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Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Argentina

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Abstract

This study aims to investigate the association patterns of a small and resident population of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio (Argentina), and assess any seasonal variation in view of the reported seasonal variation in the population's grouping behavior. The estimation of social differentiation (S) was 0.29 (SE = 0.08), suggesting a homogenous society. The half-weight index (HWI) averaged 0.23 (± 0.06), with evidence of long-term preferred associations. However, data showed seasonal variation in the association patterns. In winter, when large groups were reported in this population, HWI values averaged 0.30 (± 0.09) with no indication of preferred or avoided associations. However, during summer, when group size was generally small, HWI values averaged 0.14 (± 0.07), with an indication of preferred/avoided associations. This study indicates that the social structure of the bottlenose dolphins in Bahía San Antonio seems relatively homogenous and flexible over time, with the formation of a random social network at times when large aggregations are formed, and a more disconnected network made up of strongly connected components when the cost of grouping is high.

Key words: associations, bottlenose dolphin, *Tursiops truncatus*, fission–fusion society, seasonality, social structure.

Being an easily accessible coastal species, the social ecology of common bottlenose dolphin (*Tursiops truncatus*) communities has been studied in many regions around the world (reviewed by Connor *et al*. 2000). Generally, research has shown that the species has a fluid social structure (Würsig and Würsig 1979, Ballance 1990, Smolker *et al*. 1992, Williams *et al*. 1993, Wilson 1995) often referred to as a fission–fusion society (Würsig and Würsig 1977, Wells *et al*. 1987, Smolker *et al*. 1992, Connor *et al*. 2000). Most detailed information originates from a handful of long-term studies (*e.g*., Wells 1991, Smolker *et al*. 1992, Connor *et al*. 2000, Lusseau *et al*. 2003), which indicate the existence of sexual segregation within the dolphin's society, as well as strong long-term male alliances and strong variability in female association patterns depending on reproductive status (Wells 1991; Connor *et al*. 1992, 2000; Lusseau *et al*. 2003). Conversely, only a few other studies have shown that such strong bonds may not occur in all bottlenose dolphin populations (*e.g*., Wilson 1995, Bearzi *et al*. 1997, Foley *et al*. 2010). Indeed, in fission–

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fusion societies it is aimed to balance the costs and benefits of grouping related to mating, predation risk, and food availability (Grove *et al.* 2012). Due to the habitat-specific nature of these pressures, fine-scale dissimilarities may occur in the grouping behavior and association patterns of different bottlenose dolphin populations (Connor *et al.* 2000).

Little is known about the social structure of bottlenose dolphins in Argentina. Nonetheless, the study population, located in the north of Patagonia, has been monitored since 2006 and is relatively well known (*e.g.*, Fruet *et al.* 2014; Vermeulen and Bräger 2015; Vermeulen *et al.* 2015, 2016). It is a small (approximately 83 individuals) and isolated population (Vermeulen and Bräger 2015), showing high levels of residency and site fidelity to the area of Bahía San Antonio (Vermeulen *et al.* 2016). This population also shows a marked seasonal pattern in grouping behavior with significantly larger groups observed in winter ($\bar{x} = 7$) and the smaller groups in summer ($\bar{x} = 3$; Vermeulen *et al.* 2015). The authors suggested this variation was caused by a seasonal variation in food availability, and regulation of feeding competition; *i.e.*, in winter prey seems to be abundant and dolphins are often engaged in cooperative surface feeding activities (in groups of on average 27 individuals, Vermeulen *et al.* 2015) believed to increase prey capture efficiency (Wells *et al.* 1980, Würsig and Würsig 1980). On the other hand, in summer prey seems to be scarcer and dolphins are frequently engaged in a "tail-out peduncle dive" foraging behavior in small groups of two individuals on average (Vermeulen *et al.* 2015), believed to be a strategy to reduce scramble competition (Pearson 2009) and increase individual fitness (Würsig 1986).

The aim of this study was to investigate this population's association patterns. Considering the population's seasonal variation in grouping behavior and the influence of grouping on associations (due to the adopted definition as membership of the same group; Whitehead 2008*b*), it was furthermore aimed to assess any seasonal variation within the dolphin's social structure.

