

Quantifying the influence of sociality on population structure in bottlenose dolphins

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Summary

1. The social structure of a population plays a key role in many aspects of its ecology and biology. It influences its genetic make-up, the way diseases spread through it and the way animals exploit their environment. However, the description of social structure in nonprimate animals is receiving little attention because of the difficulty in abstracting social structure from the description of association patterns between individuals.

2. Here we focus on recently developed analytical techniques that facilitate inference about social structure from association patterns. We apply them to the population of bottlenose dolphins residing along the Scottish east coast, to detect the presence of communities within this population and infer its social structure from the temporal variation in association patterns between individuals.

3. Using network analytical techniques, we show that the population is composed of two social units with restricted interactions. These two units seem to be related to known differences in the ranging pattern of individuals. By examining social structuring at different spatial scales, we confirm that the identification of these two units is the result of genuine social affiliation and is not an artefact of their spatial distribution.

4. We also show that the structure of this fission-fusion society relies principally on short-term casual acquaintances lasting a few days with a smaller proportion of associations lasting several years. These findings highlight how network analyses can be used to detect and understand the forces driving social organization of bottlenose dolphins and other social species.

Key-words: bottlenose dolphin, network theory, population ecology, social structure, *Tursiops*.

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Introduction

Social animals tend to organize in units that can react differently to various density-dependent and density-

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independent factors (Bronikowski & Altmann 1996; Whitehead & Rendell 2004). It can therefore be misleading to assess the dynamics of populations without considering the heterogeneity imposed by social structure. For example, different social units, or communities, can have varying foraging success depending on environmental conditions (Whitehead & Rendell 2004), which in turn can produce stratification of the survival and reproductive successes of their members. Social animals must make choices to join and leave groups of conspecifics throughout their life (Krause & Ruxton 2002). The way that individuals interact with conspecifics is influenced by intrinsic factors such as the presence or absence of preferred associates. In turn, these intrinsic factors are shaped by extrinsic habitat

characteristics including both density-dependent factors such as prey availability (Baird & Dill 1996; Fritz & deGarinéWichatitsky 1996; Honer *et al.* 2002; Lusseau *et al.* 2004; Vucetich, Peterson & Waite 2004) and density-independent pressures such as landscape complexity (Bronikowski & Altmann 1996; Templeton & Giraldeau 1996; Lusseau *et al.* 2003). The resulting social structure of an animal population becomes a fundamental component of its biology, influencing its genetic make-up (Pusey & Wolf 1996; Sugg *et al.* 1996; Krutzen *et al.* 2003), the spread of diseases (Newman 2002b; Corner, Pfeiffer & Morris 2003), pathways of information transfer (King 1991; McComb *et al.* 2001; Leavens 2002; McComb *et al.* 2003), and the way that the population exploits its environment (Hoelzel 1993; Baird & Dill 1996; Connor *et al.* 1998). Identifying the occurrence, number and composition of social groupings helps reveal individual association preferences, and is an important prerequisite for characterizing the social structure of a population (Whitehead 1997). However, in this process it is important to tease apart aggregative behaviour driven by an external force, such as prey distribution or landscape structure, and those resulting from genuine social preferences.

In his seminal 1976 article, Robert Hinde described a conceptual framework for studying the emergence of social organization and structure in animal populations. Thirty years later, this framework is still a landmark and regularly used (Sambrook, Whiten & Strum 1995; Gamble 1998; de Waal 2000; Gowans, Whitehead & Hooker 2001; Kappeler & van Schaik 2002; Kozłowska & Hanney 2002; Sigurjonsdottir *et al.* 2003). However, the latter part of this framework, the study of animal social structure, has received little attention in nonprimates (Whitehead 1997). The structure, that is 'understanding the patterning of relationships independently of the particular individuals concerned' (Hinde 1976), can be problematic to determine in species for which meaningful relationships are difficult to describe. In particular, to abstract the patterning of relationships in a model, one must first describe these patterns in what Hinde called the surface structure.

Quantifying the surface structure of an animal society is difficult, because it represents a complex agglomeration of objects (individuals, also called vertices thereafter) in which relationships change in time and space. Network analyses developed in physical sciences, and more recently furthered in social sciences, provide a set of tools with a proven track record for dealing with such complex adaptive systems (Watts & Strogatz 1998; Newman 2001, 2003b; Newman *et al.* 2001). They can help to describe the architecture of networks of animal social relationships, and also find the features driving them (Lusseau & Newman 2004). In most animal studies, the relationship between pairs of individuals (dyads) is defined by time spent together using an association index (Whitehead & Dufault 1999). Various studies have shown that individuals

spending more time together than would be expected by chance tend to be socially associated; for example, forming alliances in bottlenose dolphins (Connor, Heithaus & Barre 1999, 2001) and chimpanzees (Mitani & Amstler 2003). Therefore it appears that measuring how much time animals spend together is a behaviourally meaningful way of quantifying their social association (Hinde 1976). The rate at which association between individuals changes over time in a society (lagged association rates) can also help abstract the social structure of a population (Whitehead 1995).

One problem with this approach is that association patterns based upon the amount of time that animals spend together are influenced both by individual ranging patterns or habitat preference, and by genuine social affiliations. Recent work on the bottlenose dolphin population studied in this paper has shown that there is considerable variation in ranging patterns. Some individuals have only been observed within a core-study area, while others range more widely and visit the core area only occasionally (Wilson *et al.* 2004). Consequently, estimates of association patterns may be biased because individuals with similar ranging patterns are more likely to be sighted together.

In this study, we used network analyses, association analyses, and estimates of lagged association rates to investigate social structuring in this population of coastal bottlenose dolphins. In particular, we focused our analyses on data collected at different spatial scales to tease apart the social component of the observed associations from the spatial segregation of animals. The goal of this study is to determine the temporal and spatial structure of social interactions in this population. First, we assess whether the observed variation in ranging pattern corresponds to separate social units or only result from aggregative behaviour and then we assess how associations among individuals are persistent with time.

Materials and methods

STUDY POPULATION AND FIELD SAMPLING

Observations were conducted in the inner Moray Firth and adjacent coastal waters of eastern Scotland (Fig. 1). This area is used by a resident population of *c.* 130 bottlenose dolphins, of which approximately 60% of individuals can be reliably distinguished over long periods using photographic documentation of natural markings (Wilson, Hammond & Thompson 1999).

