALL, GFH, and GFS) were compared with those of an expected network based on 1000 permutations (until the P value stabilized; see Bejder et al. 1998; Whitehead 2008b). All network analysis was also run in SOCPROG 2.3 (Whitehead 2008b).

Temporal stability of associations

Finally, temporal patterning in social relationships, that is, changes in association rates over time, was calculated for all groups of individuals using the LAR (Whitehead 1995). LAR for any time lag t represents an estimate of the probability that 2 individuals associated at a particular time are still associated t time units later. LAR was initially compared with the null association rate to determine whether nonrandom patterns of associations occurred over the entire study period. The null association rate indicates the expected value of the LAR if there are no preferred associations; in other words, if the associations are random. Mathematical models proposed and used by Whitehead (1995) describing different rates of exponential decay, that is, models of temporal stability, were then fitted to the observed data, to assess the probability of 2 animals remaining associated after various time lags. The components constituting the models tested included (sensu Whitehead 1995): constant companions (CC; stable associations over time, i.e., who stay together permanently), casual acquaintances (CA; nonpermanent relationships, which decay over various time lags but may reassociate at a later time point, i.e., who associate for some time, disassociate, and may reassociate), and rapid disassociations (RD; some associates disassociate very quickly, within one time period). The model best describing the temporal dynamics of association patterns was indicated by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007). Jackknife standard errors for the LAR were calculated by sequentially omitting data from 30-day periods (Whitehead 1995).

Table 1
Number and average size of bottlenose dolphin groups during the study period

Year	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	
Number of groups												Total
Observed	38	64	70	77	20	2	86	87	61	37	34	576
Selected	8	11	40	33	10	2	7	4	7	12	17	151
Group size (selected)												Overall
Mean ± SD	5.25 ± 3.1	5.81 ± 2.82	6.23 ± 3.88	5.66 ± 2.49	3.50 ± 2.06	6.01 ± 1.41	5.87 ± 2.23	6.43 ± 2.88	4.40 ± 1.57	5.66 ± 2.26	6.82 ± 3.77	5.74 ± 3.21
Median	5	5	5	6	3	6	5.5	6.5	4.5	5	5	5
Range	2–12	2–13	2–17	2–12	2–7	5–7	3–10	3–10	2–7	3–20	2–17	2–20

Temporal stability analysis was also run in SOCPROG 2.3 (Whitehead 2008b). All other statistical analysis were performed by SYSTAT 12.

RESULTS

A total of 151 groups was selected for this study of 576 observed between July and September each year (Table 1), with a number of 95 (defined as GHF) not encountered at human feeding stations and a number of 56 (defined as GFS) encountered at human feeding stations. All selected groups met the photo-identification standards (only good quality images of distinctive fins; see MATERIALS AND METHODS).

Seventy-one individuals (of a total of 148) were used in this association study based on the condition that each was seen at least 3 times between 1996 and 2006, with a number of 55 (defined as Y individuals) observed at feeding stations at least once during the study (25 at trawls, 4 at fish farm, and 26 at both) and 16 (defined as N individuals) never seen in association with either anthropogenic activity. GHF groups, that is, those not encountered at feeding stations, may include not only 16 N individuals but also 54 Y individuals because they were not exclusively observed following trawls and/or near the fish farm.

No detectable differences were found in the average group size between GHF (mean = 6.09 ± 3.37, median = 5, range 1–17) and GFS (mean = 5.39 ± 2.75, median = 5, range 1–20) groups (Mann–Whitney U test: $U = 2280$, $P = 0.134$), with an overall value of 5.74 ± 3.21. Observed group size from 1996 to 2006 changed significantly between years (Mann–Whitney U test: $U = 1127$, $P < 0.001$), with a lowest yearly mean of 3.5 ± 2.06 in 2000 ranging up to 6.82 ± 3.87 in 2006, though a distribution over the 11 years ranged from pairs of animals to 20 individuals (Table 1).

As for measurements estimated to understand if sighted groups (and their memberships) were influenced by the higher possibility to encounter animals at human feeding stations, no detectable differences between GHF and GFS groups were observed in RAI values (0.22 and 0.20, respectively) and in both capture rate and average time spent in GHF groups for Y and N individuals (capture rate: $Y = 3.62$, $N = 3.57$; average time: $Y = 332.4$, $N = 328.3$ min). However, Y animals were located with higher rate in GHF than in GFS groups (GHF: mean = 3.62 ± 0.19, median = 4, range 0–12; GFS: mean = 2.81 ± 0.24, median = 2, range 0–6; Mann–Whitney U test: $U = 876$, $P < 0.001$), with higher amount of time spent in GHF groups (GHF: mean = 332.4 ± 0.37, median = 300; GFS: mean = 279.9 ± 0.18, median = 240; Mann–Whitney U test: $U = 986$, $P < 0.001$).

