# **Sexual Segregation of Coastal Bottlenose Dolphins** (Tursiops truncatus) in the Southwestern Gulf of Mexico

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## Abstract

Cetaceans are highly mobile species with complex social structures, aspects that play an important role in their fitness such as survival and offspring production. Population dispersal influences the dynamics of social species, which may vary with age, sex, or individual status, thus resulting in segregation; however, sex-related dispersal and social affiliations have been studied only in a handful of species at few locations. We conducted a 2-y photographic survey in an open habitat off the coast of Mexico to determine if site fidelity, residency, and social affiliations in male and female bottlenose dolphins (Tursiops truncatus) revealed sexual segregation. Forty-one surveys yielded 167 h of field effort and 61 h of observations. From 174 different individuals, we sexed 38 females and 11 males (45% positively and 55% tentatively). Females were more resident (p <0.05), had higher site fidelity (p < 0.05), and had weaker associations (p < 0.05) with a higher number of partners (p < 0.05) than males and putative males. Associations were not dictated by differences in sample size or temporal patterns between sexes, and 53% of recorded partnerships were preferred/ avoided relationships. Although the composition of social interactions in the community was highly dynamic, it unveiled evidence of sexual segregation. Temporal and social patterns suggest that males may be primarily responsible for gene flow among adjacent locations. Female associations occurred within a large but unstable network, potentially resembling "bands"; conversely, males and putative males only grouped in pairs or trios, showing significant temporal changes in their relationships, and potentially resembling first- and second-order alliances. Detailed behavioral and genetic data are needed to unravel the social dynamics of this dolphin community and the mechanisms driving their evolutionary change.

Key Words: alliances, bands, residency, sex, site fidelity, social affiliations

## Introduction

Dolphin fidelity towards coastal systems has been recognized as highly variable among individuals, sexes, and populations, ranging from strong long-term residency in small areas to long distance movements of some dolphins (Connor et al., 2000). The term residency does not necessarily imply an indefinite permanence of individuals in a given space but the existence of limited movements reflected in an increased frequency of sightings in a given area, with a concomitant lower level of movements outside of that area. Bottlenose dolphins (Tursiops truncatus) are highly mobile cetaceans, living in fission-fusion societies with strong social bonds (Connor et al., 1992), whose spatial and temporal distribution patterns are often related to environmental features such as sea surface temperature (SST), depth, presence of predators, and abundance and distribution of prey (Wells et al., 1987; Ballance, 1990; Whitehead et al., 2000; Rogers et al., 2004). The causes for individual movements are difficult to assess, but they have been related to changes in environmental parameters and sex-based differences in access to resources (more relevant in females) and mates (more relevant in males) as well as to levels and types of human activities (Ballance, 1990; Wells, 1991, 2003; Lusseau, 2004; Möller & Beheregaray, 2004; Morteo et al., 2004, 2012b).

Data on individual dolphin movements over the last two decades have produced further insight into their social ecology. For instance, along the west coast of Florida, males have been found to have larger ranges than females (Wells, 2003; Urian et al., 2009). The smaller distributional ranges and

longer presence within feeding areas of females may promote frequent interactions with other females (Quintana-Rizzo & Wells, 2001) and larger networks of associates, including mostly other females (Smolker et al., 1992; Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Krützen et al., 2004; Rogers et al., 2004). Conversely, larger ranges in males decrease the possibility of having frequent associations with numerous partners (Quintana-Rizzo & Wells, 2001; Krützen et al., 2004). Thus, some male bottlenose dolphins form strong alliances with only a few male individuals, involving collaborative behaviors (Wells et al., 1987; Smolker et al., 1992; Connor et al., 2000, 2006; Möller et al., 2001; Owen et al., 2002).

Since females and males may use productive areas with different purposes, sex-related differences in access to resources may be reflected in the duration and frequency of area occupancy. In addition, given that differences in individual movements may change the community structure (sensu Wells et al., 1987) and alter individual association patterns (Smolker et al., 1992; Bräger et al., 1994), dolphins from open communities, living in habitats with strong seasonal fluctuations, are expected to experience shifts in their residency patterns and social structure, thus leading to potential sexual segregation. In most cases, whether such sexual differences in individual movements are the cause or the consequence of their social patterns is unclear, but the movements have different demographic effects (e.g., in population stability) depending on environmental pressures and, therefore, are an important driver of evolutionary change among communities (e.g., genetic structure and variability).

Bottlenose dolphins along the coastal waters off Alvarado, Mexico, in the Gulf of Mexico, have been studied intermittently since 1993, and the high and relatively stable levels of abundance underline the importance of the area as habitat for this species (García, 1995; Del Castillo, 2010; Morteo et al., 2012b). Recent information indicates that this is an open community, and temporal patterns for these dolphins range from transient and seasonal visitors to year-round and long-term residents (Morteo, 2011). However, no detailed information is available regarding sex-related patterns of residency and associations among individuals. Consequently, we set out to determine sex-related differences in temporal and social patterns of bottlenose dolphins off Alvarado under the hypothesis that given the open nature and the seasonality of their habitat, male bottlenose dolphins will have lower residency and only a few strong associates, whereas females will have stronger residency and many more associations, thus potentially promoting sexual segregation.