MATERIALS AND METHODS

Study Area and Fieldwork

Bahía San Antonio (40°45′S, 64°54′W; Fig. 1) is a shallow bay of approximately 200 km^2, an average depth of 6 m, and a maximum depth of 30 m (SHN 2000). The bay is located at the northern end of Golfo San Matías, Patagonian Argentina, and is known for its large tidal differences (Perier 1994, SHN 2000). The area is believed to be the core habitat within the larger home range of a community of bottlenose dolphins (Vermeulen and Cammareri 2009, Vermeulen *et al.* 2016).

A total of 129 boat-based surveys were conducted from a small, outboard-powered, inflatable boat between August 2008 and December 2011. The effort totaled 587 h during which 155 dolphin groups were observed. Table 1 presents the distribution of effort over the different years and seasons.

All survey effort was restricted to calm seas of Beaufort state ≤ 3, periods of no or little precipitation, and good visibility. During each survey, the boat was maintained at a steady speed of 4–5 knots, with the same 2–3 observers maintaining a continuous visual search for dolphins. The course of the boat-based survey could not be standardized; the area was surveyed nonsystematically until a bottlenose dolphin group was found. This was due to logistical limitations, and decisions were made by the skipper based on fuel availability and weather conditions (*e.g.*, if there was

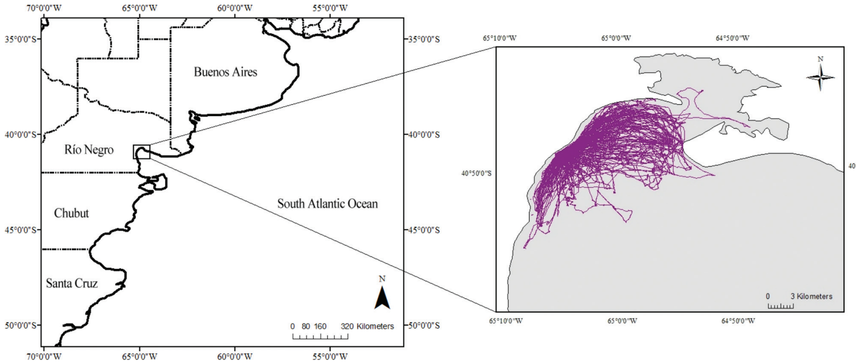

Figure 1. Map of Argentina indicating the provinces, detailing the study area Bahía San Antonio and the boat-based survey tracks.

Table 1. Hours of photo-identification survey effort in Bahía San Antonio (h) and cumulative number of individuals identified over the different years and seasons.

	Summer	Autumn	Winter	Spring
2008	0 h/0	0 h/0	31 h/91	53 h/44
2009	67 h/67	40 h/46	37 h/73	18 h/36
2010	31 h/18	14 h/16	143 h/220	22 h/26
2011	78 h/89	33 h/15	20 h/74	0 h/0
Total	176 h/174	87 h/77	231 h/458	93 h/106

strong onshore wind, the course of the survey remained closer to shore, whereas when weather conditions allowed, the survey was conducted more offshore; when fuel availability was low, survey effort had to be decreased). Nonetheless, with each survey we aimed to ensure the best possible coverage of the entire bay.

A dolphin group was defined as a collection of dolphins within a 100 m radius of each other (Wells *et al*. 1987) that operated in a coordinated way (Lusseau *et al*. 2003), interacting or engaged in similar activities (Irvine *et al*. 1981, Wells *et al*. 1987, Wilson 1995, Connor *et al*. 2000, Lusseau *et al*. 2006). Once a bottlenose dolphin group was encountered, group size was estimated by two researchers independently, and verified subsequently using photographs obtained for photo-identification.

For each dolphin group encountered, as many high-quality photographs as possible were taken of the dorsal fins of all individuals in the group for later identification of individuals, regardless of the presence of obvious marks (Würsig and Würsig 1977, Würsig and Jefferson 1990). These photographs were taken using a digital DSLR camera Nikon D90 and a 200 mm Nikor zoom lens (f/2.8) and a 1.7× teleconverter. The quality of these photos was graded based on Urian *et al*. (2015). Dolphins identified to be closely accompanied by a calf on at least two different occasions were assumed to be females (Mann and Smuts 1999, Grellier *et al*. 2003). In addition, the sex of 14 dolphins was determined through genetic sampling as part of another study (Fruet *et al*. 2014). Seasons were defined as follows: (1) summer: January to March, (2) autumn: April to June, (3) winter: July to September, (4) spring: October to December.