Association levels

The eigenvector method of Newman and Modularity 1 (from gregariousness) divided the Lampedusa population into 6 clusters (clustering using average linkage; cophenetic correlation coefficient = 0.8037), with 3 individuals showing eigs near zero. This division specifically corresponds to differences in the interaction with human activities of the individuals, with one group of 4 animals exclusively composed by N dolphins, one group of 8 animals mostly composed by N individuals ($n = 6$), 3 clusters including a total number of 44 Y individuals only and one mixed group of 15 individuals (10 Y and 5 N). With a value of 0.289, modularity of this arrangement was close to the suggested 0.3 value, which represents a good division (Newman 2006). Sociograms (Figure 2) illustrate relationships between individuals in ALL (a), GHF (b), and GFS (c) groups (study animals are represented by their ID codes; codes without parentheses indicate N individuals).
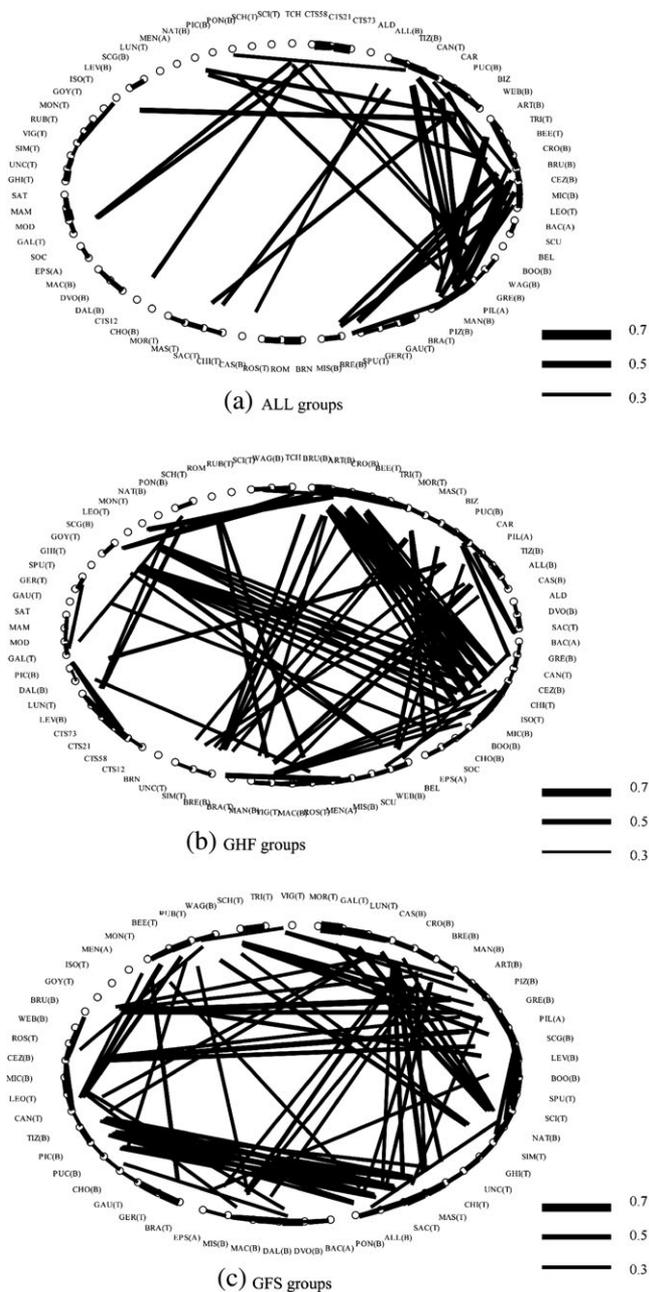
Figure 2
Sociograms showing the associations in ALL (a), GHF (b), and GFS (c) groups. Lines of increasing thickness correspond to increasing pairwise associations. Study animals are represented by their ID codes; codes without parentheses indicate *N* individuals.

Within (a), 2 *N-N* dyads and 4 *Y-Y* dyads had the highest association, with maximum values of 0.67, while among (b), 2 *N-N* dyads, 8 *Y-Y*, and 2 *N-Y* dyads had stronger HWIs, and 16 *Y-Y* within (c). No remarkable changes in the interactions between pairs of individuals were observed after the removal of the fish farm, with only one dyad no longer seen associated again.

Overall association indices were quite low, with a mean association rate of 0.06 (SD = 0.3) (Table 2a). However, max levels of individual's associations, with values of 0.41, 0.44, and 0.55 in ALL, GHF, and GFS groups, respectively (Table 2b), indicate that some individuals formed strong bonds. Significantly,

higher mean levels of association (mean = 0.0634, random = 0.060; *P* < 0.001) and CV of association indices (CV = 1.69042; random CV = 1.16075; *P* < 0.001) in ALL groups indicate that long-term preferred companions between periods are present in the population (Whitehead et al. 2005). A total of 628 preferred associations (25.2%) were identified out of a possible 2485 dyads, that is, they had HWIs above twice the mean index including all zero values (see MATERIALS AND METHODS). All 71 individuals formed at least one preferred association.