Observational data on the associations of these individuals were made during boat-based surveys carried out during summer months (May to September) from 1990 to 2002 (Wilson, Thompson & Hammond 1997). The primary goal of these surveys was to estimate the abundance of bottlenose dolphins using photographic mark-recapture techniques (Wilson *et al.* 1999). Most surveys were conducted within a 250-km² core-study area within the Moray Firth (Fig. 1), which was further

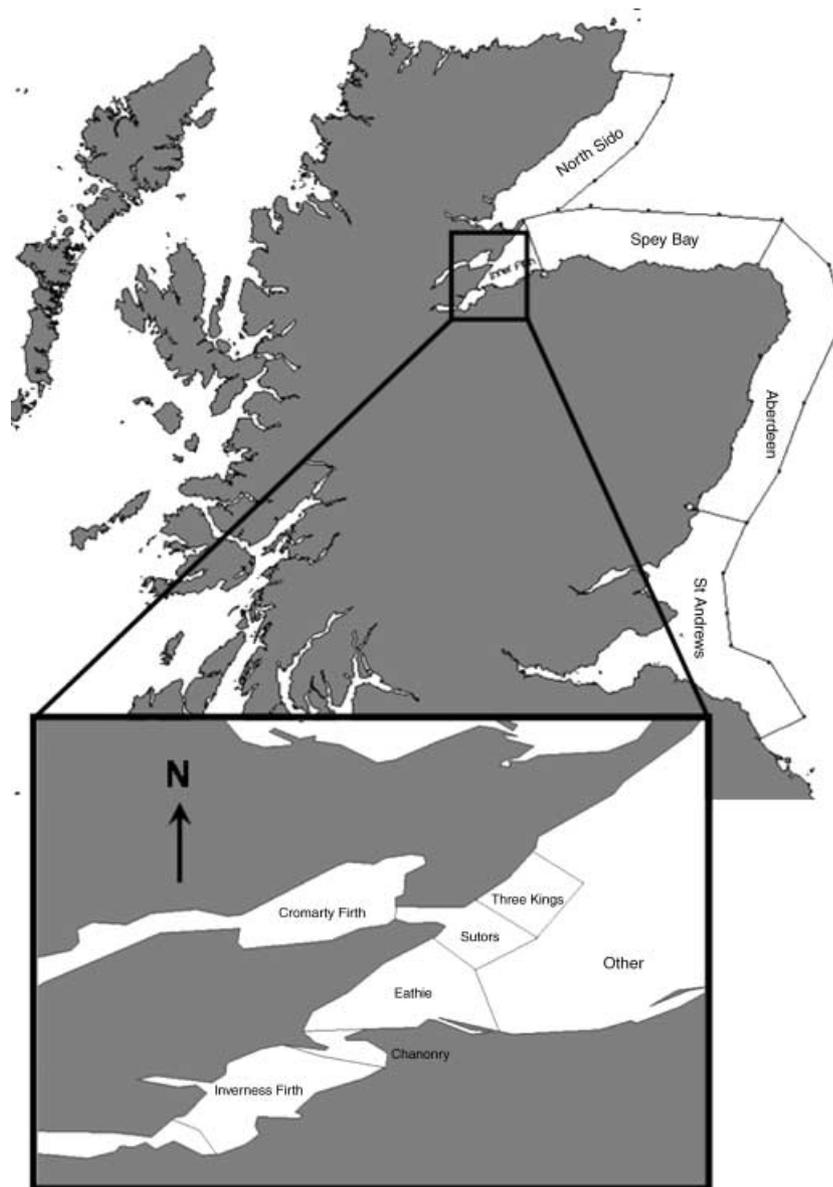


Fig. 1. Map of the study area. The home range of the population extends from the Moray Firth to the Firth of Forth (St Andrews subarea). Most of the sampling took place in the inner Moray Firth (inset) which was divided into several subareas.

subdivided into six subareas. Wider-scale surveys were also conducted along the coast south from the Moray Firth to the Firth of Forth on a less regular basis. Survey design and effort has varied between years, in response to variations in weather and attempts to increase recapture probabilities as the use of the core study area has declined (see Wilson *et al.* 2004). However, in summers (May–September) of all years we made at least 10 surveys within the core study area, with all except the Inverness Firth subarea being visited in each year.

In all cases, once a school was encountered, individuals were photographed and later identified using natural markings on their dorsal fins such as scars, nicks and lesions (Wilson *et al.* 1999). A school was defined as individuals within 100 m of one another behaving in a co-ordinated fashion (Wells, Scott & Irvine 1987).

DEFINING RELATIONSHIPS BETWEEN INDIVIDUALS

We used only high-quality photographs to distinguish individuals in the encounter based on the pattern of nicks, lesions, scars and variation in dorsal fin shape (Wilson *et al.* 1999). Association analysis were only conducted for individuals with reliable markings that were known to last for several years (Wilson *et al.* 1999), but the photographs of all individuals were used to assess which groups were used in the analyses of social structure. Specifically, we only used data from encounters in which at least 50% of all dolphins estimated to be present were photo-identified. Of these encounters, all individuals present were photo-identified in 50% of schools, and 72% of the schools had three-quarters of the individuals identified.

For the association analysis of reliably marked individuals, individuals were defined as associated if they were present in the same school. We assessed the relationships among dyads in the social network of the population using the half-weight index of association (Cairns & Schwager 1987) that quantifies associations on a scale from 0 (two individuals never seen together) to 1 (two individuals always seen together). The half-weight index ($\text{HWI} = 2X/[A + B]$, where X is the number of times dolphins A and B were seen together and A and B are the total number of times dolphins A and B were sighted) was used to minimize bias due to sampling techniques (Cairns & Schwager 1987) and to enhance comparability with other bottlenose dolphin studies (Wells *et al.* 1987; Smolker *et al.* 1992; Lusseau *et al.* 2003). Individuals were only used in the analysis if they had been observed more than five times during the study period (Chilvers & Corkeron 2002). Almost all individually recognizable animals have spent at least some of their time within our core study area in the inner Moray Firth (Fig. 1 inset). However, using repeated observations from within and outside this area, we divided individuals into two broad categories: those that have only ever been observed in the inner Moray Firth and those that have been observed in both the inner Moray Firth and other parts of the population's home range (Wilson *et al.* 1997, 2004).