Data Selection

All individuals within a group were considered to be associated with each other, a spatial definition of association commonly used in studies of vertebrate social structure (Whitehead and Dufault 1999). The more frequently two dolphins were sighted together in the same group, the more strongly they were associated. Only Q1 and Q2 pictures were used for analysis (Urian *et al.* 2015). All sightings of groups were selected to be at least a day apart to ensure independent sampling periods (Bejder *et al.* 1998; Chilvers and Corkeron 2002; Whitehead 2008*a,b*). Groups sighted on the same day remained in analyses as they were pooled within the same sampling period (see below for details on sampling period). Furthermore, only identified dolphins resighted ≥ 5 times were selected for social association analysis. Within the data set, this selection procedure was believed to result in a sufficient number of individuals for the analysis (both highly resident and less resident individuals), while ensuring the identifiability of the individuals. Calves were excluded from the analysis due to their dependence on their mothers.

Defining Associations and Social Organization

Half-weight index (HWI) values were calculated using SOCPROG 2.6, a Matlab program for analyzing social organizations within animal societies (Whitehead 2009, 2015). The HWI was chosen as a measure of association, because it tends to correct for missed identifications of one member of a pair (which is inherent in photo-identification techniques) including within-group sampling errors and within-community sampling errors (Cairns and Schwager 1987, Ginsberg and Young 1992, Smolker *et al.* 1992). The HWI can vary from 0.0 for individuals never seen together to 1.0 for individuals always seen together. It has been applied at various times to evaluate the association patterns of bottlenose dolphins (*e.g.*, Wells *et al.* 1987, Weller 1991, Connor *et al.* 1992, Smolker *et al.* 1992, Bräger *et al.* 1994, Lusseau *et al.* 2006, Cantor *et al.* 2012). To calculate the association index values for each dyad (pair of individuals), a daily sampling period was chosen. In order to ensure more than one dolphin group was observed within a sampling period (thus more than one occasion to observe associations), and in view of the spread of the selected data, a monthly sampling period was chosen to perform the permutation test (of groups within samples).

To test the accuracy of representing the true social system (power of analysis), the correlation coefficient r between the true association indices (proportion of time dyads actually spend together, Cairns and Schwager 1987) and the estimated association indices were calculated, using the likelihood approximation (Whitehead 2008*a*). Values of r close to 1.0 indicate an excellent representation, close to 0.8 indicate a good representation, whereas values close to 0.4 indicate a somewhat representative pattern. Values close to 0.0 indicate no power (Whitehead 2008*b*, 2015). The social organization of the population was analyzed by estimating the "social differentiation" (S) using the likelihood approximation (including bootstrap standard errors), which is the coefficient of variation of the true association indices (Whitehead 2008*a*). It is a measure of how varied the social system is; values <0.3 indicate a homogeneous society whereas values >2 indicate extremely differentiated societies (Whitehead 2015). Subsequently, in order to ensure the statistical power of the permutation test, $S^2 \times H$ was calculated based on Whitehead (2008*a*) in which H is the mean number of associations per individual. Sufficient statistical power to reject the null hypothesis of no preferred/avoided associations was assumed when $S^2 \times H > 5$ (Whitehead 2008*a*).

A Monte Carlo randomization technique was employed to test the significance of all possible dyads of animals within the sample by comparing any association pattern in real data with a distribution of random data (Manly 1995, Bejder *et al.* 1998). This permutation test (of groups within samples) is used to test the null hypothesis that individuals associate at random. Following the methods of Bejder *et al.* (1998) and Whitehead and Dufault (1999), the number of permutations performed in this test was increased until the P value obtained from the Monte Carlo simulation stabilized and the confidence intervals decreased. This occurred at 20,000 permutations with 1,000 trials per permutation.

