



## Social structure of Atlantic spotted dolphins, *Stenella frontalis*, following environmental disturbance and demographic changes

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### ABSTRACT

Extreme environmental events and demographic changes can have variable effects on the social structure of animal populations. This study compared the social structure of a community of Atlantic spotted dolphins in the Bahamas before and after two hurricanes. Approximately 36% of the individuals were lost, with no subsequent increase in immigration. The majority of the social structure characteristics were consistent with results from a long-term study covering the previous 12 yr, including community structure with definitive social clusters, sex preferences and overall association patterns. However some changes occurred, though still constrained within sex preferences. Posthurricane there was a decrease in social differentiation and increased cohesion within clusters and across age class. Males retained or made new first order alliances, however, only one second order alliance was evident, revealing a simplified alliance structure. Juvenile individuals made alliance level associations, unprecedented from long-term analysis. Although other studies have shown stark restructuring, this study showed that less drastic changes within overall social structure stability can occur. Persistence and evolutionary changes in populations through environmental and/or demographic perturbations may depend on the social structure of a population or community. Understanding the processes involved in social development is paramount for conservation of diverse populations.

**Key words:** *Stenella frontalis*, Atlantic spotted dolphin, community structure, social structure, association patterns, coefficients of association, SOCPROG, demography, environmental disturbance.

Environmental disasters, both human and natural, can affect animal populations in many ways, including alterations of behavior, death of individuals (small and large scale), emigration, immigration, and changes in food abundance and distribution. In highly social mammals, these changes can affect the social structure of the

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population. Lack of long-term baseline information limits the ability for researchers to assess damages that may occur, particularly in cetacean populations (Matkin *et al.* 2008). This paper describes the effects of demographic changes, following two major hurricanes, on the social structure of a community of Atlantic spotted dolphins, *Stenella frontalis*.

The fission/fusion dynamics (Aureli *et al.* 2008) of spotted dolphin society (Elliser and Herzing 2012, Elliser and Herzing in press) are similar to those of bottlenose dolphins and chimpanzees, where membership in groups is continually changing (Connor *et al.* 2000). Associations may involve many age and sex combinations of individuals, but long-term affiliations are generally correlated with age, sex, reproductive status, and kinship (Wells *et al.* 1999), including female networks (Wells 1991, Möller *et al.* 2006) and male alliances (Wells *et al.* 1987; Connor *et al.* 1992; Möller *et al.* 2001; Parsons *et al.* 2003; Rogers *et al.* 2004; Elliser and Herzing, in press). Although these patterns are similar across many bottlenose dolphin populations in different habitats (Quintana-Rizzo and Wells 2001), as well as spotted dolphins (Elliser and Herzing, in press), some extreme ecological constraints may be important factors shaping social interactions in cetaceans (Lusseau *et al.* 2003, Karczmarski *et al.* 2005). Alterations and/or reduction of habitat can cause severe changes in behavior and patterns of intra- and interspecies breeding (Strier 2002).

Similar effects can also result from changes in community size and composition, which can alter the social organization of a species (Lehmann and Boesch 2004). The loss of a single individual in a community or population has been shown to alter behavior, associations, and group and community structure (marmosets, *Callithrix jacchus*: Lazaro-Perea *et al.* 2000; bottlenose dolphins, *Tursiops truncatus*: Lusseau and Newman 2004). Likewise, the loss of many individuals can also greatly affect the associations and social structure of the population (chimpanzees, *Pan troglodytes verus*: Lehmann and Boesch 2004; bottlenose dolphins: Elliser and Herzing 2011; killer whales, *Orcinus orca*: Matkin *et al.* 2008).

These demographic changes can also have variable effects on social structure, depending on the species and population studied. In a chimpanzee community a decrease in community size led to increased party cohesion and enhanced cohesiveness between the sexes (Lehmann and Boesch 2004), similar to association patterns seen in dolphin populations inhabiting geographically isolated areas (Lusseau *et al.* 2003, Karczmarski *et al.* 2005). Bottlenose dolphins in the Bahamas lost 30% of their resident individuals, with an influx of almost the same number of immigrants after two major hurricanes impacted the area (Elliser and Herzing 2011). This resulted in a split of the community into two units, which were distinct and more homogenous in nature (Elliser and Herzing 2011). After the extreme environmental disturbance of the oil spill from the *Exxon Valdez*, killer whales suffered similar losses and a split in a matriline occurred (Matkin *et al.* 2008). It is evident that demographic and/or environmental factors can help shape the social structure of a given population. How individuals adjust to these changes may depend on the species, habitat, and social structure of the population.

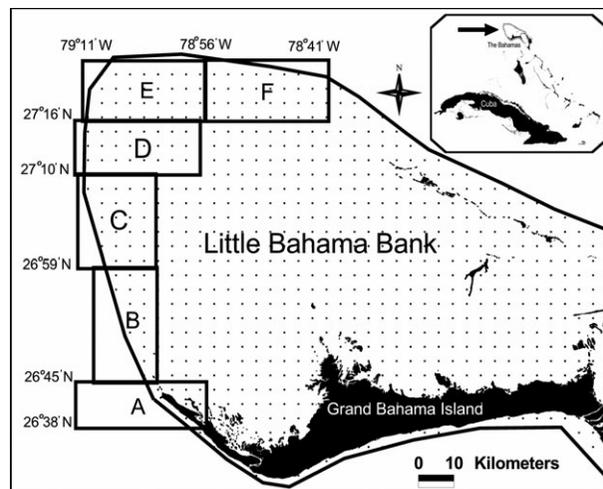
This study reports on a large loss of individuals from a small stable, resident, community of Atlantic spotted dolphins and the subsequent effects on their social structure. This community has been studied since 1985 (Herzing 1997, Herzing and Brunnick 1997). Long-term association patterns reveal a society remarkably similar to well-studied coastal bottlenose dolphin societies, including female networks, male alliances, and no long-term associations between sexes (Elliser and Herzing, in press). This community is divided into three social clusters with overlapping ranges where

mixed-cluster groups occur, but associations are stronger within clusters than between (Elliser and Herzing 2012). In 2004 this community was impacted by two major hurricanes within three weeks of each other. Following the hurricanes this community had a decrease in community size, either through mass mortality, displacement, or other correlated events. Due to the synchronous and sharp decline and lack of resightings of individuals that disappeared after 2004 (as of 2012 none have been resighted), the reduction in community size was most likely due to the hurricanes. The goal of the present study was to quantitatively describe the differences in social structure of this community of spotted dolphins before and after the hurricanes in 2004.

