Patterns of association and alliance formation between reproductive males in a North Sea coastal bottlenose dolphin community

Bachelor Thesis

By
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I, Sandra Hoerbst, hearbly declare that this thesis is my own work. Where I have used the work of other persons or quoted the work of other persons the sources of the other work or information have been referenced in the text and listed in the reference section.

Date

Signature

Abstract

Social behaviour in mammals has been observed and analysed in both terrestrial and aquatic mammalian taxa. In marine ecosystems, highly social members of the order Cetacea are particularly well suited to behavioural studies. Bottlenose dolphins (*Tursiops truncatus*), for example, typically live in interactive social groups within a complex, fission-fusion society. Male bottlenose dolphins are highly competitive and exhibit form associations for different reasons such as herding females. The goal was to find out if such male-male bonds exist in the Bottlenose population of the Moray Firth in Scotland.

For this purpose I tested if male bottlenose dolphins from the outer Moray Firth preferentially associate and form alliances in the coastal population. For the study I used photographic data of well-marked bottlenose dolphins (*Tursiops truncatus*), collected through boat based surveys in the outer Moray Firth, Scotland. A dataset over eighteen years (1997 to 2014 inclusive) is used in this study to determine the incidence and stability of detected male alliances. Social structure analyses were completed using the software SOCPROG v2.5 developed for MATLAB.

The results from this study demonstrate that association between males from this population exist. The males in this study form “friendships” that last for several years, but they are not as strong as in other bottlenose dolphin populations. However, this population has a fission–fusion social structure with fluid associations among individuals (half-weight index = 0. 09) like other bottlenose dolphin communities.

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Introduction

The bottlenose dolphin (*Tursiops truncatus*) is one of a few mammalian taxa where males cooperate within their social groups. The social structure of coastal bottlenose dolphins has been characterized as fission-fusion society (Connor *et al.,* 2000) (Parsons *et al.,* 2003), consisting of small groups that constantly exchange individuals (Goodall *1986;* Wells *et al.,* 1987*;* Connor *et al.,* 1992). The bottlenose dolphins are also known for males cooperating with other males and forming social groups. Male alliances are usually found consisting of dyads or triplets, but in some cases they can form super-alliances (Connor *et al.,* 2001). These friendships are primarily formed to herd females but may also be beneficial for travelling and foraging together. Due to unpredictable distributions of reproductively available females, reportedly such alliances are a response across a populations range resulting in aggressive interactions amongst competing males. The bonds between males can last for just a few days but also for several years or more (Connor *et al.,* 1992, 2001*)*. Alliances are usually found in long-term and strongly associated dyads and triplets that cooperatively herd single/non-pregnant females for mating (Connor *et al.,* 1992).
According to Hinde (1976) measuring how much time animals spend together is a behaviourally meaningful way of quantifying their social interactions.

Kin selection theory has often been used to explain the formation of alliances between reproductive adult males (Hamilton, 1963). However, genetic studies in bottlenose dolphins have revealed that the majority of male pairs within recognized alliances, are in fact randomly related (Möller *et al.,* 2001) and therefore mechanisms aside from kinship, including sociological and ecological factors, may be responsible for these associations. Associations between male bottlenoses have been found in four different populations in Sarasota Bay, Florida Wells *(*1986*) cited in:* Duffield and Wells *(*2002), Shark Bay, Australia (Connor et *al.,*1992), Port Stephens, Australia (Möller *et al.,* 2001), and Little Bahama Bank, Bahamas (Parsons *et al.,* 2003). For animals such as bottlenose dolphins that are hard to observe, however as most of their interactions are under water, associations being known individuals are a good way to model social structure in these mammals.

Study Area

In the present study, long-term photo-identification data were provided for individually recognised adult males from a 200 strong coastal bottlenose population using the Moray Firth in northeast Scotland. The Moray Firth is a large coastal embayment in north-east Scotland measuring approximately 5230 km^2 (Eleftheriou *et al.,* 2004). The area can geographically be separated into the “inner” (from Helmsdale to Lossimouth) and “outer” Moray Firth (from Lossiemouth to Fraserburgh) shown in figure 1, stretching outwards to Duncansby Head in the north and Fraserbrugh in the south (Harding- Hill, 1993).

The waters in the firth are a combination of brackish and coastal waters. Twelve major rivers flow into the Moray Firth, ten of them discharge their freshwater into the inner area which substantially reducing the salinity of the coastal waters (Holmes *et al.,* 2004).

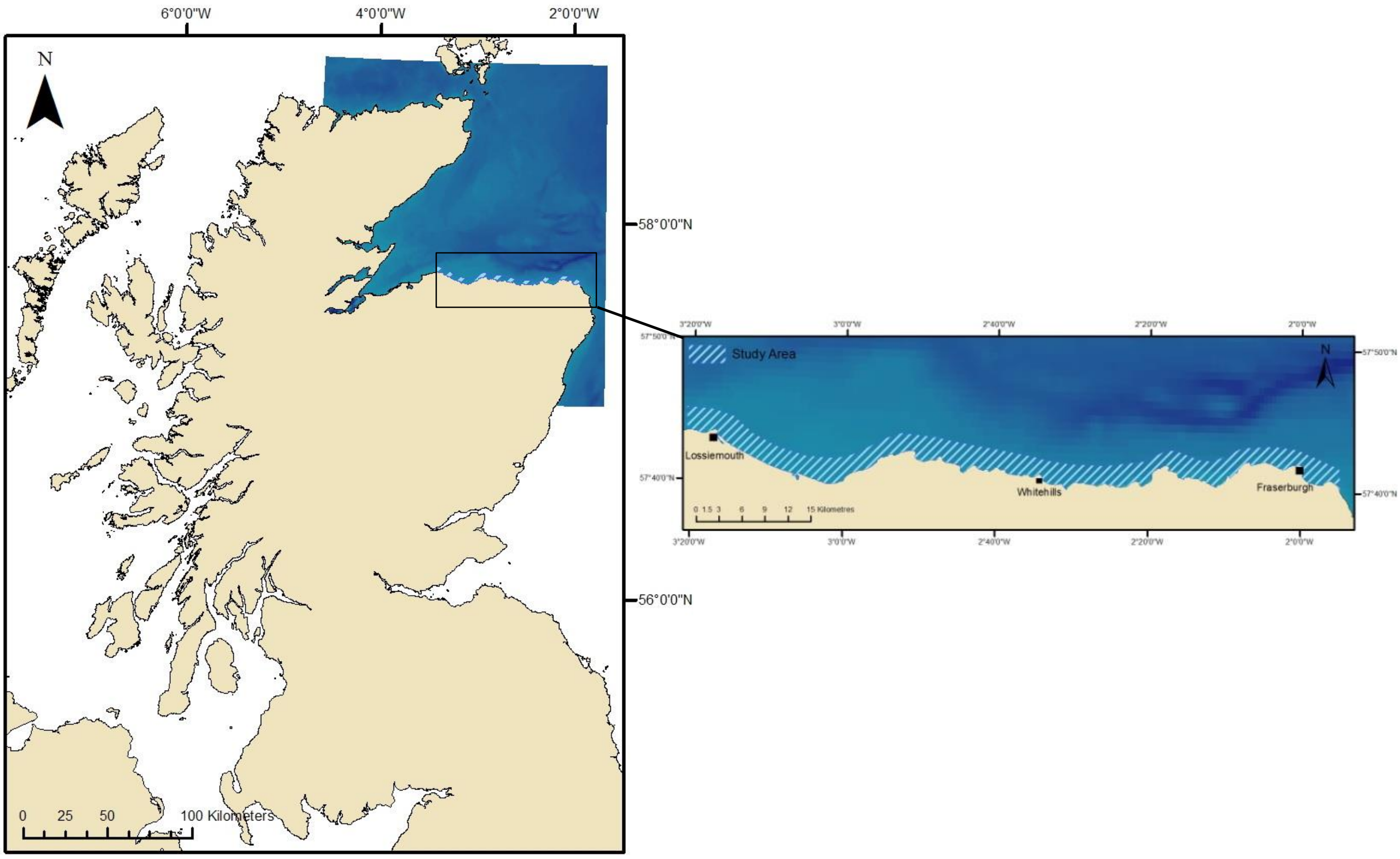


Fig. 1. Map of the Moray Firth in north-east Scotland showing the Moray Firth and the position of the study area from where the dataset used in the present study was collated.

Study Species

Tursiops truncatus. is perhaps one of the best studied marine mammals. The species is found in both temperate and tropical waters in all Oceans (Mitchell *et al*., 1975). These delphinids are long-lived mammals living in a fission-fusion society, where individuals typically associate in groups that may change in size and composition over periods of time. (Wells *et al*., 1987; Smolker *et al*., 1992; Conner *et al*., 2000). In the Moray Firth, the resident bottlenose dolphin population is estimated, to be around 195 animals. (Cheney *et al*., 2013). This bottlenose population is one of 7 bottlenoses in British waters, and the only population in the North Sea. Representing the species at the very northern extreme of its range, the Moray Firth population is both national and international importance.