Mantel tests (Table 3) demonstrated significantly higher association values among and between classes for different class of individuals seen in ALL and GHF groups. As expected, no differences were seen in GFS groups. The null hypothesis is that associations between classes and within classes are similar; the null hypothesis can be rejected if it does not fall between 0.025 and 0.975 (Whitehead 2003). Interclass associations (*N-Y*) were less strong that intraclass association, with a significant tendency for *Y-Y* associations to be strongest.

The CV of true association indices using maximum likelihood was 0.69 (standard error [SE] = 0.051), indicating a well-differentiated population. With a mean of 0.45 associations per dyad, the correlation between true and estimated association indices was moderate at 0.57 (SE = 0.039), showing that the data set has reasonable power to provide a good representation of social structure (Whitehead 2008b).

Network metrics

The 3 selected network measures showed differences in social behavior between class of individuals and from random expectations. Strength and affinity were always related, meaning that the "important" individuals were preferentially linked with each other, which is known as assortative mixing, a situation that seems generally characterized of social networks (Newman 2002). *Y* individuals had higher values of strength and affinity in ALL and GHF groups than *N*, whereas values significantly lower than expected were observed in GFS (Table 4a). The clustering coefficient remains rather constant at low level (individuals only associate with neighbors); however, an individual's direct associates were less likely to be connected than expected in a random network in ALL and GHF groups for *Y* animals (Table 4a). Within-classes comparisons showed distinctly different patterns between *Y* and *N* individuals, with *N* individuals having a significantly lower strength and affinity than expected by chance, whereas higher significant departure from random was detected in each measure in *Y* animals (Table 4b). The clustering coefficient revealed a denser structure in *N* individuals, although significant lower values than expected in ALL and GHF groups were observed for *Y* animals.

Temporal stability of associations

LAR analysis first indicated that nonrandom associations persisted over the entire study within individuals (Figure 3). LAR for bottlenose dolphins in Lampedusa island showed a decrease in dyads being sighted together again after more than a few weeks. However, the LAR appeared to stabilize above the null association rate (i.e., the rate if animals were randomly associating) as time increases, indicating that the population contains and maintains stable relationships for multiple years. The best fitting model curve (lowest QAIC; Table 5), represented by the equation $a_2 + a_3 * \exp(-a_1 * td)$ of SOCPROG, indicates 3 levels of associates found in this population, consisting of CC (long-term), CA (short-term; individuals associate for a certain length of time and then disassociate), and rapid dissociations (RD; some associates leave very quickly)

Table 2

Mean (a) and max (b) level of associations between and within classes of individuals (Y = individuals seen at anthropogenic feeding stations; N = individuals never seen at anthropogenic feeding stations)

Class of individuals

Groups	n	i	N	Y	N-N	N-Y	Y-Y	Within	Between	Overall
(a) Mean
ALL	151	71	0.04 (0.02)	0.07 (0.03)	0.05 (0.03)	0.04 (0.02)	0.08 (0.03)	0.07 (0.03)	0.04 (0.02)	0.06 (0.03)
GHF	95	70	0.04 (0.02)	0.06 (0.03)	0.05 (0.03)	0.04 (0.03)	0.07 (0.04)	0.06 (0.04)	0.04 (0.03)	0.06 (0.03)
GFS	56	55	—	—	—	—	—	—	—	0.06 (0.03)
(b) Max
ALL	151	71	0.48 (0.16)	0.39 (0.08)	0.47 (0.17)	0.23 (0.11)	0.38 (0.08)	0.40 (0.11)	0.25 (0.11)	0.41 (0.11)
GHF	95	70	0.45 (0.13)	0.44 (0.16)	0.37 (0.18)	0.28 (0.14)	0.43 (0.16)	0.41 (0.15)	0.30 (0.14)	0.44 (0.15)
GFS	56	55	—	—	—	—	—	—	—	0.55 (0.16)

The table shows groups (ALL groups, groups not observed at feeding stations [GHF], and groups observed at feeding stations [GFS]), sample size (n), and total number of individuals (i) seen in groups. SDs are given in parentheses.

(see Whitehead 1999). This suggests that typically individuals remained with a set of associates over periods of days (a mix of CA and CC); however, by the end of some weeks, they had largely disassociated from all individuals except a smaller number of CC. As the smallest difference in QAIC was ΔQAIC = 5.3375, there was no support for any of the other models.

DISCUSSION

This study reveals several important outcomes on how trawl fishery and fish farming can affect grouping patterns for common bottlenose dolphin at the island of Lampedusa. Our results suggest that the presence of anthropogenic food patches can model behavioral repertoire and social structure of the species and that the animals can adjust group cohesiveness flexibly in ways that could have considerable impact on their long-term survival. These findings have both theoretical and practical implications.