Within the permutation test, short-term (within sampling periods) preferred/avoided associations are indicated by a significantly lower mean of the observed *vs.* random association index (for more detail see Whitehead *et al.* 2005, Whitehead 2008*b*). Additional evidence for the presence of avoided associations is found when this decrease of the proportion of nonzero association index values is significant when comparing the observed *vs.* random data (Whitehead 2008*b*). In general, long-term (between sampling periods) preferred/avoided associations are indicated by a significantly higher Standard deviation and coefficient of variation of the observed *vs.* random association index values (Whitehead *et al.* 2005).

To assess differences in association by sex, a Mantel test (Mantel 1967) was carried out. The statistical significance of each Mantel test was tested against the null hypothesis in which the number of preferred associations was unrelated to the sex, using 1,000 random permutations. To validate the use of HWI *vs.* HWIG (half-weight index standardized for gregariousness; for more detail see Godde *et al.* 2013) to assess association patterns, a variation in individual gregariousness was tested. This test searches for individuals that may be consistently found in groups larger or smaller than the typical (Jarman 1974, Whitehead *et al.* 2005). The null hypothesis is that all individuals are found in groups with a similar size distribution, and it is rejected when the SD of the typical group size (tgs: mean group size for any given individual) is unexpectedly high and significantly different from the permutated data (Whitehead 2015). When the variation in individual gregariousness is unsubstantial compared to the variation in affinity, the HWI is believed to be suitable for the assessment of association patterns, with no need to standardize for gregariousness (see Godde *et al.* 2013).

All data were analyzed in combination across seasons as well as for each season separately.

Temporal Association Pattern

In order to examine the temporal stability of associations between individuals, the standardized lagged association rate (SLAR) was calculated. This is appropriate relative to the lagged association rate when potentially not all associates are recorded on every monitoring occasion (Whitehead 1995). The precision of this process was estimated by jackknifing over the sampling periods (Efron and Stein 1981). The resulting proportion was then compared to the null association rate (Whitehead 1995) which represents the association rate over time if individuals are associating at random with no preferred companions. The rate of decay of the SLAR was then compared with a number of mathematical models describing different rates of exponential decay (see Whitehead 1995). The quasi Akaike information criteria (QAIC)

Table 2. Average half-weight index values (HWI) with SD as well as average of maximum HWI values with SD for all individuals calculated in general as well as for the seasons. The number of possible dyads and the amount of dyads for which the HWI > 0 (number of nonzero dyads) are also given. The separate data sets that were not accepted with sufficient power of analysis to detect the true social system, and thus excluded from farther analyses, are written between brackets (see text for farther details).

Season	Average HWI for all dyads	SD	Average of maximum HWI of all dyads	SD	Number of nonzero dyads	Number of possible dyads
Summer	0.14	0.07	0.62	0.19	486	1,081
(Autumn)	(0.14)	(0.07)	(0.63)	(0.19)	(213)	(561)
Winter	0.30	0.09	0.61	0.12	1,420	1,596
(Spring)	(0.22)	(0.10)	(0.86)	(0.15)	(406)	(946)
Total	0.23	0.06	0.50	0.08	1,468	1,596

was used to select the model with the lowest theoretical expected error (Whitehead 2008*b*), which then provided an estimate of the decay of associations. For this analysis, no data selection was performed to avoid a positive bias (Whitehead 2008*b*); *i.e.*, 155 groups and 64 identified individuals were used for this analysis.

RESULTS

After data selection, 116 groups were selected for analysis of the social organization. Out of these groups, 57 identified dolphins seen ≥ 5 times were selected. Twelve of these individuals were males and 15 were females; the remaining 30 individuals were of unknown sex.