Defining preferred companionships

Preferred companionships, i.e. associations occurring more often than expected by chance, were defined in two ways. First, all dyads with an HWI greater than HWI_{null} were defined as preferred companionships, where $\text{HWI}_{\text{null}} = n_{\text{associate}}/[N - 1]$ relates to the average association index obtained if an individual associates at random in the population (N is population size) (Whitehead 1995) and therefore has $n_{\text{associate}}$, which is the average school size in which the individual is found.

Dyads occurring more often than expected by chance were also defined using the Manly Bejder permutation technique (Bejder, Fletcher & Brager 1998). This technique tests the significance of these associations by randomly permuting individuals within schools, keeping the school size and the number of times each individual was seen constant using SOCPROG 1.3 (Whitehead 1999) (available at <http://www.dal.ca/~hwhitehe/social.htm>). This is achieved by switching two individuals present in two different schools. After each permutation the HWI for each pair was calculated and the observed HWI was compared with expected values of the HWI. If more than 95% (one-tailed test) of expected HWI were smaller than the observed HWI, the pair of dolphins was defined as a preferred companionship. The number of permutations was set to 500 000 to allow for an average of 200 permutations per dyad.

The first technique is advantageous because it relies directly on the association indices. However, association indices are proportions and therefore provide only

an indication of the association strength between two individuals that relies on the number of times individuals have been observed (which is why we restricted the data to individuals observed at least five times). The second technique takes this uncertainty into consideration. However, it does not rely directly on the association indices and may be affected by spatial structuring of the samples. It also depends on an arbitrary cut-off point (the acceptable level of type II errors). It is therefore valuable to compare the results obtained using both these techniques.

COMMUNITY STRUCTURE AND GEOGRAPHICAL ASSORTATIVE MIXING

We used the Girvan–Newman algorithm to detect community structure within the network (Girvan & Newman 2002; Lusseau & Newman 2004; Newman & Girvan 2004). The method finds natural divisions of networks into tightly knit groups by looking for the boundaries that run between groups. Boundaries were identified using a ‘betweenness’ measure (Freeman 1977). Betweenness quantified how often an edge between two individuals, which is a preferred companionship here, was crossed when moving between any pair of individuals on the network graph. The more often an edge was passed, the higher its betweenness; it therefore identified bottlenecks in the network. In other words, the technique finds pairs of dolphins that are often used in the network graph when moving from one dolphin to another. Edges with the highest betweenness scores were removed from the network, leaving behind the groups themselves. The algorithm breaks the network into a number of communities (= groups), from one to n communities, where n is the number of individuals studied. To select the best division, i.e. the division which provides the most edges within communities and the least between, we calculated a modularity index, Q (Newman 2003a). The modularity index quantified the number of edges running within and between communities:

$$Q = \sum_i (e_{ij} - a_i^2),$$

where i (rows) = j (columns) is the number of communities, e_{ij} is the proportion of edges running between communities i and j , and $a_i = \sum_j e_{ij}$. A good community division should have many edges within communities and few between, leading to high Q -values. The first local peak in Q -values indicates divisions between communities (Newman 2003a; Lusseau & Newman 2004).

Here we are interested not just with the fact that divisions exist within our network, but also with understanding whether the ranging pattern of individuals plays a part in defining those communities. We are therefore looking for geographical homophily, or assortative mixing, the preferential association of individuals with others who are like them in some way (Newman 2002a). Using the two broad ranging pattern

categories, this effect can be quantified using an assortativity ‘correlation’ coefficient (Newman 2003a). Let e_{ij} be the fraction of ties in the network that connect individuals of type i to individuals of type j . Then the assortativity coefficient is defined as

$$r = \frac{\sum_i e_{ii} - \sum_{ijk} e_{ik} e_{jk}}{1 - \sum_{ijk} e_{ik} e_{jk}}$$

This quantity equals 1 when we have perfect assortative mixing (all individuals associate solely with others of the same type as themselves) and zero when mixing is random. Partial mixing gives values between 0 and 1. The standard deviation of r was calculated as described in Newman (2003a).

Teasing apart spatial from social structure

If the movement of some dolphins is restricted in space, e.g. confined to the inner Moray Firth, these dolphins are more likely to be found in the same school just by chance. If any homophily is detected in the previous analysis (see section above) it may be related to spatial sampling bias because some individuals were more likely to be observed in some locations than in others. We therefore performed the same analyses using only data collected in those areas where individuals with both types of ranging patterns (inner Moray Firth only or inner Moray Firth and elsewhere) were equally likely to be encountered (Wilson *et al.* 1997), having therefore an equal chance to interact. Therefore, if any assortativity by home range characteristics emerged in the schools encountered there, it should be the result of social structure. To detect these areas, and confirm that the findings in Wilson *et al.* (1997) remained consistent throughout the study period, we calculated for each subarea (Fig. 1) the proportion of encounters with both types of individuals.

MODELLING THE SOCIAL STRUCTURE OF THE POPULATION

Network properties

Defining the local and global structure of the social network can help elucidate the dynamics of affiliations, illustrating how individuals associate with their neighbours and how they relate to other communities. We focused on three properties of the network architecture. First we calculated the clustering coefficient, C , which is a measure of the likelihood that, if two individuals α and β are associates and α is associated with γ , then β and γ are also associated. The quantity C therefore measures the number of triads in the network compared with the total possible number of triads given the number of individuals present. We also calculated the average shortest path, l , between all individuals; that is if we ‘travel’ from one individual to the next on the network, on average how many individuals

do we go through on the way. These two measures provide clues to the shape of the network; essentially they help classify the network as being either random, ordered or a small world (Newman 2003b). Small world networks share properties with both random and ordered networks as they have a high clustering coefficient (characteristic of ordered networks) and a short average shortest path (characteristic of random networks). That is, they are highly clustered yet all individuals can be reached in only a few steps. We therefore compared the properties of the social network with random networks that were designed to have the same number of vertices and edges but where edges were randomly distributed among vertices. The properties were calculated using Ucinet (Borgatti, Everett & Freeman 2002), the networks were drawn using Netdraw (Borgatti 2002), and the random networks were designed using Pajek (Batagelj & Mrvar 2002).

Finally, recent studies show that affiliation processes can also be derived from degree homophily (Newman 2003b). The degree of a vertex (an individual in the network graph) is the number of edges (preferred companionships) linking it to other vertices (Newman 2003b). Using the same assortativity technique as described above we determined whether individuals tended to associate with others that had similar degree values.