## METHODS

### *Study Area and Hurricane History*

Little Bahama Bank (LBB) is about 64 km from the east coast of Florida, and just north of West End, Grand Bahama Island. The study area spans 60 km north to south and 8 km east to west and encompasses 480 km<sup>2</sup>. The sandbank is shallow, between 6 and 16 m deep, and is surrounded by deep water (steep drop off to over 500 m into the Gulf Stream). It has a mostly sandy bottom, scattered with areas of rock, reef, and patches of seagrass (*Thalassia testudinum*). The entire study area was divided into six sections, A–F (Fig. 1). Effort was not evenly distributed throughout every area (% of total effort: A = 3.5%, B = 10.2%, C = 31.8%, D = 51.4%, E&F = 3.1%) due to physical attributes of the environment as well as rough weather which prohibits boat movement (Elliser and Herzing 2012). This type of varied effort is evident in other social analysis studies in similar size study areas (Shane 2004, Lusseau *et al.* 2006, Kent *et al.* 2008, Elliser and Herzing 2011).



*Figure 1.* Study area broken into six segments: A, B, C, D, E, and F. Arrow on the insert indicates the Bahamas study area.

The study area was directly hit by two strong hurricanes, Frances (strong category two, five mph below category three) and Jeanne (category three), within three weeks of each other in 2004 (Elliser and Herzing 2011). Previously, the most recent hurricane directly over this area was in the early 1900s (National Hurricane Center: <http://www.nhc.noaa.gov/HAW2/english/history.shtml>). The 40–50 yr life span of most dolphins (Connor *et al.* 2000) means that this community of dolphins has not encountered storms of this intensity before.

### Data Collection

Through repeated observations over many years, these dolphins are habituated to the presence of boats and people in the water. Data for this study was collected between 80 and 100 d from May to September each year from 2002 to 2007. Observations were conducted in all but rough weather conditions (over Beaufort 3 and/or intense rain squalls) from 0700 to 2000 by a single observer for each one hour shift, scanning 180° while underway, and 360° while anchored. More frequent rough weather (strong winds, seas, and storms) in years following the hurricanes, 2005–2007, made it difficult for offshore field work and restricted the ability to get into the field, and/or collect data on certain days (Table 1).

A group was defined as all dolphins in sight, moving in the same direction, typically involved in the same activity (*e.g.*, group or pod, Shane 1990). Upon sighting, group size was determined from the surface. Individuals were considered associated when identified with the group. Two to five researchers then entered the water with underwater video and Nikon V 35 mm or Sony Cyber-shot digital cameras to document behavior. An encounter was defined as a group of dolphins that were observable underwater for more than 2–3 min (Elliser and Herzing 2012). If the composition of the group changed by 50% or more (determined during field photo identification), they were considered a different group and a new encounter began.

Atlantic spotted dolphins show the four developmental color phases described by Perrin (1970) for the pantropical spotted dolphin (*Stenella attenuata*) and have been adapted for the Atlantic spotted dolphin by Herzing (1997). The four age classes include: two-tone (calves,  $\leq 4$  yr), speckled (juveniles, 4–9 yr), mottled (young adult, 10–16 yr) and fused (adult,  $\geq 16$  yr). Every identified individual was assigned to an age class and these data were updated each year. Individual identification was accomplished by comparing spotting patterns between individuals. Additional body

Table 1. Field effort and number of encounters for 2002–2007 and pooled years prehurricane (2002–2004) and posthurricane (2005–2007).

Season	# days at sea	# encounters	# days with encounters	Total hours	% hours underway (anchored)
2002	73	50	34	895	54.0 (46.0)
2003	71	49	33	779	59.5 (40.5)
2004	73	54	33	793.5	62.9 (37.1)
2002–2004	217	153	100	2,467.5	58.6 (41.4)
2005	55	30	24	592	70.4 (29.6)
2006	60	31	22	619.75	65.4 (34.6)
2007	61	37	27	654	68.5 (31.5)
2005–2007	176	98	73	1,865.75	68.1 (31.9)
Total	393	251	173	4,333.25	62.7 (37.3)

marks were also used, including nicks and scars on the dorsal fin, flukes and pectoral fins as well as marks or scars on the body. Females were identified by observation of mammary slits or observation of nursing by a calf. Males were identified by a gap between the genital slit and the anus, or observation of an erection.

### *Data Analysis*

Differences in group size were first analyzed to determine if there was a change in average group size following the hurricanes. No significant difference was found, so further analysis on differences in group size in relation to calf presence and behavioral category were conducted on all encounters (2002–2007) with ANOVA and Tukey tests using SPSS 16 software. Behavior was categorized as forage, travel, social, forage/travel, social/travel, social/forage, and social/forage/travel. The latter four categories capture the fact that dolphin groups often displayed multiple behavioral states within an encounter.

Coefficients of association (CoAs) were calculated using the half-weight index (Cairns and Schwager 1987) with the software program SOCPROG 2.3 (Whitehead 2009). Encounters were only included in the analysis if more than 50% of individuals were identified. Due to these restrictions, the number of encounters used in the CoA analysis was less than the total number of encounters observed. Calves were not included because their associations are dependent on their mothers' associations. Annual CoAs for each year between 2002 and 2007 were calculated for noncalf individuals of known sex sighted three or more times within that year. Pooled CoAs were calculated for noncalf individuals of known sex sighted six or more times per pooled period (prehurricane 2002–2004, posthurricane 2005–2007). These sighting requirements have given reliable, representative data (Whitehead 2008*a, b*) for these spotted dolphins (Elliser and Herzing 2012; Elliser and Herzing, in press) and the sympatric bottlenose dolphins (Elliser and Herzing 2011). If an individual changed age class within the pooled period, they were classified as the age class that they were two out of the three years. Observed associations were defined as all non-zero CoAs. Strong associations were defined as greater than twice the average CoA of the study group (Gero *et al.* 2005, Whitehead 2008*a*).

SOCPROG was used to conduct permutation tests to determine if associations were nonrandom and if there were preferred/avoided companions (Christal and Whitehead 2001, Whitehead 2009). The sampling period was set to “day” and the number of permutations was increased until the *P*-value for the Standard Deviation (SD) stabilized at 10,000 permutations, with 100 flips per permutation (Whitehead 2009). The “permute all groups” test was chosen for the annual analysis, and the “permute groups within samples” test was used for the pooled data sets, to account for lack of individuals due to birth, death, migration, *etc.* Significantly high SD or CV of the real association indices indicate long-term preferred companionship and nonrandom associations (Whitehead 2009). If associations were found to be nonrandom, Mantel tests were conducted to examine whether differences in association occur between classes (*e.g.*, sex and age classes).