Long-term site fidelity is a characteristic of many bottlenose dolphin populations (Wells et al. 1987; Smolker et al. 1992), and Lampedusa Island appears to be no exception. Several individuals were resighted on repeated occasions, both within 1 year and over a span of 11 years, suggesting that the studied dolphins were members of at least one resident population. It is not known whether these dolphins are seasonally resident or remain at Lampedusa Island year round; our data showed that, during summer months, the waters around the island appeared to be favorable for sighting dolphins and areas used intensively by the animals had a significantly higher degree of feeding behavior, whether in association with human activities or not. Because these dolphins exhibit long-term site fidelity and their numbers are relatively small, it is reasonable to as-

sume that common bottlenose dolphins at Lampedusa Island should have ample opportunity to establish bonds and exhibit preferred and/or avoided associates, therefore presentation a certain degree of social stability.

Animals observed around Lampedusa show nonrandom sociality. The eigenvector method of Newman and Modularity 1 (from gregariousness) divided the Lampedusa population into 6 clusters, indicating a society structured by the individuals' aptitude for interacting with human activities, with individuals probably showing genuine social preference rather than simply being a consequence of the gregarious behavior of the individuals. This is made possible by the ability of bottlenose dolphins to recognize and discriminate conspecifics. Association with individuals that have similar foraging preferences and experience may provide substantial benefits, possibly expanding the efficiency of the structured feeding processes needed to safely interact especially with trawling nets. These findings are in contrast with Díaz López and Shirai (2008), who found association strength among preferred associates considerably lower when individuals were opportunistically feeding near fish farms, hypothesizing that during opportunistic behaviors, the benefits derived from cooperation decrease, as it is easier to capture prey, and the costs associated with increased competition among group members increase.

The Lampedusa population appears to be organized in communities (sensu Wells et al. 1999, i.e., regional assemblage of animals that share ranges, interact socially, but do not represent closed reproductive units) composed by 16 animals never observed associated with trawls or fish farm (N individuals) and 55 animals that do so (Y individuals), with mixed assemblages also recorded. This structure seems to be similar to the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population in Moreton Bay, Southeast Queensland (Australia), where animals occur in 2 distinct communities influenced differently by human activities (Chilvers and Corkeron 2001, 2003). Despite their overlapping distributions and observed interaction for possible mating purposes, these 2 communities (identified as "trawler" and "nontrawler" dolphins) showed a certain degree of social segregation, with no interactions between members in other circumstances. As it is highly improbable that this noninteraction occurs by chance, it appears that the members of the 2 communities usually ignore each other. This kind of condition does not seem to characterize the Lampedusa population, where associations between the Y and N individuals are regularly seen in GHF groups, thus having opportunities for social relationships to develop between them. These interclass associations may be a facilitating factor in information exchange for food acquisition and thus

Table 3

Differences in HWI association

Groups	n	t	r	P
ALL	151	5.3981	0.1878	0.999*
GHF	95	2.7932	0.1018	0.989*
GFS	56	0.9332	0.0410	0.759

The table shows groups (ALL groups, groups not observed at feeding stations [GHF], and groups observed at feeding stations [GFS]), sample size (n), results of Mantel tests (t), matrix correlations (r), and P values (p) (H_0 associations between and within classes of individuals are similar).

*Significant differences ($P > 0.95$).

Table 4
Strength, clustering coefficients, and affinity of individuals averaged over (a) and within (b) class of individuals in ALL, GHF, and GFS groups

	Strength			Affinity			Clustering coefficient		
	ALL	GHF	GFS	ALL	GHF	GFS	ALL	GHF	GFS
(a) Class of individuals									
N	2.98 (1.47)	3.06 (1.68)	2.98 (1.47)	3.94 (1.12)	3.99 (1.16)	3.94 (1.12)	0.22 (0.07)	0.20 (0.06)	—
Random	3.32 (1.55)	4.04 (1.90)	3.32 (1.55)	4.92 (0.60)	4.74 (0.82)	4.92 (0.60)	0.21 (0.05)	0.20 (0.06)	—
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	ns	ns	—
Y	4.69 (1.92)	4.10 (2.27)	3.31 (1.75)	5.10 (0.96)	5.05 (0.90)	4.01 (0.83)	0.17 (0.04)	0.21 (0.09)	0.17 (0.04)
Random	4.29 (1.85)	3.80 (2.11)	3.37 (1.81)	4.78 (0.49)	4.40 (0.89)	4.13 (0.85)	0.19 (0.04)	0.24 (0.09)	0.19 (0.04)
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
(b) Within classes									
N-N	1.03 (0.45)	0.86 (0.43)	—	1.16 (0.26)	1.10 (0.16)	—	0.38 (0.16)	0.36 (0.12)	—
Random	2.36 (0.58)	1.58 (0.61)	—	2.89 (0.32)	2.33 (0.20)	—	0.39 (0.17)	0.37 (0.14)	—
P	<0.001	<0.001	—	<0.001	<0.001	—	ns	ns	—
Y-Y	4.12 (1.81)	3.45 (2.11)	3.18 (1.74)	4.63 (0.89)	4.39 (0.95)	4.03 (0.95)	0.19 (0.06)	0.23 (0.10)	0.24 (0.11)
Random	3.95 (1.97)	3.21 (2.36)	3.34 (1.80)	4.38 (0.97)	4.05 (1.01)	4.37 (0.96)	0.22 (0.07)	0.27 (0.09)	0.24 (0.12)
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	ns