#### Methods

### Study Area

The study area is an open ocean coastal habitat in the southwestern Gulf of Mexico (Figure 1). Water depth reaches 20 m, and SST ranges from 20° to 32.5° C, with an annual average of 27° C.



Figure 1. Location of study area; dashed lines show depth contours every 5 m.

The regional climate is tropical with three seasons: (1) a rainy season (July-October), in which runoff into the adjacent lagoon and mangrove forest causes high organic matter and nutrient input into coastal waters; (2) a windy season (November-February), featuring strong winds (up to 80 km h<sup>-1</sup>) associated with the incursion of northern cold fronts, which may last several days; and (3) a dry season (March-June) with a significant reduction in average precipitation. Coastal artisanal fisheries are the most important commercial activity, taking place year-round, depending on weather and market demands. Fisheries activities are relevant to coastal bottlenose dolphin populations in light of the frequent adverse interactions between dolphins and local fishers through incidental mortalities of dolphins in nets (Morteo, 2011; Morteo et al., 2012b).

# Surveys

Surveys covering 9 km along the coastal waters on both sides of the entrance to the Alvarado Lagoon were conducted twice per month from 25 May 2006 to 24 April 2008. The extent of the surveyed area was constrained by the duration of daily operations and was intended to maximize the chance of encountering coastal bottlenose dolphins, based on their habitat preferences (Ballance, 1990; Fazioli et al., 2006). Surveys were carried out at constant speed (15 to 18 km h<sup>-1</sup>) always under Beaufort sea state 3 or lower (wind speed < 15 km h<sup>-1</sup>) on board a 7-m outboard motor boat (40/60 hp). When dolphins were sighted, they were approached with caution to avoid disturbing them as group size and behavior were recorded. We used an inclusive definition of group, consisting in all dolphins observed in apparent association, moving in the same direction, and often, but not always, engaged in the same activity (Bräger et al., 1994); however, some groups included only one dolphin (Fazioli et al., 2006). Dolphins were followed until all dorsal fins were photographed (digital SLR cameras Canon Rebel XT and Nikon D50, 70 to 300 mm lenses) or until they were lost. The entire study area was surveyed each time.

## Data Analyses

*Photographic Identification*—Individual bottlenose dolphins were identified by marking patterns on their dorsal fins (Würsig & Würsig, 1977; Würsig & Jefferson, 1990; Wells, 2009; see also Morteo, 2011). Dolphins lacking conspicuous identifying markings (excluding tooth rakes, scars, pigmentation marks, superficial wounds, and epiphytic organisms) were considered unidentifiable and were excluded. Additionally, we assessed the probability of photographing marked dolphins in each sighting by computing the number of high-quality pictures from each individual; four or more pictures from each animal have been shown empirically to afford a 95% chance of photographing every dolphin in the group (Ballance, 1990; Bejder & Dawson, 2001). Individual sex was first determined in the field through direct observations of the genital area, and it was confirmed in photographs when available (Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Rogers et al., 2004). In the absence of direct evidence, females were also identified as individuals associating consistently with a calf or a young animal (Connor et al., 2000; Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Rogers et al., 2004). On the other hand, putative males were identified as individuals that (1) were never found associated with calves or young animals (Felix, 1997), and (2) consistently displayed synchronized swimming (Connor et al., 2000, 2006) with at least another adult that was not classified as female. Since calving intervals for females might be longer than the studied period, the latter criteria were expanded to individual data from 2002 to 2003 and 2009 to 2010, increasing the certainty that female sex classification was correct. This also allowed searching for graphic evidence confirming the sex of putative male dolphins over a larger database. Dolphins without conspicuous identifying markings (ca. 23% of the total) were excluded from subsequent analyses. Sexed individuals were included only if they were adults (based on their total length relative to the research vessel) and sighted in five or more survey days (Bräger et al., 1994; Felix, 1997; Bejder et al., 1998; Maze-Foley & Würsig, 2002; Rogers et al., 2004); thus, analyses were performed only in dolphins with a certain degree of residency.