SOCPROG was used to determine the power and precision of the CoA analysis by calculating the social differentiation ( $S$ , which indicates the variability of association indices within a population),  $S^2 \times H$  ( $H$  is the mean number of observed associations per individual), and the correlation coefficient (CC) between the true association indices and their estimated values, the association indices (Whitehead 2008*a, b*). This information revealed how reliable the results were, if there was enough data to be

representative and aided in determining which data set (annual or pooled) was more representative. Standard Errors (SE) were calculated from 1,000 bootstrap replications. Data sets with intermediate ( $S \sim 0.5$ ) to high ( $S$  close to or above 1.0) social differentiation need far fewer associations than data sets with low differentiation to detect preferred companionship (Whitehead 2008a).

This community is made up of three social clusters: Northern, Central, and Southern (Elliser and Herzing 2012). In order to correctly interpret the pattern of social associations, it was important to determine whether these social clusters were still present before and after the hurricanes. Cluster definition was confirmed using non-metric multidimensional scaling (MD) and hierarchical agglomerative cluster analysis conducted with SOCPROG 2.3. In a MD plot, strongly associated individuals were plotted together and weakly associated were farther apart (Whitehead 2009). A plot with stress  $< 0.1$  is considered a good ordination (Whitehead 2008a). Hierarchical agglomerative cluster analysis produced a dendrogram where the individuals were arranged on one axis and their degree of association on another (Whitehead 2009). The Average-linkage method was used. The cophenetic correlation coefficient (CCC) determined how well the dendrogram matched the association matrix. A CCC of  $> 0.8$  indicates a good match, (Whitehead 2008a). These clusters overlapped in range and associations and have been confirmed to be part of one community (Elliser and Herzing 2012); therefore all individuals were analyzed together for CoA analysis.

## RESULTS

### *Resighting*

In 393 d at sea there were 173 d with encounters, with a total of 251 encounters (Table 1). A total of 89 individuals were identified and sex was determined for 96% of the community. There were 43 females, 42 males, and 4 of unknown sex. Fifty-six individuals (63%) were sighted in every year of this study that was possible for that individual (*i.e.*, they had been born and they were not considered lost—indicated by no sightings for more than 3 yr in a row).

Before the hurricanes an average of 103 individuals were identified per year. After the hurricanes, this number dropped dramatically to 67.7 individuals (Fig. 2). Thirty-six regularly seen individuals (16 females and 20 males) disappeared and have not been resighted to date (through the 2012 field season). Losses were fairly consistent over age classes: 9 two-tones, 11 speckled, 6 mottled, and 10 fused individuals. However the percentage loss per age class decreased with increasing age: 50% of two tones, 44% of speckled, 35% of mottled, and 26% of fused individuals. Of these missing individuals, 30 had been seen every year since they were first identified, some since 1985. It is highly unusual for these regularly seen individuals to not be sighted for over three years in a row, indicating these dolphins may have been lost to the community. Despite the loss of roughly 36% of the community, immigration remained low, with an average of 2.3 prehurricane to two individuals per year posthurricane (Fig. 2).

### *Group Size*

Group size ( $n = 251$ ) ranged from one to 56,  $\bar{x} = 10.9 \pm 8.9$ . The majority (67.7%) included 11 or fewer individuals. There was no difference between pre- and

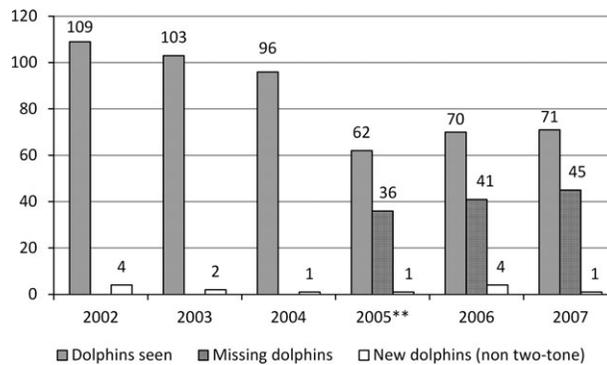


Figure 2. Number of individuals identified per year, number of missing individuals and new non-two-tone (calf) individuals for 2002–2007. Starred year indicates the year following the hurricanes.

posthurricane group size ( $df = 1$ ,  $F = 0.354$ ,  $P > 0.50$ ), so further analysis was conducted on all groups 2002–2007. Groups were significantly larger with calves ( $n = 143$ ,  $\bar{x} = 14.3 \pm 9.9$ ) than without calves ( $n = 108$ ,  $\bar{x} = 6.4 \pm 4.6$ ,  $df = 1$ ,  $F = 9.261$ ,  $P < 0.005$ ). There was no difference in group size relating to behavior or pre/posthurricane ( $df = 6$ ,  $F = 0.836$ ,  $P > 0.50$ ). There was no significant interaction between calf presence, behavior, and pre/posthurricane on group size ( $df = 6$ ,  $F = 0.816$ ,  $P > 0.50$ ).

#### Pre- and Posthurricane Associations

The total number of noncalf individuals, males, and females for each data set are given in Table 2. In the prehurricane analysis there were 22 speckled, 16 mottled, and 36 fused individuals. In the posthurricane data there were 16 speckled, 6 mottled, and 25 fused. For both annual and pooled data sets, permutation tests revealed nonrandom associations, indicating preferred and/or avoided companions (Table 2). The pooled data (compared to the annual data sets) were the best representation of the true social system with the highest social differentiation (S) and correlation coefficient (CC) (Table 2), thus pooled data was used in all subsequent analyses.

The percentage of observed associations and overall mean CoA greatly increased from prehurricane (66.7%, CoA =  $0.14 \pm 0.05$ ) to posthurricane (87.6%, CoA =  $0.24 \pm 0.06$ ). Due to this increase the number of strong associations accordingly decreased from 24% to 9%. Table 3 shows CoA analysis and Mantel tests broken down by age and sex class. With-in associations were consistently higher than between-sex for both data sets, due to the high male-male CoA (particularly fused and mottled males) compared to female-female and mixed sex CoA. CoA were significantly higher within age classes (0.16) compared to between age classes (0.13) for the prehurricane years (again due to high fused and mottled male-male CoA). No significant difference was found posthurricane (within age classes CoA = 0.27, between age classes CoA = 0.24), however when broken down by sex, once again the male-male associations within age class were significantly higher than between age classes, similar to the prehurricane years, there was no difference for female-female CoA (Table 3).