Lagged association rate

We plotted the lagged association rate in relation to time both for all relationships (all dyads) and for within and between communities relationships using SOCPROG. We then tested various social structure models (Whitehead 1995) and selected the best fitting and most parsimonious model using Akaike Information Criteria (AIC) (Burnham & Anderson 1998). The models tested were developed using exponential decay and constants to mimic the dynamic of association patterns between pairs of individuals (Whitehead 1995). The models are composed of three components and any meaningful combination of those. These components are constant companionships, rapid disassociation (that is association lasting less than a few hours), and casual acquaintances that can last from a few days to a few years. For this latter component, the duration of the acquaintances is directly approximated from the exponent of the exponential function (τ , in days). We tested eight social structure models ranging from societies composed only of constant companionships (in which the association rate, $g(d)$ in days (d), remains constant through time $g(d) = 1$) to models considering two levels of casual acquaintances and some rapid disassociation ($g(d) = ae^{-d/\tau_1} + be^{-d/\tau_2}$), where a and b are the proportion of animals with which an individual associates at rates given by the exponential functions). The error around both the duration of the acquaintances and the proportion of relationships within the society that are represented by the components was estimated using jack-knifing (see Whitehead 1995 for more details).

Results

COMPARING SOCIAL NETWORKS

Between 1990 and 2002, there were 930 encounters with dolphins during which school composition information was collected during the summer months. Of those, 809 schools were suitable for analyses given our selection criteria. Using both network construction techniques, all of the 124 reliably identified individuals observed during the study period were linked in one network. The permutation technique linked them with 738 preferred companionships, or edges, while the HWI_{null} cut-off technique linked them with 3138 edges. Both techniques yielded similar, high and significant assortativity coefficients by ranging pattern ($r = 0.61 \pm 0.026$ for the permutation technique and $r = 0.55 \pm 0.012$ for the HWI_{null} technique). Both networks could be best described as being composed of two communities (first maxima: $Q = 0.46$ and 0.39 , respectively) (Newman 2003a) and only 10 of the 124 individuals (8% of individuals) were classified differently by the two association techniques. These individuals were located at the periphery of the communities (Fig. 2). The sex of 36 individuals was known from field observations, but sex of individuals did not appear to explain communities; of the eight known males, two and six were in each community, and of the 28 known females, 12 and 16 were in each community. Following the homophily result, the two communities could be broadly described as (1) individuals only observed in the inner Moray Firth (the inner community thereafter), and (2) others (the outer community thereafter). For 87.1% and 83.9% of individuals, the ranging pattern matched the social community to which they belonged using the HWI_{null} and permutation techniques, respectively.

RELATING THE SOCIAL STRUCTURE TO GEOGRAPHICAL PREFERENCES

During the survey years, 610 dolphin encounters were documented in the Sutors, Three Kings and Eathie subareas (Fig. 1 inset), where dolphins of both types of ranging patterns are likely to be encountered (Wilson *et al.* 1997; Fig. 3). Using only these 610 encounters, the community structure of the network created was very similar to that described in the previous section (Fig. 2). The dichotomy in two communities remained apparent when restricting the data set to schools observed in these areas (first maxima: $Q = 0.45$ for the network based on the permutation technique and $Q = 0.42$ for the other network). The HWI_{null} technique linked all individuals with 2474 edges based on the schools encountered in the Eathie, Sutors and Three Kings subareas. The permutation technique yielded a network composed of 91 individuals linked by 312 edges (some individuals were not commonly observed in these subareas). The relationships were again well explained by the ranging pattern of individuals (geographical

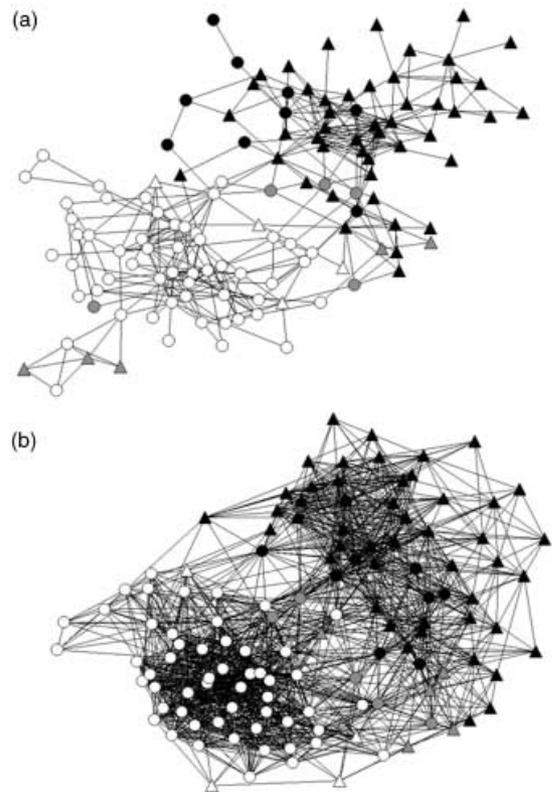


Fig. 2. The social network of bottlenose dolphins occupying the Moray Firth, Scotland resolved using (a) the Manly Bejder permutation technique, and (b) by applying a cut-off based on the average null half-weight index of the population. The Girvan–Newman algorithm defined two communities in both networks (white and black vertices) and only 10 vertices were classified differently in both networks (grey vertices). In both cases, the two communities seem to be composed of individuals that have a different ranging pattern. There appears to be an inner community composed mainly of individuals that have only been seen in the inner Moray Firth (triangles) and an outer community composed mainly of individuals that have been observed in other parts of the population's home range as well as in the inner Moray Firth (circles).

assortative mixing: $r = 0.50 \pm 0.040$ for the permutation technique, $r = 0.54 \pm 0.014$ for the HWI_{null} technique). For 86.3% and 83.6% of individuals, the ranging pattern matched the social community to which they belonged using the HWI_{null} and permutation techniques, respectively.