Data

The data set used in this study was provided by the Cetacean Research & Rescue Unit (CRRU), a small non-profit research institution in Scotland, with research interests in Scotland, Thailand, Gibraltar and Greece. Since July 1997, the unit has conducted extensive studies of the whales and dolphins in the Moray Firth and has compiled along term database of individually identifiable bottlenose dolphins primarily using the southern coastline of the outer Moray Firth region, using photo identification and mark recapture studies (Wilson et al., 1999). The data was collected during boat based transect surveys during the summer months May – October) from 1997 to 2014. The individuals also have been photographed during the survey and later on identified by individual marking patterns on their dorsal fin and variation in dorsal fin shape (Würsig & Jefferson *et al.,* 1990, Wilson *et al.,* 1999). Individual dolphins can be reliably distinguished over a long period of time, using their natural markings especially on the distal edge of their dorsal fin. Further to distinguish individuals scientists use facilitating focal studies of their individual movements, reproductive histories and long-term social interactions.

The dataset provided for this study was collected during dedicated boat based survey work conducted from May to October, 1997 to 2014 inclusive. A total of 74 known males were provided for the present analysis from a total of 458 encounters. For this study, 63 male dolphins where selected, 11 others were excluded because they are either too young or were deceased.

Methods

Survey Methods

Mark-recapture data were collated from dedicated boat survey work by the CRRU in the outer southern Moray Firth between the months of May and October from 1997 to 2014 inclusive. Small (5.4 metre), rigid-hulled inflatable vessels were used to search for bottlenose dolphins following inshore linear survey routes positioned parallel to the adjacent shoreline. Both the design and frequency of surveys conducted varied greatly during the 18-year study period. Between 1997 and 2001 boat surveys were largely opportunistic, and primarily concentrated to the west of the survey area between Spey Bay and Cullen (Figure 1). From 2001 to 2007 however, fixed routes were followed along the entire coastline, either east of west from the central port of Whitehills (Robinson *et al*., 2007). From 2008 onwards, more flexible surveys were adopted, with selected routes aiming to maximise capture probabilities and minimise heterogeneity within the core areas used by the dolphins along the outer firth coastline.

All data were collected using standardised photo-identification procedures (e.g. Culloch & Robinson, 2008). Transparency film was used for photography up until 2006, after which digital imagery was used. Images were maintained within a comprehensive photo-identification database (see Eisfeld, 2003) providing a retrievable record of the long-term sightings histories of all known males in the population.

Data Analysis

SOCPROG

The software SOCPROG v2.5 developed by Hal Whitehead (1999, 2014) was used to test the observed association patterns in the field of male bottlenose dolphins.

Strengths of association among dyads were calculated using the half-weight index (Cairns & Schwager, 1987). To diagnose significant associations between dyads, the permutation test suggested by Bejder et al. (1998) and implemented in SOCPROG v2.5 was applied permuting association values within samples. The tests were run 5 times with 1000, 5000, 10000, 15000 and 20 000 permutations, to see when the p- value of the test stabilized. Each test was repeated 1000 times. To avoid autocorrelation bias, sampling was restricted to a daily basis (Smolker *et al.,* 1992). To look at the temporal scale of the male bottlenose population in the Moray Firth the lagged association rate was calculated in SOCPROG v2.5 using a standardized lagged association rate and standardized null association rate. The use of this for fission-fusion societies is recognised in (Whitehead, 1995).

Defining Association

To calculate associations, the half weight index (HWI) was used. Using the HWI makes it also easier to compare with other bottlenose dolphin studies (e.g. Wells *et al*., 1987; Smolker *et al*., 1992; Lusseau *et al*., 2003).

The HWI is defined (after Cairns & Schwager, 1987):

$$HWI = \frac{X}{X + y_{AB} + 1/2\,(y_A + y_B)}$$

where:

X is the number of times both individual (dolphins) A and B were seen together in the same group,

yA is the number of times individual a was seen, and

yB is the number of times individual b was seen.

The Index ranges from 0, where two individuals are never seen together in a group to 1 where two individuals are always seen together in the group.

Association indices are only an indication of the association strength amongst dyads, which relies on the number of times individuals have been observed and therefore must be proportional (Lusseau *et al.,* 2006).

Temporal scale: Association Rates

This method is to show how the social structure and the relationship between animals change over a period of time such in fission-fusion societies. According to Hinde (1976), temporal patterns are characteristic of social relationships. The lagged association rates, which are based on the methods of Underwood (1981) and Myers (1983) and developed by Whithead (1995), are designed to address the scale of temporal patterns in social relationships. Lagged association rates estimate the possibility that two animals sighted together at a particular time will still be associated at some time lag later (Whithead, 1995; Gowans *et al.,* 2001). Lagged association rates at 1.0 show little/no disassociation between dyads, whilst a falling rate over the range of lag shows that associations are breaking up over the time scale. (Whithead, 1999)

However, for this study the standardized lagged association rate and the null association rate were used. The standardized association rate was plotted against lag of time. The standardized null association rate helps to interpret the standardized association rate, as it helps to reflect the value individuals would have if they would randomly associate. The null association rate is the ratio of gregariousness of the population to the number of identified individuals minus one. The standardized null association rate does not change over time and is the inverse of the number of identified individuals minus one (Whitehead, 1995). Further, the jack-knife technique was used in the present study to calculate the standard error of the model, providing a conservative estimate of the precision of the terms (Sokal & Rohlf, 1995). The temporal pattern of association of the dataset used in the present analysis was then compared to models of social organisation, as developed by Whitehead (1995). These models consider four types of associates: preferred companions, casual acquaintances, preferred companions and casual acquaintances, and two levels of casual acquaintances.

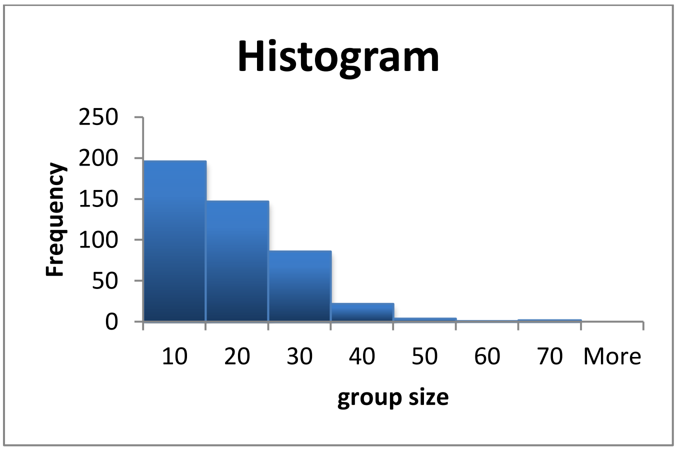
Results

Group size and composition

For the period 1997 to 2014, a total of 458 encounters with bottlenose dolphins were recorded.

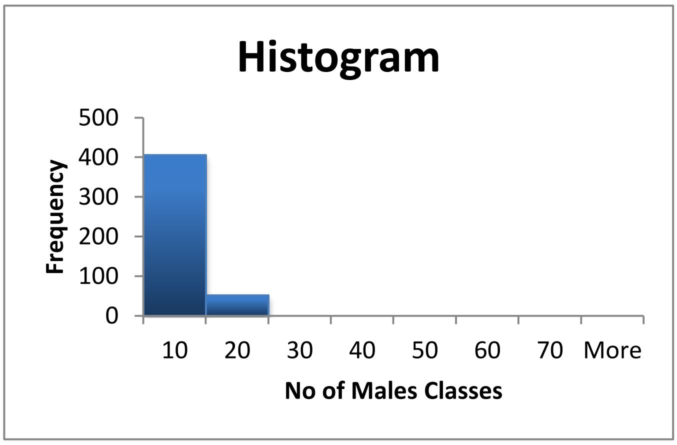
In this thesis, the average observed group size over all years (1997 to 2014 inclusive), including females, was 14.30 animals. The average number of males observed was 4.88 per group.

The groups observed in the study area are most of the time small and contain only up to 10 animals (Figure 2). Big groups with up to 40 or more individuals are seen more infrequently during the sampling period. There was no group observed over all the years with more than 20 males at a time (Figure 3). However the number of males is usually between 1 and 10 males per group.



group size classes	*Frequency*
10	196
20	147
30	86
40	22
50	4
60	1
70	2
More	0

Fig. 2. Frequency distribution histogram of the observed group size of bottlenose dolphins in the MF population during the sampling period. Bins for group sizes include the value of the label (e.g., 1–10, 11–20, etc.).



No of males Classes	*Frequency*
10	406
20	52
30	0
40	0
50	0
60	0
70	0
More	0

Fig. 3. Frequency distribution histogram of the observed No of Males of bottlenose dolphins (Tursiops truncatus) during the sampling period. Bins for group sizes include the value of the label (e.g., 1–10, 11–20, etc.).