*Table 2.* Number of groups, individuals, mean CoA, *P*-value for permutation tests and test statistics for power and precision of social structure analysis.  $S > 0.50$  = well differentiated society,  $CC = 0.40$  CoA matrix is somewhat representative,  $CC = 0.80$  CoA matrix is a good representation, and  $S^2 \times H > 5$ , good ability to reject the null hypothesis of no preferred companions.

Year	No. groups	No. Individuals	Males	Females	Mean		<i>P</i> -value	<i>S</i> ± (SE)	<i>H</i>	CC ± (SE)	$S^2 \times H$
					COA ± (SD)	<i>S</i> ± (SE)					
2002	48	54	21	33	0.17 ± (0.20)	0.83 ± (0.31)	<i>P</i> < 0.001	0.46 ± (0.22)	47.33	0.62 ± (0.05)	32.2
2003	45	56	27	29	0.20 ± (0.20)	0.46 ± (0.22)	<i>P</i> < 0.001	0.58 ± (0.17)	57.79	0.43 ± (0.09)	12.4
2004	45	48	17	31	0.22 ± (0.20)	0.58 ± (0.17)	<i>P</i> < 0.001	0.94 ± (0.15)	66.33	0.56 ± (0.06)	22
2002–2004	141	74	32	42	0.14 ± (0.14)	0.94 ± (0.15)	<i>P</i> < 0.001	0.00 ± (0.24)	139.38	0.80 ± (0.02)	123.2
2005	28	37	16	21	0.33 ± (0.20)	0.00 ± (0.24)	<i>P</i> < 0.005	0.00 ± (0.16)	61.68	0.00 ± (0.18)	0
2006	27	39	23	16	0.32 ± (0.18)	0.00 ± (0.16)	<i>P</i> < 0.001	0.46 ± (0.19)	69.9	0.00 ± (0.13)	0
2007	35	44	20	24	0.21 ± (0.21)	0.46 ± (0.19)	<i>P</i> < 0.002	0.44 ± (0.09)	48.41	0.44 ± (0.09)	10.2
2005–2007	91	47	23	24	0.24 ± (0.16)	0.52 ± (0.07)	<i>P</i> < 0.001	0.70 ± (0.03)	162.43	0.70 ± (0.03)	44.4

Table 3. Mean CoA for age-classes and sex with standard deviation (SD). MM = male-male, MF = mixed sex, FF = female-female associations. Fus-Fus = fused only, Mort-Mort = morttled only, Spec-Spec = speckled only associations. Bold indicates highest CoA and significant Mantel tests.

Year	Sex class	Fus-Fus	Mort-Mort	Spec-Spec	Within age class	Between age class	Mantel
2002–2004	MM	<b>0.39 (0.05)</b>	<b>0.24 (0.11)</b>	0.14 (0.05)	<b>0.28 (0.13)</b>	0.18 (0.08)	<b>P &lt; 0.001</b>
	MF	0.12 (0.07)	0.13 (0.07)	0.13 (0.04)	–	–	–
	FF	0.11 (0.03)	0.17 (0.04)	<b>0.21 (0.08)</b>	0.15 (0.07)	0.13 (0.05)	<b>P = 0.14</b>
2005–2007	Mantel	<b>P &lt; 0.001</b>	<b>P &lt; 0.03</b>	<b>P &lt; 0.03</b>	–	–	<b>P &lt; 0.03</b>
	MM	<b>0.34 (0.06)</b>	<b>0.60 (0.06)</b>	0.32 (0.11)	<b>0.38 (0.13)</b>	0.29 (0.08)	<b>P &lt; 0.03</b>
	MF	0.21 (0.10)	0.33 (0.17)	0.28 (0.07)	–	–	–
	FF	0.20 (0.06)	0.17 (0.00)	0.23 (0.11)	0.20 (0.08)	0.22 (0.06)	<b>P = 0.79</b>
	Mantel	<b>P &lt; 0.05</b>	<b>P &lt; 0.05</b>	<b>P = 0.43</b>	–	–	–

Multidimensional scaling (Fig. 3) and hierarchical agglomerative cluster analysis (Fig. 4) showed one community with three social clusters, Southern, Northern, and Central consistent for both pre- and posthurricane years. Mantel tests ( $P < 0.001$ ) revealed stronger associations within clusters (prehurricane CoA = 0.25, posthurricane CoA = 0.35) than between clusters (prehurricane CoA = 0.07, posthurricane CoA = 0.14) for both pooled periods.

*Female-female associations*—The average CoA of female-female associations was below the mean for the community for both pre- and posthurricane. Generally

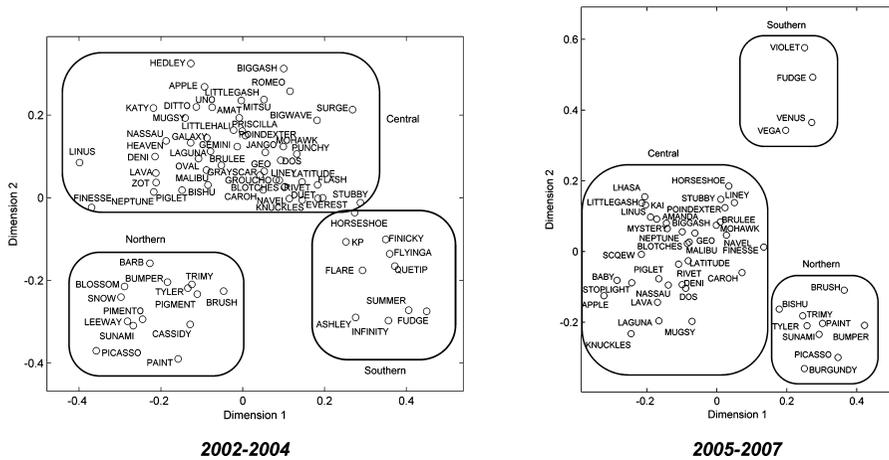


Figure 3. Representative plot of multidimensional scaling showing one community, with three clusters, Northern, Southern and Central for 2002–2004 pooled years (Stress = 0.085, with 200 iterations in five dimensions) and 2005–2007 pooled years (Stress = 0.099, with 200 iterations in five dimensions).