NETWORK PROPERTIES

The social network of the dolphins displayed features of small worlds; that is it was highly clustered yet all individuals could be reached in only a few steps. The average shortest path was similar to that of a random network with the same number of vertices and edges (3.9 vs. $\bar{\tau} = 2.9 \pm 0.001$ for the permutation technique and 2.1 vs. $\bar{\tau} = 1.8 \pm 0.001$ for the HWI cut-off technique: 10 random networks in each case), but the network's clustering coefficient was much higher (0.412 vs. $\bar{C} = 0.048 \pm 0.001$ for the permutation technique and 0.584 vs. $\bar{C} = 0.206 \pm 0.001$ for the HWI cut-off

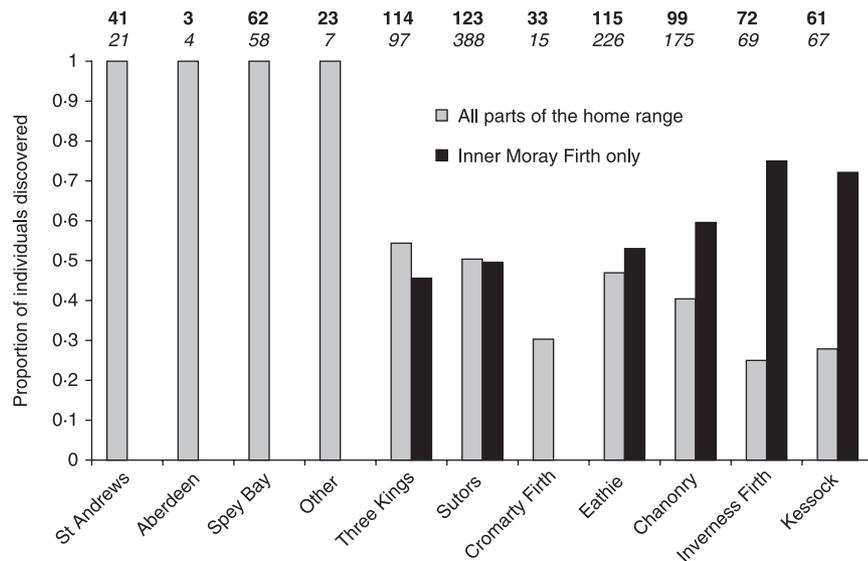


Fig. 3. The proportion of individuals from each ranging pattern seen between 1990 and 2002 in each subarea of study. Bold numbers above each subarea represent the total number of individuals identified in that subarea and numbers in italics are total number of encounters of schools in that subarea. See Fig. 1 for location of different sampling areas.

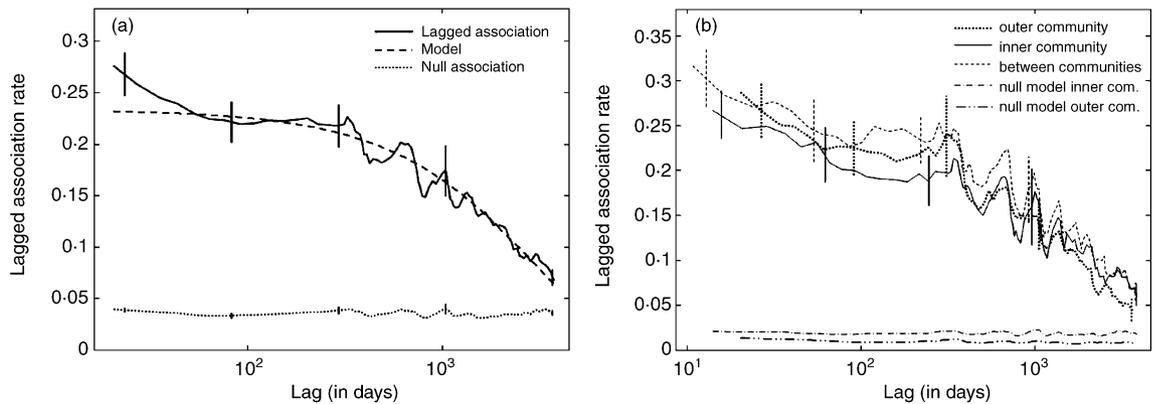


Fig. 4. Lagged association rates for (a) all individuals and (b) among and between social communities. These association rates are compared with the null association rate. Error bars are 1 SE and were obtained by jack-knifing. Best model explaining the observed association rates (the two casual acquaintances model) is displayed for (a).

technique: 10 random networks in each case). There was some degree of homophily in this network ($r = 0.170$), which means that individuals tended to associate with others that had similar numbers of associates as they had.

THE LAGGED ASSOCIATION RATE OF INDIVIDUALS WITHIN AND BETWEEN COMMUNITIES

Association rate remained higher than expected by chance (null association model) for the whole study period (Fig. 4). Both within and between social communities interactions could be described with a similar model (Fig. 4b), which also fitted best the overall pattern of association (Fig. 4a). A model containing two levels of acquaintances, a short, casual level of association and a longer-term one, described all four lagged association rates (Fig. 4a and Table 1). Not only did

the same model describe all interactions, its parameters were also similar across all types of association (Table 1). The social structure therefore appeared to be mainly driven by short-term relationships, which tended to last a few days. Individuals also had longer-term companions, roughly one-quarter of individuals with whom they were in a school, with whom they have relationships that last 7–8 years (Table 1). The long-term relationships of the outer community seemed to be shorter-lasting, averaging 5 years compared with the 8 years of the inner community (Table 1).

Discussion

Bottlenose dolphins live in fission-fusion societies (Connor *et al.* 2000). That is, they live in large communities whose members form frequently changing schools (White 1992). This definition has been used to describe the social structure of many species ranging

Table 1. The lagged association rate of individuals in the population is best explained by a model including two levels of casual acquaintances. This table provides the parameters of this model for each type of association; within and between the two communities, and overall. The association rate between individuals, $g(d)$, is given as a function of the time lag, d and is related to a proportion, p_{cas} , of short-term relationships that last τ_{cas} days and a proportion, $p_{\text{perm}} = 1 - p_{\text{cas}}$, of longer-term relationships that lasted τ_{perm} days: $g(d) = p_{\text{cas}}e^{-d/\tau_{\text{cas}}} + p_{\text{perm}}e^{-d/\tau_{\text{perm}}}$. The standard error (SE) of each parameter was estimated by jack-knifing. The SE for the time lag is given as a ± 1 SE interval around the mean. For a more detailed description of the model refer to Whitehead (1995)

Association type	p_{cas}	τ_{cas} (days)	p_{perm}	τ_{perm} (years)
Outer community	0.76 (0.024)	1.3 (0.3–100.0)	0.24 (0.024)	5.43 (4.73–6.37)
Inner community	0.79 (0.020)	1.3 (1.0–1.8)	0.21 (0.020)	8.00 (7.09–9.16)
Between communities	0.75 (0.017)	1.3 (0.9–2.8)	0.25 (0.017)	7.08 (6.51–7.76)
Overall (all individuals)	0.77 (0.016)	1.3 (0.7–10.0)	0.23 (0.016)	7.92 (7.24–8.72)