The groups observed in the study area were seen to be mostly small and contain only up to 10 animals (Figure 2). Large groups, with up to 40 or more individuals, were found to occur less frequently during the sampling period. There was no group observed over all the years with more than 20 males at a time (Figure 3). However the number of males was typically seen to be between 1 and 10 males per group.

The average group size and average number varied widely between each encounter however, as reflected by the high standard deviation observed. Total group size ranged from 1 to 70 individuals. Males were found to be present throughout the whole sampling period and there was no significant correlation between certain months and the presence of males.

Generally, with increasing group size, the number of male dolphins was also seen to increase (Figure 4), but the number of males was not dependent upon the group size, as sometimes there were more males found in small groups than in large groups.

On average, males were present in 37% of all recorded groups.

The mean group size versus the number of males per group, expressed as the average ± standard deviation (± SD), is illustrated in figure 5.

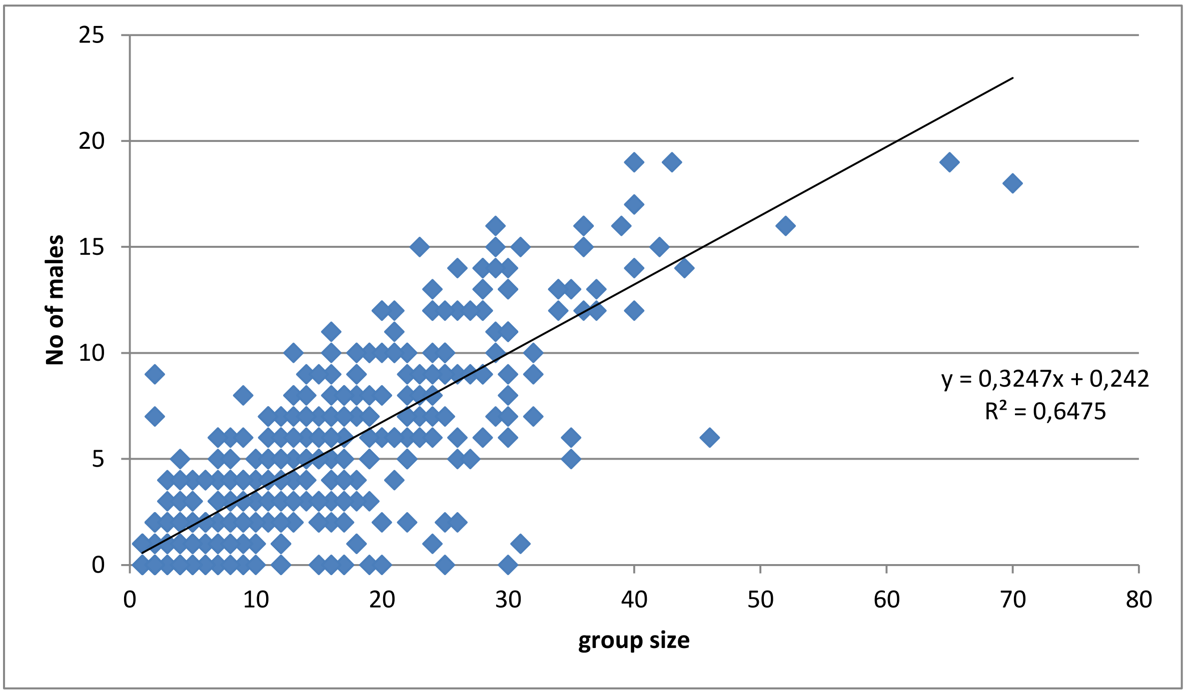


Fig. 4: No of males and the group size of all bottlenose dolphin encounters.

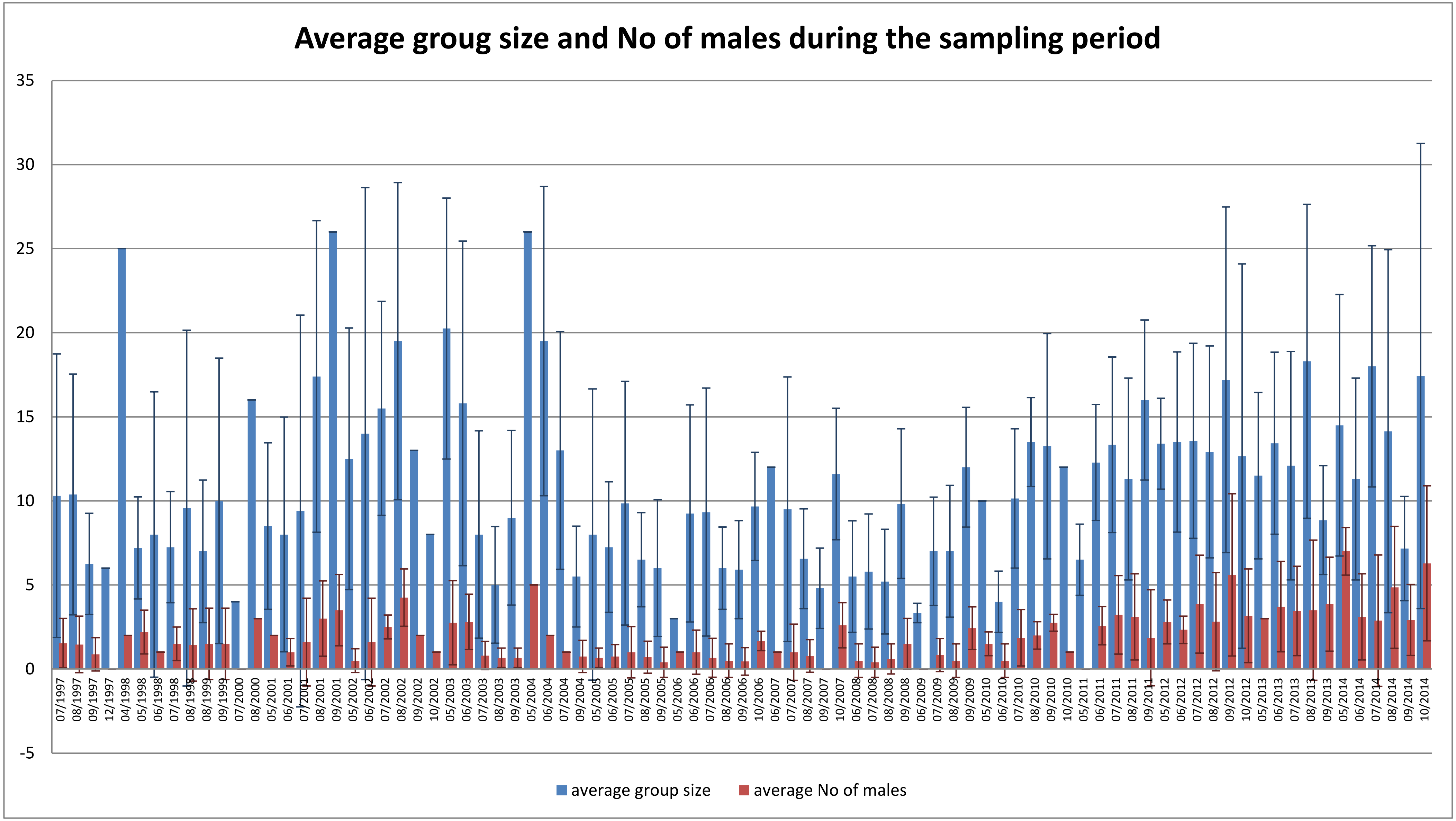


Fig. 5: Average group size of all encounters in each survey month during the sampling period (1997 – 2014 inclusive) in comparison with the average number of males and the standard deviation.

Association Analysis

A social dendrogram for the dataset, produced in SOCPROG v2.5 from an average linkage cluster analysis, showed that most of the associations between males were not that strong. Only a few male dyads were found to be over 0.5, meaning they spent over 50% of their time together. Some males were, however, more frequently sighted together e.g. ID#s 9 and 10 (two adults) and ID#s 448 and 478 (two sub-adults). The highest association index (Table 2.0) was 1.00 and was found to occur between the dyad ID # 407 and 409. Those two males were sighted the first time together in 2006. Furthermore they form a triad with dolphin ID #134 (HWI of 0,67), who is and adult male first sighted in 1998. However, this is not very significant as we only have one sighting of 407 and 409 is dead and 134 is thought to be dead as well.

Coefficients of association for individuals ranged from 0.00 to 1.00. The most frequently occurring levels were 0.00 - no association (Figure 8).

The distributions of the mean Coefficients of association and the maximum Coefficients of association for each male dolphin (adult and sub-adult) are shown in table 1 individually.

In figure 7, the associations between all males are illustrated as a sociogram. It shows that some males preferentially associated more often than others, but there is a complex network between the males in the outer, southern Moray Firth. Some of the males never associated during the sampling period. However, most of the males of the population have been associated with each other of variable strength. Comparing both, the hierarchical clusters and sociograms over the study period of each year, the association rate between males are not always the same. However some of the “friendships” last for years and some only last for a year or a shorter period of time.