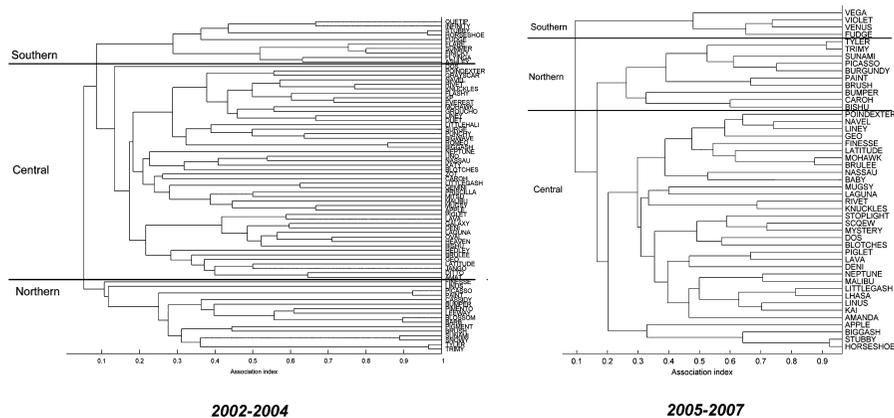


Figure 4. Hierarchical agglomerative cluster analysis for 2002–2004 (CCC = 0.78) and 2005–2007 (CCC = 0.81), revealing one community with three social clusters Northern, Southern, and Central for both pooled periods.

females associated with most other females in their cluster, with few strong associations across clusters. The two highest female-female CoAs both pre- and posthurricanes were between mothers and their speckled offspring. Every female prehurricane and 19 of 24 females posthurricane had at least one CoA that was more than twice the community average, involving all age class combinations. Many of these pairs include older offspring (up to mottled age class) associating highly with their mothers, as well as with their mother's associates and their older offspring. For both pooled periods, the majority of the females with strong female-female associations were reproductively active. Many of the speckled with strong female-female associations had mothers that were pregnant or had a new calf.

*Male-male associations*—The average CoA of male-male associations was higher than the community average for both pre- and posthurricane. A sociogram of male-male strong associations for pre- and posthurricane years is shown in Figure 5. The base CoA for each sociogram was at least twice the mean male-male CoA for that period, indicating strong associations. In order to compare relationships of similar strength between the pooled periods, the baseline CoAs for the sociograms are different, accounting for the increase in mean CoA for the posthurricane years (because the level of associations considered strong varies in relation to the mean CoA). In both pooled periods the majority and strongest of the associations involve fused and mottled males.

In the prehurricane years, first order alliances were made up of pairs/trios (some since 1991) and some alliances had strong associations with other alliances, within and between clusters (Fig. 5). The posthurricane sociogram shows a more simplified association pattern. Contrary to prehurricane data, there was only one strong association between alliances (alliances 2 and 5), however, this association is not observed on the sociogram because one of the male individuals was not seen enough under the data restrictions to be included in analysis (nonetheless, it was seen in 68% of encounters with his alliance partner). There were only three long-term alliances that survived the hurricanes (alliances 2, 3, and 5). The male, Liney, (alliance 9) lost his



Figure 5. Sociograms of strong CoA (0.50 and higher) for male spotted dolphins 2002–2004 and sociogram of strong CoA (0.65 and higher) for male spotted dolphins 2005–2007. A thicker line indicates a stronger CoA. Arrows indicate social cluster. Letters in parentheses indicate age: S = speckled, M = mottled, F = fused. Number in parentheses indicates alliance number. \* and \*\* indicate alliance pairs/trios with CoA 0.70 and above.

partner, Duet, after the hurricanes and began another primary pair with Navel, a lesser associate since 2000, along with a third male Poindexter. Two new primary pairs were formed between mottled and fused individuals, alliances 1 and 4). The final two primary alliances that formed were very unusual since they were all speckled males (alliances 6 and 8).

*Mixed sex associations*—In both pooled periods the mixed sex mean CoA was less than the community average (and close to the female-female mean CoA) and associations involved every age class combination. In prehurricane years all but three males and four females had strong mixed sex associations, whereas in posthurricane years only 15 of 23 males and 14 of 24 females had strong mixed sex associations. All other data were similar for both data sets and is presented together. The vast majority of associations were within social clusters, the few that were cross cluster involved Central males with Northern and Southern females. The highest CoAs were between mothers and speckled offspring, and one association of an uncle and niece (known through documented multigenerational maternal-offspring relationships). The majority of first order alliances did not have equally strong CoAs with females, indicating they were not always together when with females. In some of the alliances, only one male had strong associations with females. The majority of the females involved in strong mixed sex associations were reproductively active (pregnant, with a calf, or both). Of those that were not involved in mixed sex strong associations, only five were of age to be reproductively active.

## DISCUSSION

Despite large changes in demography, the basic pattern of social structure characteristics of this community remained consistent with previous long-term analyses, including definitive social clusters (Elliser and Herzing 2012), sex preferences, and overall association patterns (Elliser and Herzing, in press). This is contrary to what has been described for other species, where demographic changes resulted in altered behavior and social structure/grouping (bottlenose dolphins: Lusseau and Newman 2004; marmosets: Lazaro-Perea *et al.* 2000; chimpanzees: Lehmann and Boesch 2004; killer whales: Matkin 2008; bottlenose dolphins: Elliser and Herzing 2011). However, some changes in spotted dolphin social structure were observed after the hurricanes. There was lower social differentiation, younger age of alliance formation and increased overall cohesion within clusters and across age class. This suggests that responses to demographic upheaval differ between populations and/or species, with varying degrees of change in social structure as they adapt to new conditions.

One of the most striking results was that despite losing many individuals and an overall decrease in community size, the Northern, Central, and Southern clusters remained discrete (although the Central cluster appeared more closely connected with the Southern cluster prehurricane and then with the Northern cluster posthurricane) and group size remained the same, even though social differentiation within the clusters decreased. Small communities of both dolphins and primates, whether resulting from demographic changes or isolated populations, have been documented to have less fission/fusion dynamics, increased group sizes, strong associations across sex class, and increased cohesiveness, with individuals spending more time with all other members of the population (Lusseau *et al.* 2003, Lehmann and Boesch 2004). Smaller social groups may be more accepting of outside individuals (such as immigrants or individuals from another cluster) to maintain normal social and behavioral functions

(such as foraging, mating, play, and calf care). This would facilitate recruitment of individuals (Schaffner and French 1997). Therefore, it might be expected that the clusters would increase their cohesiveness and combine together; however, the lack of increased number of associations between clusters indicated that the clusters remained an integral part of the community structure.