Social Organization

The correlation coefficient r between the true association indices and the calculated association indices was 0.73 (SE = 0.03), suggesting a relatively good representation of the true social structure. The estimation of social differentiation (S) resulted 0.29 (SE = 0.08), indicating a rather homogenous society (*i.e.*, no apparent differentiated social groups within the population). The mean number of observed associations per individual (H) was 209.73. Based on guidelines developed by Whitehead (2008*a*), the data appear to have the power to reject the null hypothesis of preferred or avoided associations ($S^2 \times H = 0.29^2 \times 209.73 = 17.6 > 5$). When subdividing the data set per season, the correlation coefficient (r) dropped to 0.64 (SE = 0.06) for winter and 0.58 (SE = 0.06) for summer, suggesting data were still somewhat representative of the true social system, although for summer the representation is weak. Due to the low social differentiation in winter ($S = 0.20$) (and thus the need for more observed associations; Whitehead 2008*a*), the power to reject the null hypothesis of no preferred/avoided associations is weak ($S^2 \times H = 0.20^2 \times 148.04 = 5.9 > 5$). On the other hand, due to the higher social differentiation in summer ($S = 0.72$) (and thus the need for fewer observed associations; Whitehead 2008*a*), there appears to be strong power to reject the null hypothesis of no preferred/avoided associations ($S^2 \times H = 0.72^2 \times 35.7 = 18.5 > 5$). Based on similar calculations, separate data sets for autumn and spring were excluded from farther analyses.

Table 3. Results of the permutation test of the overall half-weight index values (HWI), and those for winter and summer. CV = coefficient of variation, SD = standard deviation, tgs = typical group size.

	Overall HWI	Winter HWI	Summer HWI
Observed mean	0.29	0.44	0.18
Random mean	0.29	0.44	0.19
(Test for presence of short-term preferred/ avoided associations) *P*	0.39	0.51	<0.01[a]
Observed SD	0.15	0.23	0.24
Random SD	0.15	0.23	0.22
(Good test for presence of long-term preferred associations) *P*	<0.05[a]	0.30	<0.01[a]
Observed CV	0.53	0.53	1.35
Random CV	0.50	0.52	1.19
(Preferred test for presence of long-term preferred associations) *P*	<0.05[a]	0.34	<0.01[a]
Observed proportion nonzero association index values	0.93	0.89	0.42
Random proportion nonzero association index values	0.93	0.89	0.48
(Additional test for presence of avoided associations) *P*	0.13	0.29	<0.01[a]
Observed SD of nonzero association index values	0.13	0.18	0.19
Random SD of nonzero association index values	0.13	0.18	0.16
P	<0.05[a]	0.41	<0.01[a]
Observed SD (tgs)	2.94	4.06	2.52
Random SD (tgs)	2.50	3.6	2.43
(Test for variation in individual gregariousness)*P*	0.15	0.11	0.35

[a]Significant *P* value.

The HWI value for all possible dyads ($n = 1{,}596$) averaged 0.23 (± 0.06 SD), whereas the maximum HWI value averaged 0.50 (± 0.08 SD). The HWI values varied over the two seasons, with the lowest average HWI value found in summer and the highest one in winter. Table 2 provides a summary.

Results of the permutation test (using a monthly sampling period; see Table 3) showed that the observed mean association index was not significantly different from the random mean, indicating that the null hypothesis of no short-term preferred companions could not be rejected. However, the null hypothesis of no long-term preferred associations could be rejected based on the available data (observed SD and CV significantly larger than random SD and CV; Table 3). The test further indicated that the null hypothesis of all individuals being found in groups with a similar size distribution (gregariousness) could not be rejected, as the SD of the tgs was relatively low and showed no difference when compared to the permuted data. This suggests that there was no need to standardize for gregariousness (*i.e.*, use of HWIG).

A permutation test was subsequently performed for data from winter and summer separately (*i.e.*, winter associations of all study years combined; see Table 3). Results indicated that in winter, the null hypothesis of no preferred/avoided companions (short- and long-term) could not be rejected (observed mean, SD, CV, and proportion of nonzero association index values did not differ from the random values). However, in summer such null hypothesis was rejected, with indications for both short- and long-term preferred (observed SD and CV > random SD and CV) and avoided (observed

Table 4. Number of dyads associating significantly different from random over the entire study period, depending on sex classes. The total number of possible dyads and the number of nonzero dyads (HWI > 0) is also given for each dyad category.

	Less than expected ($P < 0$)	More than expected ($P > 0.975$)	Total possible dyads	Number of nonzero dyads
Male–male	0	0	66	66
Female–female	1	0	105	98
Male–female	0	0	180	173
Male–unknown sex	0	1	360	345
Female–unknown sex	5	0	450	396
Unknown sex–unknown sex	2	0	435	387
Total	8	1	1,596	1,465

proportion of nonzero association index value < random proportion of nonzero association index value) associations. Results of the test farther showed that regardless of season, the null hypothesis of all individuals being found in groups with a similar size distribution could not be rejected (observed SD[tgs] = random SD[tgs]; Table 3).