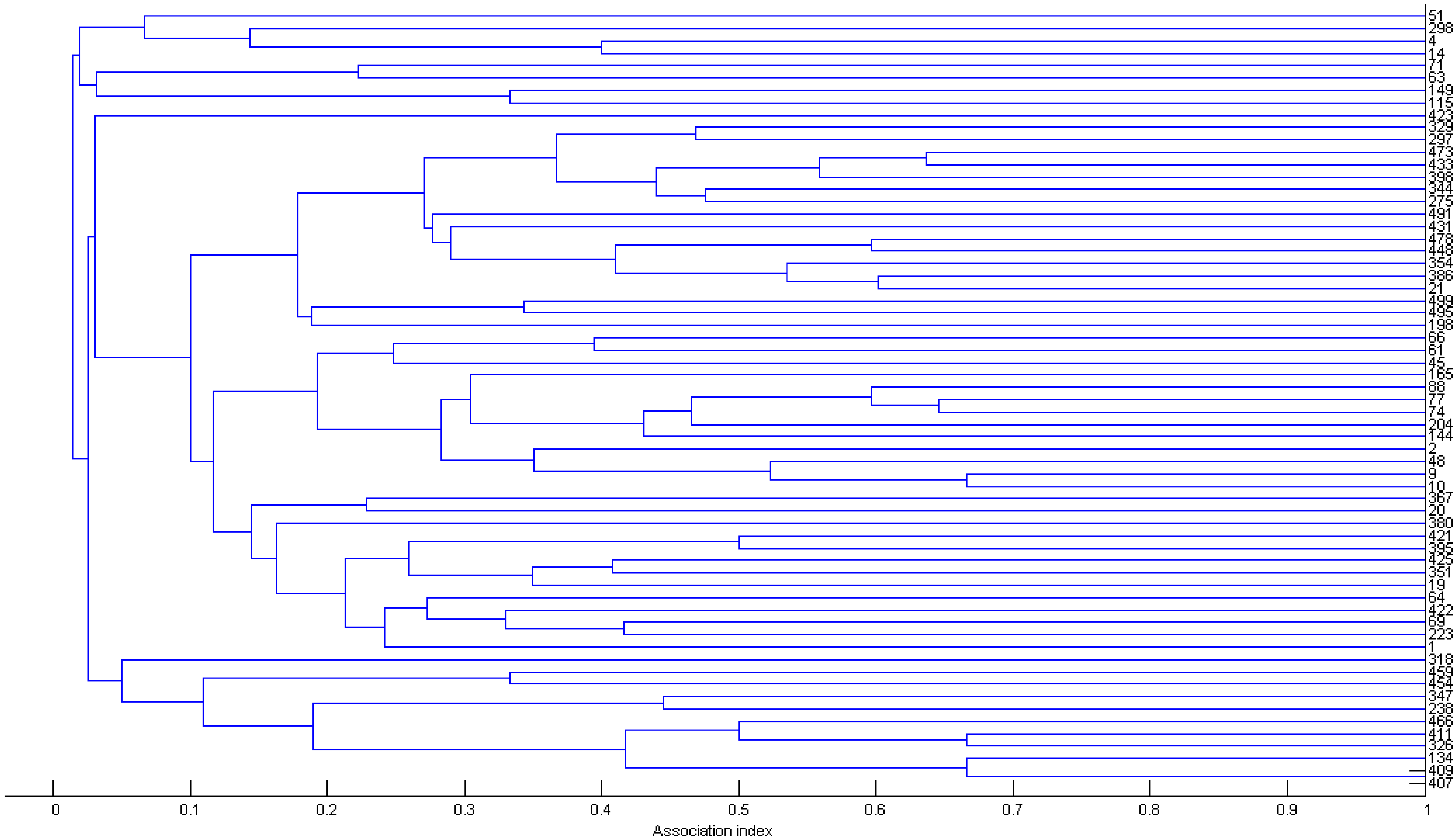


Fig. 6: Dendrogram (hierarchical cluster) showing the average-linkage cluster analysis of associations between well-marked male bottlenose dolphins (Tursiops truncatus) in the outer Moray Firth.

Table 1: The mean and maximum coefficients of association (half-weight index) for male bottlenose dolphins used in the present study, as derived from SOCPROG v2.5.

ID #	Age	Mean Assoc. (sd)	Max. Assoc. (sd)
1	adult	0.12	0.32
2	adult	0.13	0.39
4	adult	0.02	0.40
9	adult	0.14	0.67
10	adult	0.15	0.67
14	adult	0.02	0.40
19	adult	0.06	0.38
20	adult	0.07	0.25
21	adult	0.14	0.60
45	adult	0.09	0.33
48	adult	0.14	0.56
51	adult	0.03	0.18
61	adult	0.09	0.39
63	adult	0.02	0.26
64	adult	0.12	0.29
66	adult	0.08	0.39
69	adult	0.14	0.42
71	adult	0.01	0.22
74	adult	0.15	0.65
77	adult	0.12	0.65
88	adult	0.13	0.60
115	adult	0.02	0.33
134	adult	0.05	0.67
144	adult	0.13	0.46
149	adult	0.02	0.33
165	adult	0.10	0.35
198	adult	0.08	0.26
204	adult	0.12	0.49
223	adult	0.12	0.42
238	adult	0.08	0.44
275	adult	0.13	0.53
297	adult	0.16	0.47
298	adult	0.01	0.29
318	adult	0.01	0.50
326	adult	0.08	0.67
329	adult	0.14	0.47
344	adult	0.14	0.48
347	adult	0.07	0.44
351	adult	0.07	0.41
354	adult	0.14	0.56
367	adult	0.06	0.23
380	adult	0.11	0.30
386	adult	0.13	0.60
395	adult	0.09	0.50
398	adult	0.14	0.60
407	adult	0.05	1.00
409	adult	0.05	1.00
411	adult	0.07	0.67
421	adult	0.11	0.50
422	adult	0.10	0.44
423	adult	0.02	0.15
425	adult	0.09	0.41
431	adult	0.09	0.41
433	adult	0.14	0.64
448	sub-adult	0.12	0.60
454	adult	0.05	0.40
459	adult	0.03	0.33
466	adult	0.07	0.50
473	adult	0.13	0.64
478	sub-adult	0.11	0.60
491	sub-adult	0.09	0.37
495	sub-adult	0.05	0.34
499	adult	0.09	0.35
Overall		0.09 (0.04)	0.46 (0.17)