There was increased cohesiveness of the associations within clusters and across age class overall. The dolphins began associating with all individuals within their cluster (some of which they were not observed to have associated previously), and a few outside their cluster, more than they had during the prehurricane years. Past research on associations from 1991 to 2002 showed observed association percentages similar to the prehurricane years of this study (Elliser and Herzing, in press), indicating a significant change posthurricane. Similarly, the mean CoA for the community posthurricane was almost twice that of prehurricane years, and more than double previous long-term work since 1991 (Elliser and Herzing, in press). Social differentiation posthurricane was much lower, by almost half, which may denote a less stratified society. Similar cohesion within units occurred in the sympatric bottlenose dolphin community. They lost 30% of their community, but an almost equal number of immigrants moved in. Their previously stable community split into two units, with increased number of associations and cohesion within units than had been seen in the previous community (Elliser and Herzing 2011). It seems that for these sympatric species the loss of individuals, regardless of the presence or absence of immigrants, will influence the surviving individuals to associate more with the other surviving members of their unit or cluster.

Similar evidence of increased cohesion has been reported in a community of bottlenose dolphins in Sarasota, Florida. During severe harmful algal blooms the connectivity, ties and density of social network measures increased significantly for both adult and juvenile bottlenose dolphins; they were more gregarious and interacting with more associates than they had previously (McHugh *et al.* 2010). Changes in human activities have also been shown to alter associations in a similar way, though this led to a large change in bottlenose dolphin community structure (Ansmann *et al.* 2012). After fisheries regulations greatly reduced trawling activities in Moreton Bay, Australia, the presence of two distinct communities of bottlenose dolphins (trawler and nontrawler dolphins) effectively disappeared. The social network was less differentiated and more compact with increased and stronger associations between individuals (Ansmann *et al.* 2012). Although there were similar association changes within the clusters of the spotted dolphin community, the clusters and the overall community structure remained intact. Together these results indicate that changes in demography, environment and human behavior can influence dolphin associations. The effects on social and community structure may vary, depending on many factors, including the nature of the disturbance/change, the species, the previously established social structure of the population or community and the social needs and flexibility of the individuals.

One of the most interesting differences between the spotted dolphin community and a similarly demographically altered chimpanzee community was that strong and/or long-lasting mixed sex associations were predominant in the latter (Lehmann and Boesch 2004), but not in the spotted dolphins. Generally strongest and/or long-term associations were between members of the same sex (Wells *et al.* 1987; Connor *et al.* 2000; Rogers *et al.* 2004; Elliser and Herzing 2011; Elliser and Herzing, in press). These sex preferences also remained evident posthurricane in the sympatric bottlenose dolphins, and may have been the driving force for the changes in social structure that

emerged because acceptance of immigrants differed between the sexes (Elliser and Herzing 2011). Despite the loss of individuals and decreasing community size, sex preferences still strongly influenced association patterns in this spotted dolphin community, further supporting that sex preferences have a primary role in cetacean social organization.

### *Female Associations*

The loss of individuals had little effect on the association patterns of the female spotted dolphins in this community. Their associations varied little from that of prehurricane years (Elliser and Herzing, in press). Associations with other females continued to be constrained within the clusters, strong associations were often between reproductively active females, strong associations were not limited to same age class pairs and strong mother/offspring relationships continued past weaning, sometimes into adulthood.

The high female mean CoA seen posthurricane indicated increased cohesiveness and may be related to female reproduction and sociality. The stress of losing so many individuals, and the lower birth rate observed in these years (DLH and CRE, unpublished data), may have initiated a social tightening between females within clusters. Females generally associate with others in the same stage of life (Wells *et al.* 1987, Herzing and Brunnick 1997). Lowered reproduction indicates that more females were in similar reproductive states during this time, allowing a greater number of females to more easily associate with one another. These females would have some level of social familiarity with each other as most females interact to some degree with all other females (and often with their offspring as well) within the cluster. Social familiarity has been shown to be important since closely associated females may have been close associates as calves or juveniles (Möller and Harcourt 2008; Elliser and Herzing, in press). In addition, allomaternal care is an important aspect of female sociality and has been documented in other bottlenose dolphin populations (Wells *et al.* 1987, Shane 1990, Mann and Smuts 1998, Rogers *et al.* 2004), this spotted dolphin community (Elliser and Herzing, in press), and primates (nursery groups in chimpanzees: Pepper *et al.* 1999; nonreproductive helpers in marmosets: Stevenson and Rylands 1988). Sociality has been documented to influence fitness traits, revealing the adaptive value of female sociality (Frère *et al.* 2010). The results of this study showed that even through demographic upheaval, normal female association patterns remain evident and further support that female sociality depends greatly on reproductive status and social familiarity.

### *Male Associations*

Spotted dolphins have male alliance social patterns like those of their closely related cousins, bottlenose dolphins (*T. aduncus*) in Shark Bay, Australia, including first and second order alliances (Elliser and Herzing, in press). Of the first order alliances, some pairs survived the hurricanes and continued their long-term associations, some since 1985, lasting up to 22 yr. Long-term alliances of this magnitude have been documented in Sarasota and Shark Bay (Connor *et al.* 2000). Other alliances changed after the loss of a member, where the surviving member began an alliance with a new individual, which has also been documented in Sarasota (Wells *et al.* 1987), Shark Bay (Smolker *et al.* 1992), sympatric bottlenose dolphins in this study area (Rogers *et al.* 2004) and previous long-term work on this spotted dolphin community (Elliser and Herzing, in press).

The greatest difference in male association patterns after the hurricanes was the decrease in complexity between male alliances. Following the storms, only one second order alliance was observed and only first order alliances remained (both old and new). In many species, alliances are usually attributed to increased access (directly or indirectly) to females (primates: Watts 1998; lions: Wilson *et al.* 2001; bottlenose dolphins: Wells 1991, Connor *et al.* 1992) and successful mating (Krützen *et al.* 2004, Wiszniewski *et al.* 2012). In this community of spotted dolphins, male coalitions often monopolize females (Herzing and Johnson 1997; Elliser and Herzing, in press). A genetic study has revealed that first order alliance membership may increase reproductive success (Green *et al.* 2011), indicating that access to mates is also a key role of alliances in spotted dolphins. These studies, along with the changes posthurricane in this study, indicate that first order alliance formation may be more critical for access to mates than second order alliances, especially when changes in demography and sex ratio occur.