Significant differences from a random network were assessed using 1000 permutations. SDs are given in parentheses. ns, not significant.
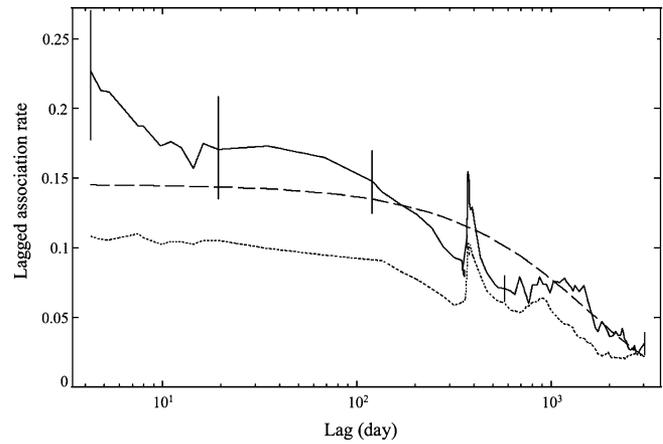

Figure 3
LAR (solid line) compared with the best fitting model (broken line) and null association rate (dotted line) in pooled sightings for all individuals. The plot shows the probability of associations persisting after increasing time lags.

in maximizing overall fitness of the population. However, Mantel tests demonstrated that interclass associations (N-Y) were significantly less strong that intraclass association, with a considerable tendency for Y-Y associations to be strongest. Since individuals were observed without any association with anthropogenic structures in GHF groups and it is possible that the population existed around Lampedusa island prior to the start of the trawl fishery in the 1960s, the opportunistic nature of the interaction and the possible display of cultural differences (Rendell and Whitehead 2001) have to be considered. The hypotheses that all individuals are gradually shifting to a complete "trawler dolphin" population or that some of them choose to not interact with human activities forming a distinct but interrelate community cannot be excluded. As we have no data on the dolphins' social structure prior to the start of the trawl fishery and prior to the beginning of this study, we cannot unequivocally demonstrate that trawling has caused the existing social structure in Lampedusa Island. However, as social interactions provide the opportunity for cultural transmission and social learning (Rendell and Whitehead 2001), with constantly changing school composition, information could have been shared rapidly throughout the population. Bottlenose dolphin populations have been already shown to evolve and transmit foraging methods via social learning and local tradition or culture (Rigley 1983; Pryor et al. 1990; Whiten and van Schaik 2007). Thus, the feeding opportunities for Y dolphins created by trawls, and aquaculture facilities may have become part of their foraging strategies, although these animals are capable of consuming other food sources as demonstrated by their presence in feeding GHF groups. Both human activities concentrate prey items; as a result, bottlenose dolphins have been observed to 1) forage in association with trawls, during which dolphins either feed on the target species or on species that are ancillary to the catch (Fertl and Leatherwood 1997; Chilvers and Corkeron 2001; Pace et al. 2003) and 2) visit fish farm, occasionally or regularly, in search of prey potentially attracted by the cages trigger trophic enrichment (Karakassis et al. 2000; Würsig and Gailey 2002; Dempster et al. 2004; Díaz López and Shirai 2008). At Lampedusa Island, where the feeding preferences of bottlenose dolphins are not known, the catch of the trawl fishery during summer consists of numerous demersal species, including some primarily targeted by bottlenose dolphin in other Mediterranean coastal waters (Bearzi et al.

Table 5
QAIC values for each fitted model of temporal patterning

Model type	Explanation	QAIC
a_1	RD + CC	1272.6750
$\exp(-a_1 * td)$	CA	1224.0172
$a_2 * \exp(-a_1 * td)$	RD + CA	1260.3025
$a_2 + (1 - a_2) * \exp(-a_1 * td)$	CC + CA	1247.7386
$a_2 + a_3 * \exp(-a_1 * td)$	RD + CC +CA	1218.6797
$a_3 * \exp(-a_1 \times td) + a_4 * \exp(-a_2 * td)$	RD + 2 levels of CA	1267.7882
$a_3 * \exp(-a_1 \times td) + (1 - a_3) * \exp(-a_2 * td)$	Two levels of CA	1313.0340