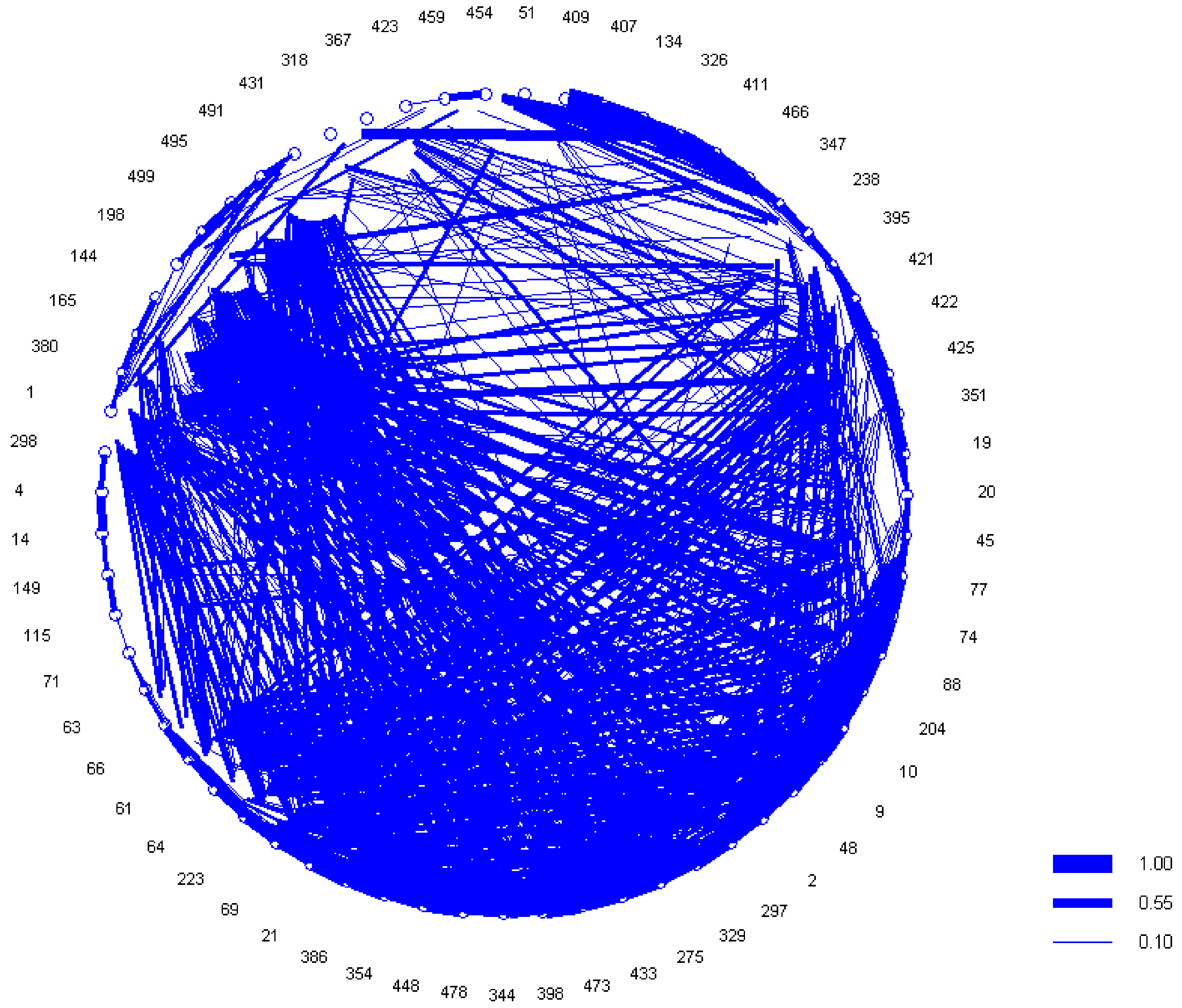


Fig. 7: Sociogram of all 63 male bottlenose dolphins observed during the study period (1997 -2014 inclusive). The key shows the thickness for the three values. The lines linking the individuals vary the precise level of association. Strong linkage (>0.5) represents clear association between dyads.

Table 2: Association matrix (symmetrical) showing the HWI for the 63 male bottlenose dolphins sampled. Resulting coefficients for pairs of individuals range from 0.00 (never sighted together) to 1.00 (always sighted together).