Alliance formation and size of the alliance are strongly affected by the mean number of males competing for a female and the factors that impact this, such as the density of females, operational sex ratio, and encounter rate with females (Whitehead and Connor 2005). Möller (2012) hypothesized that the development of male alliances in delphinids is related to both small male-biased sexual size dimorphism and male-biased operational sex ratio (due to differences in parental investment). Alliances and/or coalitions will form when the female encounter rate increases such that the cost of sharing copulations is outweighed by the benefits of cooperative female defense (Connor and Whitehead 2005). Coalitional mate guarding, previously unknown in chimpanzees, was found to develop in large mating parties when the groups had too many males for single males to maintain exclusive access to estrous females (Watts 1998). Prior to the hurricanes, the sex ratio of spotted dolphins was skewed towards females (32 males, 42 females), possibly supporting the formation of both first and second order alliances as more females were available. After the hurricanes, the sex ratio was reduced to roughly 1:1 (23 males, 24 females). In this scenario the cost of sharing mating opportunities with other alliances may be too great as the encounter rate with different females is much lower, especially within clusters. The benefits of having one or two other males to aid in gaining access to females may still outweigh the costs of sharing mating opportunities; however, the cost may be too high to share with another entire alliance while female numbers are reduced.

This fitness cost could also be related to the kinship level of alliances, which varies between and even within populations (*e.g.*, Möller *et al.* 2001, Krützen *et al.* 2003). Genetic relatedness of the alliances in this study is currently unknown. However, the lack of second order alliances after the hurricanes could be explained if the first order alliances were more highly related than the second order alliances, increasing the individual fitness cost of second order alliances during posthurricane years. Further genetic analysis will help determine whether kinship played a role in these changes in alliance membership.

Spotted dolphin alliances are also important for interspecific interactions with sympatric bottlenose dolphins on LBB (Herzing and Johnson 1997; Elliser and Herzing, in press). Behavioral research on regularly occurring interactions has shown bottlenose dolphins, which are larger and more dominant, are usually the aggressors (Herzing and Elliser, in press) and that it takes six spotted dolphins to chase away one bottlenose dolphin (Herzing and Johnson 1997). After the hurricanes, however, these types of interactions decreased significantly becoming almost nonexistent (Elliser 2010). During this time of restructuring for both communities, these interspecific

interactions may not have been a priority for either species. The lack of second order alliances after the hurricanes may have occurred if a primary reason for second order alliance membership is to aid each other (similar to aiding in consortships seen in Shark Bay) during these interspecific encounters.

Alliance-strength relationships are rare in young juveniles and have not been previously documented in this spotted dolphin community (Elliser and Herzing, in press). The bonds between males apparently grow from relationships developed in subadult groups or earlier and crystallize during sexual maturity (Wells 1991; Elliser and Herzing, in press). More affiliative associations between juveniles, which are less constrained by the mating system and social organization of adults, may indicate the early stages of alliance formation (Gero *et al.* 2005). The dynamics controlling alliance formation may have been altered after the hurricanes so that the loss of individuals effectively sped up the development of alliance formation. Juvenile social behavior has been shown to change due to other environmental disturbances. Increased sociality (and increase in number of associates) was documented in juvenile bottlenose dolphins after severe harmful algal blooms in Sarasota, FL (McHugh *et al.* 2010). Factors that alter social behavior may affect young animals to a greater degree, due to the fact that juveniles typically socialize at higher rates than adults (McHugh *et al.* 2010). Alternatively, the strong alliance level associations between juveniles in this study may be due to lack of individuals. With fewer choices, individuals that associated previously may increase their associations to a stronger level. Future work detailing the stability and processes of juvenile and alliance development will shed light on the origin of alliance formation.

### *Conclusion*

This study reveals that although large changes in social and community structure can occur following demographic changes, overall stability (with some changes) can occur as well. Despite demographic upheaval, sex preferences, social clusters and overall community structure remained the same for these spotted dolphins. The changes in social structure that occurred remained constrained within sex preferences and mating strategies. This contrasts with the changes that occurred in the sympatric bottlenose dolphin community during the same events. Differences between the social structures of various populations may play an important role in their survival through environmental perturbations and/or demographic changes, increasing the need to understand the processes involved in social development for conservation of diverse populations.

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## LITERATURE CITED

- Ansmann, I. C., G. J. Parra, B. L. Chilvers and J. M. Lanyon. 2012. Dolphins restructure social system after reduction of commercial fisheries. *Animal Behaviour* 84:575–581.
- Aureli, F., C. M. Schaffner, C. Boesch, *et al.* 2008. Fission-fusion dynamics: New research frameworks. *Current Anthropology* 49:627–654.
- Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. *Animal Behaviour* 35:1454–1469.
- Christal, J., and H. Whitehead. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. *Ethology* 107:323–340.
- Connor, R. C., and H. Whitehead. 2005. Alliances II. Rates of encounter during resource utilization: A general model of intrasexual alliance formation in fission-fusion societies. *Animal Behaviour* 69:127–132.
- Connor, R. C., R. A. Smolker and A. F. Richards. 1992. Two levels of alliance formation among bottlenose dolphins (*Tursiops sp.*). *Proceedings of the National Academy of Sciences of the United States of America* 89:987–990.
- Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91–126 in J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. *Cetacean societies: Field studies of whales and dolphins*. The University of Chicago Press, Chicago, IL.
- Elliser, C. R. 2010. Intra and interspecies association patterns of Atlantic spotted dolphins, *Stenella frontalis*, and Atlantic bottlenose dolphins *Tursiops truncatus*, and the effects of demographic changes following two major hurricanes. Ph.D. dissertation, Florida Atlantic University, Boca Raton, FL 176 pp.
- Elliser, C. R., and D. L. Herzing. 2011. Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes. *Marine Mammal Science* 27:39–59.
- Elliser, C. R., and D. L. Herzing. 2012. Community structure and cluster definition of Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. *Marine Mammal Science* 28: E486–E502.
- Elliser, C. R., and D. L. Herzing. In press. Long-term social structure of a resident community of Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas 1991–2002. *Marine Mammal Science*.
- Frère, C. H., M. Krützen, J. Mann, R. C. Connor, L. Bejder and W. B. Sherwin. 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences of the United States of America* 107:19949–19954.
- Gero, S. L., H. Bejder, J. Mann Whitehead and R. C. Connor. 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops sp.* *Canadian Journal of Zoology* 83:1566–1573.
- Green, M. L., D. L. Herzing and J. D. Baldwin. 2011. Reproductive success of male Atlantic spotted dolphins (*Stenella frontalis*) revealed by noninvasive genetic analysis of paternity. *Canadian Journal of Zoology* 89:239–253.
- Herzing, D. L. 1997. The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): Age classes, color phases, and female reproduction. *Marine Mammal Science* 13:576–595.
- Herzing, D. L., and B. J. Brunnick. 1997. Coefficients of association of reproductively active female Atlantic spotted dolphins, *Stenella frontalis*. *Aquatic Mammals* 23:155–162.
- Herzing, D. L., and C. R. Elliser. In press. Directionality of sexual activities during mixed-species encounters between Atlantic spotted dolphin (*Stenella frontalis*) and bottlenose dolphin (*Tursiops truncatus*). *International Journal of Comparative Psychology*.
- Herzing, D. L., and C. M. Johnson. 1997. Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985–1995. *Aquatic Mammals* 23:85–99.