Table 2. Statistics for the Moray Firth bottlenose dolphin social network and a number of other published social networks, including another bottlenose dolphin population. The table provides the number of vertices in the network (n), the number of edges (m), the average shortest path between vertices in the network (l), the clustering coefficient (C), and the degree correlation coefficient (r)

Network	n	m	l	C	r	References
Moray Firth dolphin association						
Permutation technique	124	738	3.9	0.412	0.170	This study
Cut-off technique	124	3138	2.1	0.584	0.222	This study
Doubtful Sound dolphin association (permutation technique)	64	159	3.4	0.303	−0.044	Lusseau (2003) Lusseau & Newman (2004)
Film actors	449 913	25 516 482	3.5	0.20	0.208	Watts & Strogatz (1998)
Biology coauthorship	1 520 251	11 803 064	4.9	0.088	0.127	Newman (2001)
Physics coauthorship	52 909	245 300	6.2	0.45	0.363	Newman (2001)
Company director	7 673	55 392	4.6	0.59	0.276	Newman <i>et al.</i> (2001)

from primates (Goodall 1986; de Waal 1997) to felids (Packer 1986) and including other cetartiodactyls such as humpback whales *Megaptera novaeangliae* (Valsecchi *et al.* 2002), red deer *Cervus elaphus* (Conradt & Roper 2000) and other ungulates (Rubenstein 1994). Under this general umbrella, bottlenose dolphin social structure varies drastically, from being mainly driven by constant companionship (Lusseau *et al.* 2003) to featuring mainly acquaintances that last a few days as in this study and others (Wells *et al.* 1987). While this umbrella definition provides a general idea of their social structure, it does not capture the surface structure of these populations, echoing findings emerging from the study of chimpanzees (Lehmann & Boesch 2004).

These quantitative techniques help define the social structure of a population more precisely, and help elucidate the dynamic processes underlying observed association patterns. For example, while our data display similar small world features to the dolphin social network in Doubtful Sound, New Zealand (Lusseau 2003), the degree homophily present in the Moray Firth was not seen in Doubtful Sound (Table 2). Degree homophily could emerge from at least two different affiliation patterns: (1) the triadic closure model, or ‘friend of a friend’, where two associates are more likely to become associates of each other’s associates (Banks & Carley 1996; Davidsen, Ebel & Bornholdt 2002), and (2) Barabasi’s preferential attachment

model of network growth (Barabasi & Albert 1999), where incoming individuals associate with individuals that already have many associates. It therefore appears that the extent of assortativity by degree can vary in bottlenose dolphins, unlike human societies (Newman 2003b) that seem to always assort by degree (see Table 2 for some examples).

One shortcoming of these techniques is that they do not lend themselves to classical significance testing. Further work is required to apply sensitivity analyses, using jack-knifing or randomization procedures, to infer the robustness of these results.

Bottlenose dolphins living off the east coast of Scotland appear to be separated into two social units, which have limited interactions. Both the techniques used to define the social network yielded very similar results in terms of both the position of individuals (Fig. 2) and the network’s structure (Table 2). Furthermore the two units appear to be related to the ranging patterns of individuals, even when the spatial structure of the data set is taken into consideration, and could be described as inner and outer Moray Firth social communities. These findings reinforce earlier hypotheses about the spatial structuring of the population representing potential competition by exclusion between social groups (Wilson *et al.* 1997). We show that individuals that are commonly seen in the inner Moray Firth are not observed in other locations and, when given the

choice to interact with individuals coming in the area during summer time, tend to stay within their community. In contrast to other studies that describe adjacent communities of bottlenose dolphins in warmer waters (Wells *et al.* 1987), the home ranges of the two social units in Scotland largely overlap. This may be related to the presence of abundant prey items in this location that allows the two communities to coinhabit in the same area at this time of year.

Foraging specializations could also explain the variation in ranging pattern between the two social units. Cultural transmission of foraging specializations has been described in another population of bottlenose dolphins (Krützen *et al.* 2005). The low mitochondrial DNA diversity in the Moray Firth population (Parsons *et al.* 2002) linked with the existence of distinct social units highlight the need to further our understanding of the role of cultural hitchhiking in the coevolution of gene and behavioural traits in this population (Whitehead 1998; Whitehead & Rendell 2004). Recent genetic studies reinforce this link as social facilitation of foraging strategies within local communities of bottlenose dolphins has been put forward as a likely explanation of the genetic structure of bottlenose dolphin populations along European coastlines (Natoli *et al.* 2005). Specializations need not be in the diet itself, but can also be related to the techniques used to capture prey (Whitehead & Rendell 2004; Krützen *et al.* 2005). The latter example may be more probable as bottlenose dolphins are generally believed to have a catholic diet (Barros & Wells 1998; Santos *et al.* 2001). However, specializations in prey preferences could reconcile both statements. Dietary studies will help elucidate this hypothesis.

The communities were not discrete, and both the techniques used to detect preferred companionship yielded an integrated network of association. This highlights the importance of some individuals that have preferred companionships in both communities and may therefore play the role of broker in the network (Lusseau & Newman 2004). The presence of brokers between two social units could hypothetically allow for information transfer at various levels (Rendell & Whitehead 2001). The social network is a small world, which is not an equilibrium state (a steady state in a thermodynamic analogy) and shows that associations between individuals do change (Newman 2003b). The analysis provides us with an idea of the central tendency of associations in this population, temporal variation analyses will help us understand the dynamics around this average (how often dyads change, and how the network copes with disappearances and appearances).

The sex of many individuals in this population is still unknown. However, the two communities do not appear to be explained by the sex of individuals because females, defined as individuals with calves (Grellier *et al.* 2003), are found in both of them. The genetic relationship of individuals is also not well known. However, a recent study based on material from bottlenose dolphins found stranded in the Moray

Firth discovered only two mtDNA haplotypes ($n = 15$ individuals), a low diversity compared with other neighbouring populations (Parsons *et al.* 2002). Unfortunately, the identity of many stranded animals was unknown, and we cannot relate this genetic information to the community structure we observed. This reinforces the need to clarify the relationship between genetic and social diversity in the population.