Associations between and within sex were not significantly different within the whole data set (Mantel test: $t = -1.75$; $P = 0.07$). Additionally, only nine dyads (0.5% of all possible dyads or 0.6% of all nonzero dyads) associated significantly more or less than expected at random over the total duration of the study (Table 4). No difference in dyad distribution (individuals associating more or less than expected) could be found in winter or spring when compared to the overall data set.

Temporal Association Pattern

The general SLAR shows a fluctuation in the duration of associations, but shows little decay over the entire study period (Fig. 2). The model with the lowest QAIC value included preferred companions and casual acquaintances, represented by the function $a2 + a3 \times \exp(-a1 \times \text{td})$. The fitted values from this model suggest a quick decrease of the SLAR over the first 2–3 mo, with values stabilizing at around 0.022, remaining slightly higher than the predicted random (null) association rate, which indicates the existence of a small proportion of long-term associations (as observed in the permutation test). The duration of casual acquaintances was estimated at 23 d, given by $1/a1$ ($a1 = 1.2649$, SE = 0.019).

DISCUSSION

The results suggest that the bottlenose dolphins in Bahía San Antonio live in a rather homogenous and flexible fission–fusion society with a few long-lasting associations. The overall average association index value (HWI) is well within the range of the values found in common bottlenose dolphin populations worldwide (Smolker *et al.* 1992, Bräger *et al.* 1994, Wilson 1995, Rossbach and Herzing 1999, Connor *et al.* 2000, Blasi *et al.* 2014).

Despite the limitations of the low sample size, the rate of associations seemed to vary between winter and summer, similarly to the dolphin's grouping behavior in

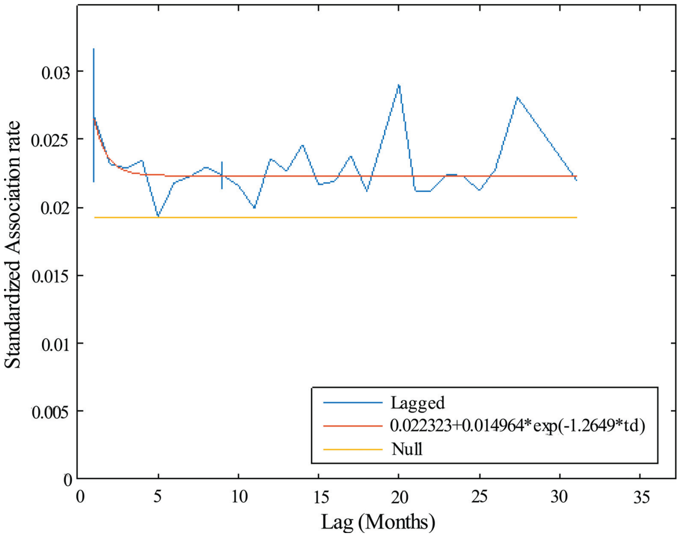

Figure 2. Standardized lagged association rate for pairs of bottlenose dolphins associated within groups in Bahía San Antonio; the plot shows the probability of associations persisting after increasing lags in time between observations (Lag). The null association rate (Null) is the expected value of the lagged association rate if there are no preferred associations. It is the inverse of the population size minus one, and so does not change with time lag. Bars represent the SE estimated using the jackknifing procedure. The maximum-likelihood best-fit model represents associations with preferred companions and casual acquaintances represented by the function $0.022323 + 0.014964 \times \exp(-1.2649 \times td)$.

these respective seasons (*see* Vermeulen *et al.* 2015). As such, in winter when average group size was reported to be largest ($\bar{x} = 7$ individuals; Vermeulen *et al.* 2015), most associations were formed (89% of all possible dyads) and the average HWI value reached its maximum of 0.30. Results further indicate that the null hypothesis of no preferred or avoided associations could not be rejected. However, because the statistical power was weak, one must be careful not to assume there are no preferred/avoided associations at this time of year. Conversely, during summer when average group size was reported to be at its minimum ($\bar{x} = 3$ individuals; Vermeulen *et al.* 2015), least associations were formed (45% of all possible dyads) and HWI dropped accordingly to a minimum of 0.14. Results further showed that during this season, the null hypothesis of no preferred or avoided associations could be rejected.