2009), for example, red mullet *Mullus barbatus*, striped red mullet *M. surmuletus*, common cuttlefish *Sepia officinalis*, European squid *Loligo vulgaris*, and common octopus *Octopus vulgaris* (Pace DS, Triossi F, personal observation). Moreover, the fish farm at Lampedusa attracted not only different sea breams and combers species *Diplodus* sp. and *Serranus* sp., respectively, saddled bream *Oblada melanura*, blotched picarel *Spicara maena*, salema, and gilthead seabream but also vorax predators like greater amberjack *S. dumerili* and atlantic bluefin tuna *Thunnus thynnus* (Pace DS, Triossi F, unpublished data), creating a specific local food web of potential interest for bottlenose dolphins. The heavy bottlenose dolphin feeding requirements (the daily food consumption by adults is calculated to be 5–6% of body weight; see Corkeron et al. 1990; Barros and Odell 1995) and the possibility to exploit both anthropogenic food patches may promote the establishment of social relationships that increases feeding efficiency via information exchanges. In fact, all individuals in this study formed long-term preferred partnerships, as revealed by significantly higher mean levels of association and CV of association indices. Higher clustering and more stable associations between individuals may increase the rate of information transfer and reciprocation of cooperative acts during feeding, which are required to exploit spatially and temporally variable prey resources (Perrin and Lehman 2001; Lusseau et al. 2003).

Delineation of community structure in a population and subsequent examination of group dynamics, association rates, and network statistics can provide novel insights into the complex nature of social interactions found in bottlenose dolphins (Wiszniewski et al. 2009). In this study, individual dolphins were sighted with a variety of associates over the study period and were linked, at least indirectly, with the majority of the members of the population to form a large social network. The dolphins associated regularly, with each individual associating with up to 35 other animals, a finding that was similarly reported for the Sarasota Bay bottlenose population, which shows associations with a large number of community members (Wells et al. 1987). One of the mechanisms for the formation of communities within a society is homophily or assortative mixing, that is, individuals associate with others who are like them in some way. The present study also looked at the potential assortativity by class of individuals (*Y* and *N*), finding that the 2 network measures "strength" and "affinity" were related. If nodes with high degree of strength also have high affinity, then the important individuals are preferentially linked with each other (Whitehead 2008a), therefore suggesting the presence of assortative mixing (although this conclusion should be considered with caution as the sex, age, and kin relatedness was still unknown for the majority of individuals in the Lampedusa bottlenose dolphin population). The clustering coefficient remained rather constant at low level, indicating a society in which individuals only associate with their neighbors, who may not associate with each other individuals. Values significantly lower than expected in both ALL

and GHF sightings were observed for *Y* animals, whereas a denser structure emerged in *N* individuals (each dolphin had fewer associates). Combining the fact that each *Y* dolphin had more preferred associates than *N* with significantly lower levels of clustering and higher levels of gregariousness, it is likely that *Y* individuals change partners more regularly. These dolphins may preferentially associate with different individuals during different sightings, whereas the choice of associates for *N* individuals may be more constrained as a result of socioecological and demographic factors. These differences within network measures could be related to the subtle social strategies that individuals employ in maintaining the cohesion of the group, with social costs and benefits probably playing an influential role in determining social unit composition in such a society (i.e., splitting and then resume the cohesion when the costs of aggregating are low or benefits of sociality are high).

The pattern of temporal association between individuals in Lampedusa Island indicated that some associations persisted over the entire study. The best-fit model predicted a general decline in the number of dyads remaining associated over time, with some dyads disassociating quickly (RD) and other individuals that associate for a certain length of time and then disassociate (CA). Nonetheless, some associations persisted throughout time, therefore maintaining stable relationships for multiple years (CC). These results are consistent with the previous findings of this study and sound with the assumption that individuals increase their fitness by choosing behavioral strategies that reduce social conflict with other members of the same population (Bergmüller and Taborsky 2010).

Delineating community structure at Lampedusa Island has offered basic information for further investigations in the area, also providing novel evidences on how disparities in association patterns between bottlenose dolphin individuals may have resulted from a combination of ecological and anthropogenic factors. The feeding opportunities for dolphins created by the constant operation of trawling fishery and by the presence of the aquaculture cage (even if limited in time and space) have become part of their "way of life," therefore directly affecting such top predators population as well as indirectly producing complex social responses.

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REFERENCES

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Condor R, Di Fiore A, Dunbar RIM, Henzi SP, et al. 2008. Fission-fusion dynamics. Curr Anthropol. 49(4):627–654.

Barros NB, Odell DK. 1995. Bottlenose dolphin feeding and interactions with fisheries in the Indian River Lagoon system. Bull Mar Sci. 57:278–285.

Barthelemy M, Barrat A, Pastor-Satorras R, Vespignani A. 2005. Characterization and modeling of weighted networks. Physica A. 346:34–43.

Bearzi G, Fortuna CM, Reeves RR. 2009. Ecology and conservation of common bottlenose dolphins Tursiops *truncatus* in the Mediterranean Sea. Mammal Rev. 39(2):92–123.

Bëjder L, Fletcher D, Bräger S. 1998. A method for testing association patterns of social animals. Anim Behav. 56:719–725.

Bergheim A, Asgard T. 1996. Waste production from aquaculture. In: Baird DJ, Beveridge MCM, Kelly LA, Muir JF, editors. Aquaculture and water resource management. Oxford: Blackwell Science. p. 50–80.

Bergmüller R, Taborsky M. 2010. Animal personality due to social niche specialization. Trends Ecol Evol. 25:504–511.