These bottlenose dolphins appear to live in schools mainly composed of individuals with whom they spend little time. The association rate model does not capture the behaviour of associations over the first month in which individuals interact. The number of associates declines sharply over that period, showing that short-term acquaintances are a strong feature of the society, even stronger than the best fitting model describes it. This study draws a picture of the Scottish east coast bottlenose dolphin society that is highly reminiscent of what is known of the well-studied bottlenose dolphin population occupying Sarasota Bay, Florida. Some associations last many years, but the overall social structure is dominated by casual acquaintances lasting short periods (Wells *et al.* 1987). The availability of food resources appears to play an important part in shaping school size in the Scottish population and seems to affect the decision that individuals make to leave or join schools (Lusseau *et al.* 2004). Here we show that during this decision process, individuals will generally not remain in the same school. This could allow information about food availability to travel quickly through the social network, which would be advantageous where food availability is patchy and varying rapidly within a season.

We can conclude that this bottlenose dolphin population lives in a fission-fusion society that is predominantly composed of short-term acquaintances lasting a few hours to a few days. Longer-lasting associations form an integrated network, which is composed of two social units largely explained by the ranging patterns of individuals. These two units have limited interactions via a few common individuals. We cannot rule out that a process very similar to human affiliation formation is taking place in the dynamics of association formation in this social network because of the degree homophily. To date the population has been managed as one entity. This study, along with others (Wilson *et al.* 2004), show that it is necessary to take into consideration the community structure of this population when trying to enhance its viability. Understanding the social relationships among individuals helps to define and target management guidelines for different sections of a population and models of population dynamics should take this segregation of individuals into consideration when assessing viability or trends in abundance.

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References

- Baird, R.W. & Dill, L.M. (1996) Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology*, **7**, 408–416.
- Banks, D.L. & Carley, K.M. (1996) Models for network evolution. *Journal of Mathematical Sociology*, **21**, 173–196.
- Barabasi, A.L. & Albert, R. (1999) Emergence of scaling in random networks. *Science*, **286**, 509–512.
- Barros, N.B. & Wells, R.S. (1998) Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, **79**, 1045–1059.
- Batagelj, V. & Mrvar, A. (2002) Pajek. Vladimir Batagelj, Ljubljana, Slovenia.
- Bejder, L., Fletcher, D. & Brager, S. (1998) A method for testing association patterns of social mammals. *Animal Behaviour*, **56**, 719–725.
- Borgatti, S.P. (2002) *Netdraw: Graph Visualization Software*. Analytic Technologies, Harvard, MA.
- Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002) *Ucinet for Windows: Software for Social Network Analysis*. Analytic Technologies, Harvard, MA.
- Bronikowski, A.M. & Altmann, J. (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, **39**, 11–25.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Cairns, J.S. & Schwager, S.J. (1987) A comparison of association indices. *Animal Behaviour*, **35**, 1454–1469.
- Chilvers, B.L. & Corkeron, P.J. (2002) Association patterns of bottlenose dolphins (*Tursiops aduncus*) off Point Lookout, Queensland, Australia. *Canadian Journal of Zoology*, **80**, 973–979.
- Connor, R.C., Mann, J., Tyack, P.L. & Whitehead, H. (1998) Social evolution in toothed whales. *Trends in Ecology and Evolution*, **13**, 228–232.
- Connor, R.C., Heithaus, M.R. & Barre, L.M. (1999) Super-alliance of bottlenose dolphins. *Nature*, **397**, 571–572.
- Connor, R.C., Wells, R.S., Mann, J. & Read, A.J. (2000) The bottlenose dolphin. *Cetacean Societies* (eds J. Mann, R.C. Connor, P.L. Tyack & H. Whitehead), pp. 91–125. University of Chicago Press, London.
- Connor, R.C., Heithaus, M.R. & Barre, L.M. (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London Series B*, **268**, 263–267.
- Conradt, L. & Roper, T.J. (2000) Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 2213–2218.
- Corner, L.A.L., Pfeiffer, D.U. & Morris, R.S. (2003) Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). *Preventive Veterinary Medicine*, **59**, 147–167.
- Davidson, J., Ebel, H. & Bornholdt, S. (2002) Emergence of a small world from local interactions: modeling acquaintance networks. *Physical Review Letters*, **88**, art. no. 128701.
- Freeman, L.C. (1977) A set of measures of centrality based upon betweenness. *Sociometry*, **40**, 35–41.
- Fritz, H. & de Garine Wicathitsky, M. (1996) Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. *Journal of Animal Ecology*, **65**, 736–742.
- Gamble, C. (1998) Palaeolithic society and the release from proximity: a network approach to intimate relations (human social evolution). *World Archaeology*, **29**, 426–449.
- Girvan, M. & Newman, M.E.J. (2002) Community structure in social and biological networks. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 7821–7826.
- Goodall, J. (1986) *The Chimpanzees of Gombe: Patterns of Behavior*. Harvard University Press, Cambridge, MA.
- Gowans, S., Whitehead, H. & Hooker, S.K. (2001) Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? *Animal Behaviour*, **62**, 369–377.
- Grellier, K., Hammond, P.S., Wilson, B., Sanders-Reed, C.A. & Thompson, P.M. (2003) Use of photo-identification data to quantify mother–calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology*, **81**, 1421–1427.
- Hinde, R.A. (1976) Interactions, relationships and social structure. *Man*, **11**, 1–17.
- Hoelzel, A.R. (1993) Foraging behavior and social group-dynamics in Puget-Sound killer whales. *Animal Behaviour*, **45**, 581–591.
- Honer, O.P., Wachter, B., East, M.L. & Hofer, H. (2002) The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology*, **71**, 236–246.
- Kappeler, P.M. & van Schaik, C.P. (2002) Evolution of primate social systems. *International Journal of Primatology*, **23**, 707–740.
- King, B.J. (1991) Social information-transfer in monkeys, apes, and Hominids. *Yearbook of Physical Anthropology*, **34**, 97–115.
- Kozłowska, K. & Hanney, L. (2002) The network perspective: an integration of attachment and family systems theories. *Family Process*, **41**, 285–312.
- Krause, J. & Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press, Oxford.
- Krutzen, M., Sherwin, W.B., Connor, R.C., Barre, L.M., Van de Castele, T., Mann, J. & Brooks, R. (2003) Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 497–502.
- Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L. & Sherwin, W.B. (2005) Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8939–8943.
- Leavens, D.A. (2002) On the public nature of communication. *Behavioral and Brain Sciences*, **25**, 630–631.
- Lehmann, J. & Boesch, C. (2004) To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, **56**, 207–217.
- Lusseau, D. (2003) The emergent properties of a dolphin social network. *Proceedings of the Royal Society of London Series B-Biology Letters*, **270**, S186–S188.
- Lusseau, D. & Newman, M.E.J. (2004) Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London Series B*, **271**, S477–S481.
- Lusseau, D., Schneider, K., Boisseau, O.J., Haase, P., Sloaten, E. & Dawson, S.M. (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion of long-