1	1.00
10	0.20	1.00
115	0.03	0.06	1.00
134	0.00	0.00	0.00	1.00
14	0.00	0.06	0.00	0.00	1.00
144	0.12	0.29	0.04	0.00	0.00	1.00
149	0.00	0.06	0.33	0.00	0.22	0.04	1.00
165	0.13	0.22	0.04	0.00	0.00	0.35	0.00	1.00
19	0.11	0.08	0.00	0.00	0.09	0.00	0.09	0.04	1.00
198	0.11	0.08	0.00	0.00	0.00	0.03	0.00	0.11	0.00	1.00
2	0.25	0.38	0.06	0.00	0.07	0.23	0.03	0.17	0.08	0.03	1.00
20	0.17	0.14	0.13	0.00	0.00	0.16	0.15	0.07	0.15	0.00	0.08	1.00
204	0.15	0.38	0.04	0.00	0.00	0.37	0.00	0.26	0.07	0.04	0.32	0.13	1.00
21	0.25	0.21	0.02	0.00	0.00	0.13	0.02	0.11	0.06	0.13	0.17	0.15	0.12	1.00
223	0.18	0.26	0.00	0.00	0.03	0.12	0.03	0.14	0.13	0.05	0.17	0.12	0.08	0.23	1.00
238	0.10	0.14	0.00	0.00	0.00	0.08	0.00	0.04	0.00	0.14	0.18	0.06	0.32	0.03	0.03	1.00
275	0.17	0.21	0.00	0.00	0.00	0.19	0.00	0.12	0.03	0.16	0.06	0.03	0.12	0.24	0.15	0.00	1.00
297	0.25	0.22	0.00	0.03	0.00	0.26	0.03	0.11	0.02	0.13	0.28	0.15	0.25	0.31	0.19	0.05	0.44	1.00
298	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
318	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	1.00
326	0.00	0.06	0.00	0.40	0.00	0.00	0.00	0.05	0.00	0.10	0.03	0.00	0.05	0.00	0.03	0.14	0.00	0.03	0.00	0.50	1.00
329	0.20	0.23	0.00	0.00	0.00	0.22	0.00	0.14	0.06	0.18	0.27	0.06	0.16	0.27	0.13	0.03	0.43	0.47	0.00	0.00	0.00	1.00
344	0.13	0.25	0.00	0.00	0.00	0.26	0.00	0.06	0.00	0.16	0.16	0.08	0.17	0.27	0.17	0.03	0.48	0.46	0.00	0.00	0.00	0.41	1.00
347	0.00	0.03	0.00	0.22	0.00	0.00	0.00	0.05	0.00	0.08	0.16	0.00	0.09	0.00	0.03	0.44	0.00	0.10	0.00	0.00	0.40	0.07	0.06	1.00
351	0.20	0.05	0.00	0.00	0.00	0.03	0.00	0.04	0.32	0.00	0.08	0.15	0.03	0.06	0.17	0.00	0.03	0.04	0.00	0.00	0.00	0.09	0.03	0.00	1.00
354	0.22	0.23	0.00	0.00	0.00	0.15	0.02	0.15	0.02	0.16	0.10	0.12	0.12	0.51	0.27	0.02	0.30	0.34	0.00	0.00	0.00	0.23	0.23	0.00	0.04	1.00
367	0.17	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.09	0.23	0.19	0.07	0.05	0.17	0.11	0.07	0.00	0.00	0.00	0.06	0.03	0.00	0.13	0.04	1.00
380	0.22	0.16	0.00	0.00	0.00	0.18	0.00	0.30	0.07	0.07	0.13	0.10	0.18	0.16	0.20	0.08	0.12	0.14	0.00	0.00	0.05	0.14	0.15	0.05	0.14	0.15	0.08	1.00
386	0.21	0.11	0.00	0.00	0.00	0.10	0.02	0.10	0.02	0.20	0.06	0.09	0.03	0.60	0.26	0.00	0.31	0.34	0.00	0.00	0.00	0.27	0.26	0.00	0.02	0.56	0.04	0.18	1.00
395	0.19	0.18	0.00	0.00	0.00	0.14	0.00	0.12	0.18	0.18	0.20	0.11	0.15	0.07	0.10	0.38	0.00	0.02	0.00	0.00	0.11	0.06	0.03	0.09	0.24	0.04	0.14	0.12	0.02	1.00
398	0.12	0.30	0.00	0.00	0.00	0.27	0.00	0.17	0.00	0.19	0.14	0.06	0.14	0.21	0.19	0.14	0.40	0.35	0.00	0.00	0.04	0.27	0.35	0.04	0.03	0.27	0.03	0.19	0.28	0.10	1.00
4	0.05	0.03	0.00	0.00	0.40	0.00	0.00	0.00	0.09	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
407	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.50	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
409	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.50	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
411	0.00	0.03	0.00	0.40	0.00	0.00	0.00	0.10	0.00	0.10	0.03	0.00	0.00	0.00	0.03	0.14	0.00	0.03	0.00	0.00	0.67	0.00	0.00	0.40	0.00	0.02	0.00	0.05	0.00	0.11	0.04	0.00	0.50	0.50	1.00
421	0.20	0.13	0.00	0.00	0.00	0.11	0.00	0.09	0.34	0.09	0.14	0.08	0.12	0.23	0.22	0.15	0.05	0.04	0.00	0.00	0.00	0.23	0.05	0.00	0.29	0.20	0.14	0.18	0.21	0.50	0.05	0.00	0.00	0.00	0.00	1.00
422	0.20	0.11	0.00	0.00	0.00	0.06	0.00	0.06	0.29	0.00	0.14	0.23	0.09	0.20	0.35	0.10	0.03	0.08	0.00	0.00	0.00	0.10	0.02	0.00	0.33	0.22	0.14	0.18	0.16	0.18	0.11	0.00	0.00	0.00	0.06	0.44	1.00
423	0.05	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.03	0.12	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.07	0.04	0.08	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.15	1.00
425	0.32	0.11	0.00	0.00	0.00	0.03	0.00	0.00	0.38	0.00	0.12	0.23	0.09	0.14	0.26	0.05	0.08	0.08	0.00	0.00	0.00	0.15	0.02	0.00	0.41	0.14	0.23	0.09	0.12	0.13	0.03	0.00	0.00	0.00	0.00	0.37	0.37	0.15	1.00
431	0.12	0.11	0.00	0.00	0.00	0.06	0.00	0.00	0.14	0.18	0.05	0.04	0.03	0.19	0.20	0.00	0.26	0.16	0.00	0.00	0.00	0.18	0.27	0.00	0.13	0.21	0.05	0.16	0.24	0.10	0.25	0.00	0.00	0.00	0.00	0.18	0.14	0.00	0.14	1.00
433	0.07	0.13	0.00	0.00	0.00	0.22	0.00	0.14	0.00	0.23	0.04	0.03	0.02	0.30	0.25	0.03	0.53	0.38	0.00	0.00	0.00	0.34	0.46	0.00	0.11	0.30	0.00	0.18	0.39	0.03	0.52	0.00	0.00	0.00	0.00	0.05	0.05	0.00	0.05	0.29	1.00
448	0.15	0.15	0.00	0.00	0.00	0.04	0.00	0.06	0.07	0.15	0.02	0.00	0.02	0.36	0.39	0.00	0.26	0.28	0.00	0.00	0.00	0.21	0.29	0.00	0.05	0.43	0.03	0.14	0.41	0.05	0.26	0.00	0.00	0.00	0.03	0.26	0.24	0.00	0.11	0.41	0.37	1.00
45	0.11	0.21	0.16	0.00	0.04	0.19	0.09	0.15	0.10	0.00	0.24	0.25	0.17	0.25	0.11	0.04	0.02	0.12	0.00	0.00	0.00	0.15	0.10	0.00	0.03	0.11	0.11	0.10	0.08	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.11	0.07	0.03	0.00	0.04	0.00	1.00
454	0.00	0.06	0.00	0.00	0.00	0.05	0.00	0.05	0.00	0.20	0.04	0.00	0.05	0.00	0.03	0.31	0.00	0.00	0.00	0.00	0.40	0.00	0.03	0.22	0.00	0.00	0.00	0.05	0.00	0.12	0.08	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
459	0.00	0.03	0.00	0.00	0.00	0.09	0.00	0.05	0.00	0.09	0.00	0.00	0.05	0.00	0.00	0.13	0.08	0.03	0.00	0.00	0.00	0.07	0.07	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.06	0.06	0.13	0.06	0.00	0.07	0.00	0.00	0.33	1.00
466	0.00	0.06	0.00	0.29	0.00	0.04	0.00	0.14	0.00	0.26	0.03	0.00	0.00	0.02	0.06	0.13	0.04	0.03	0.00	0.00	0.50	0.04	0.03	0.33	0.00	0.02	0.00	0.10	0.02	0.10	0.12	0.00	0.33	0.33	0.50	0.06	0.00	0.00	0.00	0.00	0.07	0.03	0.00	0.29	0.00	1.00
473	0.11	0.22	0.00	0.00	0.00	0.25	0.00	0.14	0.00	0.22	0.09	0.00	0.11	0.20	0.14	0.13	0.49	0.29	0.00	0.00	0.00	0.30	0.40	0.00	0.07	0.20	0.04	0.24	0.23	0.19	0.60	0.00	0.00	0.00	0.00	0.15	0.09	0.00	0.00	0.22	0.64	0.24	0.00	0.00	0.05	0.10	1.00
478	0.17	0.15	0.00	0.00	0.00	0.06	0.00	0.04	0.00	0.17	0.05	0.00	0.00	0.41	0.29	0.00	0.32	0.26	0.00	0.00	0.00	0.20	0.32	0.00	0.02	0.36	0.00	0.16	0.48	0.03	0.30	0.00	0.00	0.00	0.00	0.04	0.04	0.03	0.00	0.41	0.48	0.60	0.00	0.00	0.00	0.00	0.30	1.00
48	0.29	0.49	0.03	0.00	0.03	0.28	0.00	0.23	0.03	0.08	0.35	0.10	0.25	0.19	0.22	0.17	0.14	0.29	0.00	0.00	0.03	0.22	0.14	0.03	0.08	0.23	0.08	0.21	0.07	0.22	0.21	0.00	0.00	0.00	0.07	0.18	0.09	0.00	0.14	0.00	0.15	0.12	0.18	0.03	0.03	0.10	0.19	0.10	1.00
491	0.18	0.04	0.00	0.00	0.00	0.06	0.00	0.06	0.00	0.17	0.07	0.00	0.00	0.17	0.09	0.00	0.32	0.21	0.00	0.00	0.00	0.25	0.21	0.00	0.04	0.29	0.00	0.12	0.30	0.04	0.24	0.00	0.00	0.00	0.06	0.14	0.13	0.05	0.07	0.25	0.30	0.28	0.00	0.00	0.06	0.00	0.27	0.37	0.07	1.00
495	0.05	0.03	0.00	0.00	0.00	0.04	0.00	0.08	0.00	0.14	0.00	0.00	0.00	0.02	0.03	0.00	0.11	0.07	0.00	0.00	0.00	0.10	0.09	0.00	0.00	0.13	0.00	0.04	0.06	0.00	0.14	0.00	0.00	0.00	0.14	0.05	0.10	0.00	0.00	0.11	0.13	0.19	0.00	0.00	0.13	0.13	0.17	0.08	0.09	0.15	1.00
499	0.15	0.07	0.00	0.00	0.00	0.06	0.00	0.07	0.05	0.24	0.03	0.00	0.06	0.19	0.05	0.00	0.35	0.27	0.00	0.00	0.00	0.32	0.22	0.00	0.05	0.23	0.05	0.10	0.22	0.00	0.17	0.00	0.00	0.00	0.00	0.11	0.04	0.00	0.11	0.12	0.32	0.23	0.03	0.00	0.14	0.00	0.30	0.23	0.07	0.33	0.34	1.00
51	0.00	0.03	0.00	0.00	0.10	0.04	0.00	0.00	0.06	0.00	0.11	0.00	0.04	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.12	0.08	0.18	0.06	0.00	0.00	0.00	0.02	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
61	0.15	0.22	0.04	0.04	0.00	0.16	0.00	0.10	0.00	0.00	0.18	0.06	0.26	0.15	0.06	0.17	0.04	0.15	0.04	0.00	0.04	0.12	0.08	0.07	0.12	0.08	0.07	0.10	0.06	0.16	0.06	0.00	0.04	0.04	0.04	0.11	0.08	0.00	0.00	0.00	0.02	0.00	0.24	0.00	0.00	0.04	0.10	0.00	0.17	0.00	0.00	0.03	0.06	1.00
63	0.02	0.00	0.00	0.00	0.00	0.04	0.00	0.04	0.07	0.00	0.00	0.00	0.04	0.06	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.14	1.00
64	0.27	0.18	0.04	0.00	0.00	0.24	0.00	0.21	0.09	0.03	0.21	0.20	0.21	0.16	0.29	0.20	0.09	0.15	0.00	0.00	0.04	0.06	0.08	0.04	0.21	0.14	0.20	0.24	0.11	0.29	0.15	0.00	0.00	0.00	0.04	0.18	0.28	0.03	0.18	0.11	0.10	0.05	0.13	0.04	0.04	0.04	0.16	0.16	0.21	0.13	0.00	0.06	0.03	0.27	0.07	1.00
66	0.16	0.16	0.05	0.06	0.00	0.14	0.00	0.15	0.04	0.00	0.19	0.04	0.26	0.12	0.00	0.05	0.05	0.14	0.00	0.00	0.00	0.15	0.12	0.06	0.04	0.02	0.05	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.04	0.18	0.39	0.26	0.13	1.00
69	0.32	0.29	0.02	0.02	0.02	0.13	0.02	0.17	0.15	0.00	0.24	0.12	0.18	0.35	0.42	0.02	0.12	0.25	0.02	0.00	0.02	0.23	0.16	0.08	0.18	0.30	0.10	0.19	0.23	0.09	0.07	0.00	0.02	0.02	0.02	0.25	0.31	0.02	0.20	0.10	0.11	0.26	0.25	0.00	0.00	0.02	0.08	0.18	0.25	0.10	0.04	0.12	0.13	0.24	0.10	0.24	0.33	1.00
71	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.22	0.04	0.11	0.06	1.00
74	0.18	0.35	0.05	0.00	0.03	0.43	0.05	0.30	0.05	0.11	0.35	0.09	0.42	0.15	0.17	0.17	0.12	0.29	0.00	0.03	0.05	0.23	0.30	0.13	0.02	0.12	0.05	0.22	0.12	0.14	0.26	0.00	0.00	0.00	0.03	0.08	0.04	0.02	0.04	0.08	0.17	0.09	0.21	0.06	0.03	0.03	0.24	0.12	0.28	0.04	0.02	0.11	0.14	0.15	0.03	0.20	0.16	0.22	0.00	1.00
77	0.13	0.33	0.06	0.00	0.03	0.46	0.10	0.31	0.03	0.00	0.39	0.16	0.49	0.11	0.09	0.09	0.06	0.33	0.00	0.04	0.04	0.25	0.27	0.13	0.00	0.10	0.03	0.11	0.06	0.03	0.08	0.00	0.00	0.00	0.00	0.02	0.02	0.03	0.02	0.00	0.04	0.00	0.33	0.00	0.00	0.00	0.02	0.00	0.29	0.00	0.00	0.03	0.14	0.20	0.06	0.14	0.29	0.25	0.00	0.65	1.00
88	0.09	0.34	0.06	0.00	0.00	0.46	0.07	0.30	0.03	0.08	0.38	0.08	0.48	0.11	0.13	0.12	0.10	0.32	0.00	0.00	0.03	0.21	0.26	0.16	0.00	0.13	0.03	0.17	0.09	0.08	0.19	0.00	0.00	0.00	0.03	0.02	0.05	0.06	0.02	0.07	0.11	0.07	0.12	0.07	0.03	0.03	0.13	0.08	0.23	0.02	0.03	0.05	0.14	0.19	0.03	0.21	0.23	0.20	0.00	0.60	0.59	1.00
9	0.27	0.67	0.05	0.00	0.05	0.27	0.05	0.17	0.07	0.02	0.32	0.11	0.29	0.20	0.30	0.10	0.17	0.28	0.03	0.00	0.03	0.18	0.20	0.03	0.07	0.22	0.14	0.17	0.06	0.14	0.14	0.03	0.00	0.00	0.05	0.10	0.12	0.02	0.12	0.04	0.15	0.12	0.19	0.03	0.05	0.03	0.17	0.08	0.56	0.06	0.05	0.08	0.02	0.22	0.00	0.20	0.18	0.34	0.00	0.24	0.26	0.27	1.00
	1	10	115	134	14	144	149	165	19	198	2	20	204	21	223	238	275	297	298	318	326	329	344	347	351	354	367	380	386	395	398	4	407	409	411	421	422	423	425	431	433	448	45	454	459	466	473	478	48	491	495	499	51	61	63	64	66	69	71	74	77	88	9