Blumstein DT. 2010. Social behaviour in conservation. In: Székely T, Moore AJ, Komdeur J, editors. Social behaviour: genes, ecology and evolution. Cambridge: Cambridge University Press. p. 654–672.

Bräger S, Wursig B, Acevedo A, Henningsen T. 1994. Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Galveston Bay, Texas. J Mammal. 75(2):431–437.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. Behav Ecol Sociobiol. 39:11–25.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35:1454–1469.

Chapman CA, White FJ, Wrangham RW. 1993. Defining subgroup size in fission-fusion societies. Folia Primatol. 61:31–34.

Chilvers BL, Corkeron PJ. 2001. Trawling and bottlenose dolphins' social structure. Proc R Soc Lond B Biol Sci. 268:1901–1905.

Chilvers BL, Corkeron PJ. 2002. Association patterns of bottlenose dolphins (*Tursiops aduncus*) off Point Lookout, Queensland, Australia. Can J Zool. 80:973–979.

Chilvers BL, Corkeron PJ. 2003. Influence of trawling on the behaviour and spatial distribution of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Moreton Bay, Australia. Can J Zool. 81:1947–1955.

Connor RC, Wells RS, Mann J, Read AJ. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. In: Mann J, Connor RC, Tyack P, Whitehead H, editors. Cetacean societies: field studies of dolphins and whales. Chicago (IL): University of Chicago Press. p. 91–126.

Corkeron PJ, Bryden MM, Hedstrom KE. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In: Leatherwood S, Reeves RR, editors. The bottlenose dolphin. San Diego (CA): Academic Press, Inc. p. 329–336.

Couzin ID. 2006. Behavioural ecology: social organization in fission-fusion societies. Curr Biol. 16(5):169–171.

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. Trends Ecol Evol. 20:187–193.

Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. Science. 305:487–491.

Dempster T, Sanchez-Jerez P, Bayle-Sempere J, Kingsford M. 2004. Extensive aggregations of wild fish at coastal sea-cage fish farms. Hydrobiologia. 525:245–248.

Díaz López B. 2006a. Bottlenose dolphin (*Tursiops truncatus*) predation on a marine fin fish farm: some underwater observations. Aquat Mamm. 32:305–310.

Díaz López B. 2006b. Interactions between Mediterranean bottlenose dolphins (*Tursiops truncatus*) and gillnets off Sardinia, Italy. ICES J Mar Sci. 63:946–951.

Díaz López B, Shirai BJA. 2008. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. Behav Ecol Sociobiol. 62:887–894.

Durrell JL, Sneddon IA, O'Connell NE, Whitehead H. 2004. Do pigs form preferential associations? Appl Anim Behav Sci. 89:41–52.

Fertl D, Leatherwood S. 1997. Cetacean interactions with trawls: a preliminary review. J Northwest Atl Fish Sci. 22:219–248.

Gero S, Bëjder H, Whitehead J, Mann J, Connor RC. 2005. Behaviourally specific preferred associations in bottlenose dolphins, Tursiops spp. Can J Zool. 83:1566–1573.

Holme P, Park SM, Kim BJ, Edling CR. 2007. Korean university life in a network perspective: dynamics of a large affiliation network. Physica A. 373:821–830.

Karakassis I, Tsapakis M, Hatziyanni E, Papadopoulou KN, Plaiti W. 2000. Impact of cage farming of fish on the seabed in three Mediterranean coastal areas. ICES J Mar Sci. 57:1462–1471.

Karczmarski L, Wursig B, Gailey G, Larson KW, Vanderlip C. 2005. Spin-ner dolphins in a remote Hawaiian atoll: social grouping and population structure. Behav Ecol. 16:675–685.

Karpouzli E, Leaper R. 2004. Opportunistic observations of interactions between sperm whales and deep-water trawlers based on sightings from fisheries observers in the northwest Atlantic. Aquat Conserv Mar Freshw Ecosyst. 14:95–103.

Krause J, Lusseau D, James R. 2009. Introduction to animal social networks. Behav Ecol Sociobiol. 63(7):967–973.

Laran S, Drouot-Dulau V. 2007. Seasonal variations of striped dolphins, fin- and sperm whales' abundance in the Ligurian Sea (Mediterranean Sea). J Mar Biol Assoc U K. 87:345–352.

Lott DF. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge: Cambridge University Press.

Lusseau D. 2003a. Male and female bottlenose dolphins Tursiops spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. Mar Ecol Prog Ser. 257:267–274.

Lusseau D. 2003b. The emergent properties of a dolphin social network. Proc R Soc Lond B Biol Sci. 270(2):S186–S188.

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson SM. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? Behav Ecol Sociobiol. 54:396–405.

Lusseau D, Whitehead H, Gero S. 2008. Incorporating uncertainty into the study of animal social networks. Anim Behav. 75: 1809–1815.

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. J Anim Ecol. 75:14–24.

Manly BFJ. 1995. A note on the analysis of species co-occurrences. Ecology. 76(4):1109–1115.