These results suggest that the bottlenose dolphins in Bahía San Antonio exhibit a temporal variability in their association rates, as also shown in the SLAR. When the benefit of grouping is high (*e.g.*, to increase capture efficiency when food is abundant or when predation pressure is high) and larger aggregations are formed (in this study population during winter; Vermeulen *et al.* 2015), it appears that a social network arises in which individuals engage in numerous and short-lived associations (Clapham 1996). Conversely, when the cost of grouping is high (*e.g.*, when food availability is low) in this study population during summer (Vermeulen *et al.* 2015), it seems a more disconnected network arises with individuals engaging with few yet long-lasting associations (Cantor *et al.* 2012). Within this study, such variation in grouping behavior seemed to be equal for all individuals included in analysis, as no individual variation in gregariousness could be found.

Such temporal shift in associations has been shown before in other fission–fusion societies (*e.g.*, chitals, *Axis axis*: Raman 1997; African elephants, *Loxodonta* sp.: Wittemyer *et al.* 2005; bottlenose dolphins: Connor *et al.* 2000), and has mostly been related to socio-ecological and/or demographic factors (*e.g.*, Aureli *et al.* 2008, Parsons *et al.* 2009, Foster *et al.* 2012, Pinter-Wollman *et al.* 2013). Vermeulen *et al.* (2015) suggested that the seasonal variation in grouping behavior of the studied population was related to a seasonal variation in food availability and the Ecological Constraints Hypothesis (Chapman 1990). Although no empirical data are available in this study to assess this hypothesis, a handful of studies have shown such a relation in other cetacean societies. For example, Foster *et al.* (2012) showed how resource availability is an important determinant of the social structure of killer whales (*Orcinus orca*). Sociality increased when food was abundant, and a less connected social network occurred when food was less abundant (Foster *et al.* 2012). Pearson (2009) indicated that coordinated foraging strategies are the primary influence on the fission–fusion dynamics of dusky dolphins (*Lagenorhynchus obscurus*). Chilvers and Corkeron (2002) reported how bottlenose dolphin social structure in Moreton Bay was related to the presence of trawlers and the associated foraging technique of certain individuals. About a decade later, Ansmann *et al.* (2012) indicated how the same dolphins restructured their social organization when these trawlers disappeared. Conversely, one cannot exclude the effect of other aspects such as demography (*e.g.*, age, sex, reproductive status) and previous social experience (Aureli *et al.* 2008, Pearson 2009, Pinter-Wollman *et al.* 2013). For example, the social structure of northern bottlenose whales (*Hyperoodon ampullatus*) does not appear to be driven by their deep-diving foraging strategy (Gowans *et al.* 2001). Undeniably, the social structure of a population should be seen as a multivariate optimization to various pressures, and does not result from one ultimate cause (Caraco 1979).

The common bottlenose dolphin is often believed to live in strongly defined social organizations, with the presence of many strong long-term male alliances and strong associations between females depend on reproductive status (Wells 1991; Connor *et al.* 1992, 2000; Lusseau *et al.* 2003). Furthermore, it is frequently argued that in small bottlenose dolphin communities, with high site-fidelity to a small area, cohesiveness increases (Connor *et al.* 2000, Lusseau *et al.* 2003, Augusto *et al.* 2011) as there are only a small number of possible associates for each individual (Bräger 1999). However, despite the study population being small, isolated and highly resident in the study area (Vermeulen and Bräger 2015, Vermeulen *et al.* 2016), results showed that its social structure is not as strongly defined as often assumed for the species. In fact, it is homogenous and flexible, reconfirming the species' potential for a high degree of fission–fusion dynamics (Aureli *et al.* 2008) to adapt to fine-scale variations in temporal and habitat-specific pressures on grouping and association patterns (*e.g.*, Lusseau *et al.* 2003, Karczmarski *et al.* 2005, Elliser and Herzing 2011).

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