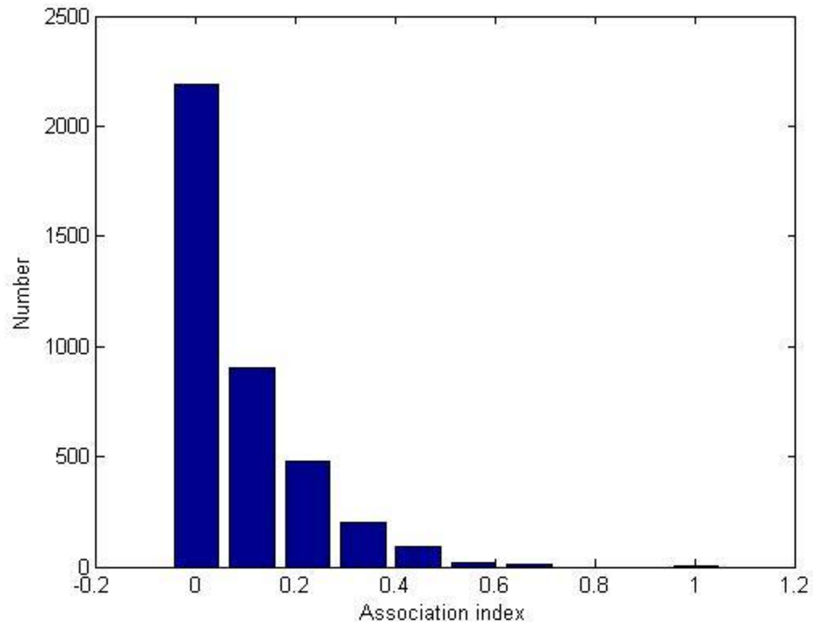


Fig. 8: Distribution of Associations between all male encounters (1997 – 2014 inclusive). Association indices (non diagonal)

Table 3:. Mean and maximum half-weight index (HWI) between and within age classes.

	Mean HWI (SD)	Maximum HWI (SD)
All ages	0,09 (0,04)	0,46 (0,17)
Adult	0,09 (0,04)	0,46 (0,17)
Subadult	0,09 (0,03)	0,48 (0,14)

Associations between adult males are the same strength as between sub-adult male bottlenose dolphins. The maximum and the mean HWI follow the same trend. Associations between both age classes had the same indices as within the age classes. However, the observed equality between age classes indicates that adults and sub-adults form strong relationships independent of age.

The association dataset was randomly permuted 20,000 times and the resulting permuted mean coefficient of association was not found to be significantly higher than the observed mean (random, permuted, mean = 0.08979, real mean = 0.08983) suggesting that observed individuals did not show preferred or avoided preference for associations, but instead tended towards random associations over the 18 years of the study.

Temporal Pattern

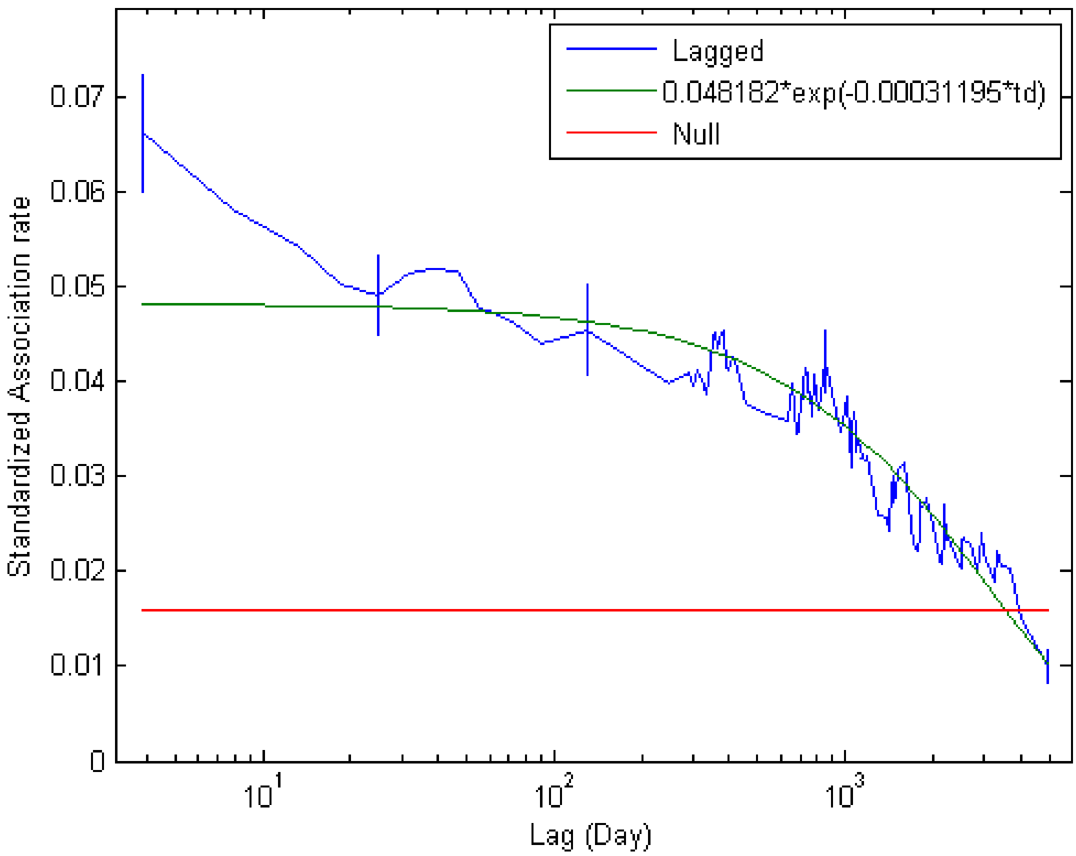


Fig. 9: Graph of the standardized lag association rate plotted against time lag (in days) for all male bottlenose dolphins (Tursiops truncatus) of all ages. Standardized association rates are shown with jackknifed estimates of precision.

The standardized lagged association rate (SLAR) was higher than the null association rate for all individuals for time lag. Standardized lagged association rates were high at the beginning where not all males were identified (Figure 9). Later on the associations last for short time lag and decreased again, this indicates that many associations between males do not last for several years. Standardized lagged association rates are high for short time lags, and decrease after approximately 10^2 (100) days which is around one field season (May – October). Over a longer period of time it is unlikely that associations amongst males will continue indicated by the decreasing SLAR.

However, the SLAR further dropped from the beginning until the association rates cross the standardized null association rate. There was relatively few data collected at the beginning of the study period. A moving average of 40000 was chosen to smooth lines, otherwise it would be to spiky. Jack-knife standard error bars are shown on the standard lagged association line (Baird *et. al.,* 2000). The lagged association rates between all males decreased during the study period. This suggests that associations did not last long over the last few years. The best fitting model type: a2*exp (-a1*td), explains casual acquaintances between all males in the bottlenose population of the outer Moray Firth.

Discussion

Long term studies are essential for understanding the social structure of marine mammals such as bottlenose dolphins. The expectation of this study was to find out more about the patterns of the associations and alliance formation in reproductive males in a population in the Moray Firth.

First of all the average group size was 14.30 individuals per group. The school size of coastal bottlenose dolphins range from 1 to over 100 individuals, but a group generally consists of between 2 and 15 dolphins (see review by Shane *et al.,* 1986). In Argentina (Würsig, 1978) and the Gulf of California (Ballance, 1990), dolphins gather in groups similar in size to those observed the outer Moray Firth. On average, males were present in 37% of the observed groups.