Möller LM, Beheregaray LB, Allen SJ, Harcourt RG. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Behav Ecol Sociobiol. 61:109–117.

Newman MEJ. 2002. Assortative in networks. Phys Rev Lett. 89:208701.

Newman MEJ. 2004. Analysis of weighted networks. Phys Rev E. 70:056131.

Newman MEJ. 2006. Modularity and community structure in networks. Proc Natl Acad Sci U S A. 103:8577–8582.

Owen ECG, Wells RS, Hofman S. 2002. Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, Tursiops truncatus, in Sarasota, Florida, provide no evidence for alternative male strategies. Can J Zool. 80:2072–2089.

Pace DS, Pulcini M, Triossi F. 1999. *Tursiops truncatus* population at Lampedusa Island (Italy): preliminary results. Eur Res Cetaceans. 13:165–169.

Pace DS, Pulcini M, Triossi F. 2003. Interaction with fishery: modalities of opportunistic feeding for bottlenose dolphins at Lampedusa Island. Eur Res Cetaceans. 17:132–135.

Perrin N, Lehman N. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. Am Nat. 158:471–483.

Pryor K, Lindbergh J, Lindbergh S, Milano R. 1990. A dolphin-human fishing cooperative in Brazil. Mar Mamm Sci. 6:77–82.

Quintana-Rizzo E, Wells RW. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization. Can J Zool. 79:447–456.

Rendell LE, Whitehead H. 2001. Culture in whales and dolphins. Behav Brain Sci. 24(2):309–382.

Rigley L. 1983. Dolphins feeding in a South Carolina salt marsh. Whalewatcher. 7:3–5.

Rogers CA, Brunnick BJ, Herzing DL, Baldwin JD. 2004. The social structure of bottlenose dolphins, *Tursiops truncatus* in the Bahamas. Mar Mamm Sci. 20:688–708.

Schnell DG, Watt DJ, Douglas ME. 1985. Statistical comparison of proximity matrices: applications in animal behavior. Anim Behav. 33:239–253.

Slooten E, Dawson SM, Whitehead H. 1993. Associations among photographically identified Hector's dolphins. Can J Zool. 71: 2311–2318.

Smolker RA, Richards AF, Connor RC, Pepper JW. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour. 123:38–69.

van Schaik CP. 1999. The socioecology of fission–fusion sociality in orangutans. Primates. 40:69–86.

van Schaik CP, van Hooff JAR. 1983. On the ultimate causes of primate social systems. Behaviour. 85:91–117.

Wells RS, Boness DJ, Rathbun GB. 1999. Behavior. In: Reynolds JE III, Rommel SA, editors. Biology of marine mammals. Washington: Smithsonian Institution Press. p. 324–422.

Wells RW, Scott MD, Irvine AB. 1987. The social structure of free-ranging bottlenose dolphins. In: Genoways HH, editor. Current mammalogy. New York: Plenum Press. p. 247–305.

Whitehead H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. Behav Ecol. 6:199–208.

Whitehead H. 1997. Analyzing animal social structure. Anim Behav. 53:1053–1067.

Whitehead H. 1999. Testing association patterns of social animals. Anim Behav. 57:F26–F29.

Whitehead H. 2003. Sperm whales: social evolution in the ocean. Chicago (IL): University of Chicago Press.

Whitehead H. 2004. The group strikes back: follow protocols for behavioral research on cetaceans. Mar Mamm Sci. 20:664–670.

Whitehead H. 2007. Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. Commun Stat Simul Comput. 36:1233–1246.

Whitehead H. 2008a. Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago (IL): University of Chicago Press.

Whitehead H. 2008b. Compiled version of SOCPROG 2.3 [computer program] and manual "Programs for analyzing social structure" [cited 2008 February 17]. Available from: http://myweb.dal.ca/~hwhitehe/social.htm. p. 73.

Whitehead H, Bejder L, Ottensmeyer AC. 2005. Testing association patterns: issues arising and extensions. Anim Behav. 69:E1–E6.

Whitehead H, Dufault S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Adv Study Behav. 28:33–74.

Whiten A, van Schaik CP. 2007. The evolution of animal 'culture' and social intelligence. Philos Trans R Soc B Biol Sci. 362:603–620.

Wiszniewski J, Allen SJ, Möller LM. 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. Anim Behav. 77:1449–1457.

Wrangham RW, Rubenstein DI. 1986. Social evolution of birds and mammals. In: Rubenstein DI, Wrangham RW, editors. Ecological aspects of social evolution: birds and mammals. Princeton (NJ): Princeton University Press. p. 452–470.

Würsig B, Gailey GA. 2002. Marine mammals and aquaculture: conflicts and potential resolutions. In: Stickney RR, McVay JP, editors. Responsible marine aquaculture. New York: CAP International Press. p. 45–59.

Würsig B, Jefferson RA. 1990. Methods of photo-identification for small cetaceans. In: Hammond PS, Mizroch SA, Donovan GP, editors. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Cambridge: International Whaling Commission. p. 43–52.