- Karczmarski, L., B. Würsig, G. Gailey, K. W. Larson and C. Vanderlip. 2005. Spinner dolphins in a remote Hawaii atoll: Social grouping and population structure. *Behavioral Ecology* 16:675–685.
- Kent, E. E., M. Mazzioli, S. D. McCulloch and R. H. Defran. 2008. Group characteristics and social affiliation patterns of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Florida Scientist* 71:149–168.
- Krützen, M., W. B. Sherwin, R. C. Connor, L. M. Barré, T. Van de Castele, J. Mann and R. Brooks. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London* 270:497–502.
- Krützen, M., L. M. Barre, R. C. Connor, J. Mann and W. B. Sherwin. 2004. ‘O father: where art thou?’—Paternity assessment in an open fission-fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology* 13:1975–1990.
- Lazaro-Perea, C., C. S. S. Castro, R. Harrison, A. Araujo, M. F. Arruda and C. T. Snowdon. 2000. Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology* 48:137–146.
- Lehmann, J., and C. Boesch. 2004. To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology* 56:207–216.
- Lusseau, D., and M. E. J. Newman. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London B* 271:S477–S481.
- Lusseau, D., K. Schneider, O. J. Boisseau, P. Haase, E. Sloaten and S. M. Dawson. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology* 54:396–405.
- Lusseau, D., F. Wilson, P. S. Hammond, *et al.* 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology* 75:14–24.
- Mann, J., and B. B. Smuts. 1998. Natal attraction: Allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour* 55:1097–1113.
- Matkin, C. O., E. L. Saulitis, G. M. Ellis, P. Olesiuk and S. D. Rice. 2008. Ongoing population-level impacts on killer whales *Orcinus orca* following the ‘Exxon Valdez’ oil spill in Prince William Sound, Alaska. *Marine Ecology Progress Series* 356:269–281.
- McHugh, K. A., J. B. Allen, A. A. Barleycorn and R. S. Wells. 2010. Severe *Karenia brevis* red tides influence juvenile bottlenose dolphins (*Tursiops truncatus*) behavior in Sarasota Bay, FL. *Marine Mammal Science* 27:622–643.
- Möller, L. M. 2012. Sociogenetic structure, kin associations and bonding in delphinids. *Molecular Ecology* 21:745–764.
- Möller, L. M., and R. G. Harcourt. 2008. Shared reproductive state enhances female associations in dolphins. *Research Letters in Ecology* vol. 2008, Article ID 498390, 5 pages, doi:10.1155/2008/498390.
- Möller, L. M., L. B. Beheregaray, R. G. Harcourt and M. Krützen. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society B* 268(1479):1941–1947.
- Möller, L. M., L. B. Beheregaray, S. J. Allen and R. G. Harcourt. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behavioral Ecology and Sociobiology* 61:109–117.
- Parsons, K. M., J. W. Durban, D. E. Claridge, K. C. Balcomb, L. R. Noble and P. M. Thompson. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour* 66:185–194.
- Pepper, J. W., J. C. Mitani and D. P. Watts. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology* 20:613–632.
- Perrin, W. F. 1970. Color pattern of the Eastern Pacific spotted porpoise *Stenella graffmani* Lonnberg (Cetacea, Delphinidae). *Zoologica* 54:135–149.

- Quintana-Rizzo, E., and R. S. Wells. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: Insights into organization. *Canadian Journal of Zoology* 79:447–456.
- Rogers, C. A., B. J. Brunnick, D. L. Herzing and J. D. Baldwin. 2004. The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science* 20:688–708.
- Schaffner, C. M., and J. A. French. 1997. Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. *Animal Behaviour* 54:171–180.
- Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pages 245–265 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Shane, S. 2004. Residence patterns, group characteristics and association patterns of bottlenose dolphins near Sanibel Island, Florida. *Gulf of Mexico Science* 1:1–12.
- Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123:38–69.
- Stevenson, M. F., and A. B. Rylands. 1988. The marmosets, genus *Callitrix*. Pages 131–222 in R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca, eds. *Ecology and behavior of neotropical primates*. Volume 2. World Wildlife Fund, Washington, DC.
- Strier, K. B. 2002. Primates past and present. Pages 73–98 in *Primate behavioral ecology*. 2nd edition. Allyn and Bacon, Boston, MA.
- Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 44:43–55.
- Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199–255 in K. Pryor and K. S. Norris, eds. *Dolphin societies*. University of California Press, Berkeley, CA.
- Wells, R. S., M. D. Scott and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247–305 in H. Genoways, ed. *Current mammalogy*. Plenum Press, New York, NY.
- Wells, R. S., D. J. Boness and G. B. Rathbun. 1999. Behavior. Pages 324–422 in J. E. Reynolds III and S. A. Rommel, eds. *Biology of marine mammals*. Smithsonian Institution Press, Washington, DC.
- Whitehead, H. 2008a. Analyzing animal societies: Quantitative methods for vertebrate social analysis. The University of Chicago Press, Chicago, IL.
- Whitehead, H. 2008b. Precision and power in the analysis of social structure using associations. *Animal Behaviour* 75:1093–1099.
- Whitehead, H. 2009. SOCPROG programs: Analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63:765–778.
- Whitehead, H., and R. Connor. 2005. Alliances I. How large should alliances be? *Animal Behaviour* 69:117–226.
- Wilson, M. L., M. D. Hauser and R. W. Wrangham. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour* 61:1203–1216.
- Wiszniewski, J., S. Corrigan, L. B. Behereharay and L. M. Möller. 2012. Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Journal of Animal Ecology* 81:423–431.

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