- lasting associations – Can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology*, **54**, 396–405.
- Lusseau, D., Williams, R.J., Wilson, B., Grellier, K., Barton, T.R., Hammond, P.S. & Thompson, P.M. (2004) Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters*, **7**, 1068–1076.
- McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001) Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**, 491–494.
- McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. (2003) Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, **65**, 317–329.
- Mitani, J.C. & Amstler, S. (2003) Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, **140**, 869–884.
- Natoli, A., Birkun, A., Aguilar, A., Lopez, A. & Hoelzel, A.R. (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London Series B*, **272**, 1217–1226.
- Newman, M.E.J. (2001) The structure of scientific collaboration networks. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 404–409.
- Newman, M.E.J. (2002a) Assortative mixing in networks. *Physical Review Letters*, **89**, art. no. -208701.
- Newman, M.E.J. (2002b) The spread of epidemic disease on networks. *Physical Review E*, **66**, art. no. -016128.
- Newman, M.E.J. (2003a) Mixing patterns in networks. *Physical Review E*, **67**, art. no. -026126.
- Newman, M.E.J. (2003b) The structure and function of complex networks. *SIAM Review*, **45**, 167–256.
- Newman, M.E.J. & Girvan, M. (2004) Finding and evaluating community structure in networks. *Physical Review E*, **69**, art 026113.
- Newman, M.E.J., Strogatz, S.H. & Watts, D.J. (2001) Random graphs with arbitrary degree distributions and their applications. *Physical Review E*, **64**, art. no. -026118.
- Packer, C. (1986) The ecology of social felids. *Ecological Aspects of Social Evolution* (eds D.I. Rubenstein & R.W. Wrangham). Princeton University Press, Princeton, NJ.
- Parsons, K.M., Noble, L.R., Reid, R.J. & Thompson, P.M. (2002) Mitochondrial genetic diversity and population structuring of UK bottlenose dolphins (*Tursiops truncatus*): is the NE Scotland population demographically and geographically isolated? *Biological Conservation*, **108**, 175–182.
- Pusey, A. & Wolf, M. (1996) Inbreeding avoidance in animals. *Trends in Ecology and Evolution*, **11**, 201–206.
- Rendell, L. & Whitehead, H. (2001) Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**, 309–382.
- Rubenstein, D.I. (1994) The ecology of female social behavior in horses, zebras, and asses. *Animal Societies: Individuals, Interactions, and Organization* (eds P. Jarman & A. Rossiter), pp. 13–28. Kyoto University Press, Kyoto.
- Sambook, T.D., Whiten, A. & Strum, S.C. (1995) Priority of access and grooming patterns of females in a large and a small group of olive baboons. *Animal Behaviour*, **50**, 1667–1682.
- Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, I.A.P., Ross, H.M. & Mente, E. (2001) Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biology Association of the United Kingdom*, **81**, 873–878.
- Sigurjonsdottir, H., Van Dierendonck, M.C., Snorrason, S. & Thorhallsdottir, A.G. (2003) Social relationships in a group of horses without a mature stallion. *Behaviour*, **140**, 783–804.
- Smolker, R.A., Richards, A.F., Connor, R.C. & Pepper, J.W. (1992) Sex-differences in patterns of association among Indian-Ocean bottle-nosed dolphins. *Behaviour*, **123**, 38–69.
- Sugg, D.W., Chesser, R.K., Dobson, F.S. & Hoogland, J.L. (1996) Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, **11**, 338–342.
- Templeton, J.J. & Giraldeau, L.A. (1996) Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, **38**, 105–114.
- Valsecchi, E., Hale, P., Corkeron, P.J. & Amos, W. (2002) Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology*, **11**, 507–518.
- Vucetich, J.A., Peterson, R.O. & Waite, T.A. (2004) Raven scavenging favours group foraging in wolves. *Animal Behaviour*, **67**, 1117–1126.
- de Waal, F.B.M. (1997) *Bonobo: the Forgotten Ape*. University of California Press, Berkeley, CA.
- de Waal, F.B.M. (2000) Primates – a natural heritage of conflict resolution. *Science*, **289**, 586–590.
- Watts, D.J. & Strogatz, S.H. (1998) Collective dynamics of ‘small-world’ networks. *Nature*, **393**, 440–442.
- Wells, R.S., Scott, M.D. & Irvine, A.B. (1987) The social structure of free ranging bottlenose dolphins. In: *Current Mammalogy* (ed. H.H. Genoways), Vol. 1, pp. 247–305. Plenum Press, New York.
- White, F.J. (1992) Pygmy chimpanzee social organisation: variation with party size and between study sites. *American Journal of Primatology*, **26**, 203–214.
- Whitehead, H. (1995) Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology*, **6**, 199–208.
- Whitehead, H. (1997) Analysing animal social structure. *Animal Behaviour*, **53**, 1053–1067.
- Whitehead, H. (1998) Cultural selection and genetic diversity in matrilineal whales. *Science*, **282**, 1708–1711.
- Whitehead, H. (1999) Testing association patterns of social animals. *Animal Behaviour*, **57**, F26–F29.
- Whitehead, H. & Dufault, S. (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior*, **28**, 33–74.
- Whitehead, H. & Rendell, L. (2004) Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, **73**, 190–196.
- Wilson, B., Thompson, P.M. & Hammond, P.S. (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, **34**, 1365–1374.
- Wilson, B., Hammond, P.S. & Thompson, P.M. (1999) Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications*, **9**, 288–300.
- Wilson, B., Reid, R.J., Grellier, K., Thompson, P.M. & Hammond, P.S. (2004) Considering the temporal when managing the spatial: a population range expansion impacts protected areas based management for bottlenose dolphins. *Animal Conservation*, **7**, 331–338.

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