Further it was found out that the males do preferentially associate with other males. The time span of these associations evidently varies, from several days to several years, however it is uncommon for such long term associations. 24 males formed dyads with a coefficient of association of 0.5 or more. However, stable alliances are pairs and triads of males (association coefficient of 80 – 100) that may last for several years (Connor *et al.,* 2000). Strong bonds have also been reported amongst pairs and triplets of male bottlenose in Sarasota Bay, Florida (Wells *et al.,* 1987). The bonds which could be found in the Moray Firth, Scotland are not as strong as the ones in Sarasota Bay, Florida and Shark Bay Australia. However, this study shows that "friendships" between males in the Moray Firth, Scotland exist. The temporal patterns in the recent study have displayed that the bonds between males last for a shorter period of time, as only a few males were found to associate over several years.

The alliance formations between the male dolphins in Shark Bay, Australia occur within a larger social network of more than 400 individuals (Connor *et al.,* 1992; 2000). According to Cheney et al. (2013), there are only around 195 bottlenose dolphins in the northeast Scottish population. What else was shown in the results is that most of the males interact with each other. Wisznewski et al. (2012) found that male bottlenose dolphins (*Tursiops sp*.) in Port Stephens, Australia form stable alliances. But dolphins from one alliance rarely associate with many others.

Additionally, herding and alliance formation in male bottlenose dolphins is believed to be age related, and mainly between adult males (Connor *et al.,* 2000). In the present study, the highest indices were typically found between mature males.

One problem with this method is that association patterns based upon the amount of time that animals spend together are influenced both by individual ranging patterns or habitat preferences, than by genuine social affiliations. (Lusseau *et al.*, 2006).
Kin selection is often used to explain the social interactions and cooperative behaviour of animals from this mammalian taxa. In Australia, according to Möller et al. (2001), studies among male alliances show a distinct lack of kinship, whilst studies in the Bahamas have shown a positive correlation between patterns of association and patterns of genetic relatedness (Parsons *et al.,* 2003).

Conclusion

To date, alliances between male bottlenose dolphins have not been reported in the Moray Firth in Scotland, however this hypothesis cannot be rejected in this study. It has been presented that the HWI for males in the population of the outer Moray Firth are not as high as the observed HWI values for male alliances in other populations, like Shark Bay, for example. Results from the Bahamas, show association coefficients HWI=0.53-1.00 (Parsons *et al.,* 2003) close to those found in the current study. Male alliances are often found while herding females (Connor *et al.,* 1992; 2000). As such, the inclusion of behavioural data in studies could help to clarify alliances and associations within study populations.

In the present results, preferred associations between male dolphins were indeed evident in the Moray Firth. These associations may have cooperative benefits for foraging, reproduction and protection from predators. However, the low level of identified male alliances in this northeast Scottish population could be directly related or consequential to the number of available females to mate with or to low levels of predation pressure in these North Sea waters. In conclusion, associations and alliances may not be so important in the Moray Firth bottlenose population as in populations in other parts of the world where lower numbers of females or increased threats of predation may be more evident. Instead, the relationships observed in the present dataset are thought to represent a more fluid, adaptive and competitive response to prospective consortships.

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Appendix

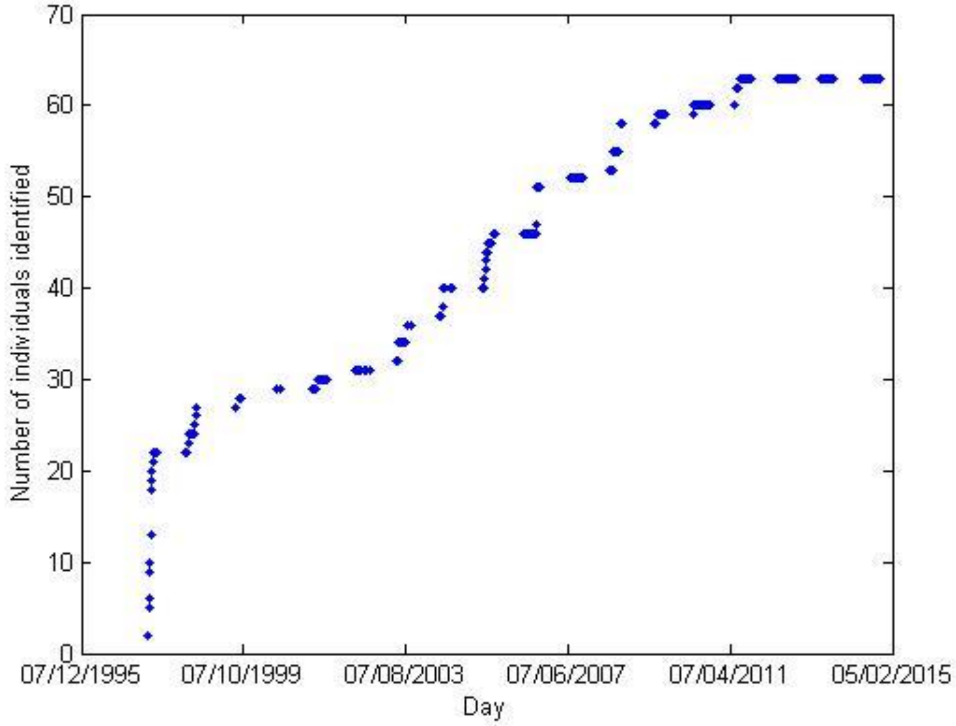

Fig. 10: Number of individuals (male dolphins) identified over the study period.

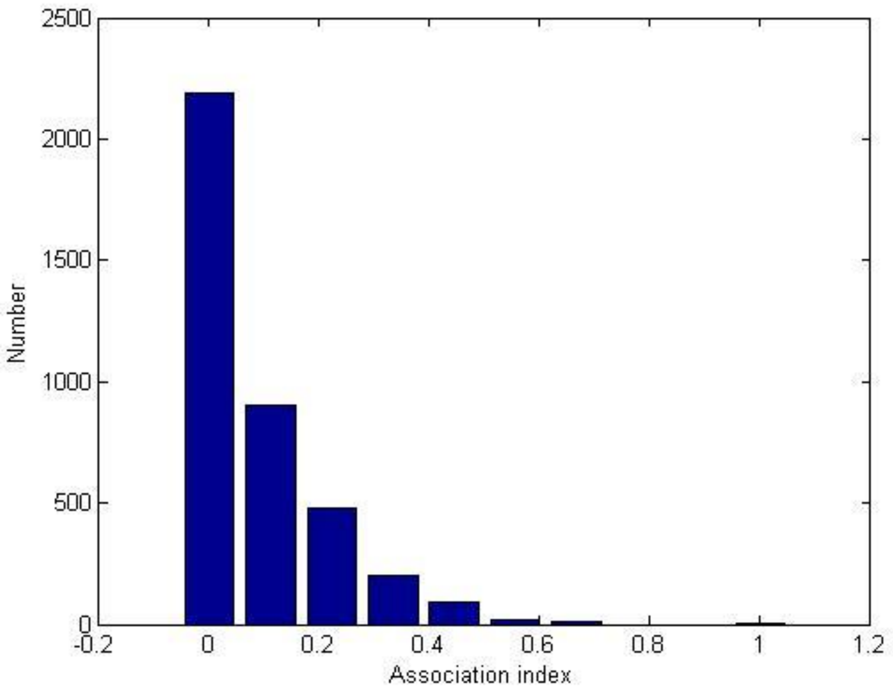

Fig. 11: Distribution of associations (Association indices non diagonal)

Table 4: Regression statistics and ANOVA

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0,804682583
R Square	0,64751406
Adjusted R Square	0,646741064
Standard Error	2,528506019
Observations	458

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	5355,502548	5355,502548	837,6686204	2,6E-105
Residual	456	2915,364265	6,393342686		
Total	457	8270,866812			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95,0%*	*Upper 95,0%*
Intercept	0,241960838	0,199215378	1,214569076	0,225159064	-0,14953	0,633454902	- 0,149533226	0,633454902
Group Size	0,324657495	0,011217325	28,94250543	2,5966E-105	0,302613	0,346701558	0,302613433	0,346701558

Table 5: Permutation tests for all individuals. Each set of permutation test was repeated 1000 times. P value stabelized between 15000 and 20000 permutations.

	Real	Mean(random)	P value
1000	0.81437	0.81085	0.0150
5000	0.81437	0.81084	0.0148
10000	0.81437	0.81093	0.0180
15000	0.81437	0.81090	0.0161
20000	0.81437	0.81093	0.0166

Table 6: Additional information for figure 9

Model type: a2*exp(-a1*td)

Explanation: Casual acqs

Start parameters: a1=0.5 a2=0.5

Number of parameters = 2

Summed Log likelihood = -467469.7742

Goodness of fit chi-squared = 6791.355 (2212 d.f.)

P = 0.0000; Variance inflation factor c = 3.07

AIC = 934943.5485

QAIC = 304519.4646

a1 = 0.00031195 (s.e. 2.7647e-05)

a2 = 0.048182 (s.e. 0.0024143)

Fitted model: association rate = 0.048182*exp(-0.00031195*td)