Site Fidelity and Residency—Individual sighting histories were used to assess site fidelity, defined as the number of recaptures divided by the number of surveys in seasons and years (Simões-Lopes & Fabian, 1999; Quintana-Rizzo & Wells, 2001; Morteo et al., 2012a). In addition, individual residency was determined by computing their occurrence (number of sighting records), permanence (days between the first and last captures), and periodicity (average days between consecutive recaptures) (sensu Ballance, 1990). Since estimation of residency parameters is prone to biases from sampling frequencies and individual recapture rates, we assessed whether the observed trends between sexes were significant using simulations (Morteo et al., 2012a). We used the program Resident 2.10 (Morteo et al., 2012a) to simulate samples for each sex based on the observed individual recapture rates (the number of sightings divided by the number of surveys)-that is, each individual was simulated using its particular recapture rate over a period with the same duration as this study and assuming a hypothetical daily sampling frequency. This procedure allowed the calculation of new scores for each residency parameter, assuming an intensive sampling, and was repeated 10,000 times for each individual. Residency scores were then individually averaged and compared between sexes (ANOVA).

Associations-Photographic data were also used to compute half-weight (i.e., controlled for sighting frequencies) coefficients of association (COA) for each dyad (pair of individuals) (e.g., Smolker et al., 1992; Bräger et al., 1994; Felix, 1997; Möller et al., 2001; Quintana-Rizzo & Wells, 2001; Parsons et al., 2003; Rogers et al., 2004) using SOCPROG 2.4 (Whitehead, 2009). COA values range from zero for dolphins that are never seen together to one for a pair that is always seen together. The number of affiliates (sensu Maze-Foley & Würsig, 2002) was calculated for each individual and compared between sexes. The number of male-male (M-M hereafter) and female-female (F-F hereafter) associates, including all putative males and females, were calculated and compared. However, since an uneven sex ratio will bias the number of available partners to associate with, we also made these computations on normalized associations based on a 1:1 sex ratio to correct for the observed bias and to provide standardization for comparison with other populations. Accordingly, the number of males and females were equalized by randomly eliminating individuals from the more abundant sex class (i.e., females), and new COA values were estimated for the balanced dataset. This procedure was repeated until all individuals from the more abundant sex class were removed at least once; we then used all the information to obtain median COA values for each dyad and compare between sexes (Mann-Whitney test).

COA values were categorized as infrequent (0.0 to 0.2), casual (0.2 to 0.4), fair (0.4 to 0.6), moderate (0.6 to 0.8), or strong (0.8-1.0) (Smolker et al., 1992; Quintana-Rizzo & Wells, 2001). Given the fluid nature of bottlenose dolphin groups, association patterns towards specific partners may change between years (Whitehead et al., 2000); therefore, year-round COA matrixes were correlated using Mantel's tests (XL-Stat 2011.1.03); the latter was performed separately for all paired relationships and for M-M and F-F dyads as well (Rogers et al., 2004). Sociograms were constructed over yearround datasets for each sex using SOCPROG 2.4 (Whitehead, 2009) as a visual aid to compare social networks. Finally, preferred and avoided companions were tested through the randomization test described by Bejder et al. (1998) using the routine in SOCPROG 2.4 (Whitehead, 2009) with two-tailed tests ( $\alpha = 0.05$ ) and 10,000 permutations (Möller et al., 2001; Maze-Foley & Würsig, 2002; Parsons et al., 2003).

# Results

# Surveys

The study area was sampled entirely on each of the 41 photographic surveys; total search effort was 167.1 h, comprising 61.0 h of bottlenose dolphin observations. Group size ranged from 1 to approximately 100 dolphins ( $\bar{x} = 9.72$ , SD = 13.11), and most aggregations (72%) had fewer than 10 members. From all sightings, dolphin pairs were the most frequent groups (18%), followed by single individuals (14%) (Figure 2).



Figure 2. Group size of bottlenose dolphins recorded along the waters off the Alvarado Lagoon in the Gulf of Mexico

## Photo-Identification

From the 14,011 available photographs, all individuals were positively identified in 77% of the groups sighted, comprising 871 dorsal fins from 174 positively identified bottlenose dolphins. Sex was tentatively assigned for 39 females and 15 males of which 15 females and 7 males were confirmed through observations and/or pictures from the genital area. Individual sexing averaged 89% (±15 SD) of the animals in each group that included dolphins recorded five or more times. The proportion of sightings composed only by females was 45%, whereas 39% were mixed sex aggregations, and groups composed only by males barely reached 5%. Of the 73 dolphins sighted in five or more occasions, only 38 females and 11 males were sexed (45% positively and 55% tentatively), and these were included in the following analyses.

Site Fidelity and Residency—The 49 sexed individuals were seen repeatedly in the 2-y study and showed no significant (p > 0.15 in all cases) differences in site fidelity or residency among

seasons or between years. However, recalculations of individual scores using the simulation software resulted in males and putative males having significantly lower site fidelity, occurrence, and periodicity (a higher average means lower periodicity) than females, whereas comparisons of permanence yielded no significant differences (Table 1).

Associations—The overall number of affiliates for the entire sample ranged from 29 to 48, averaging 43.3 (± 4.8). Males and putative males had 34 to 47 ( $\bar{x} = 41.4 \pm 4.6$ ) associates, whereas females and putative females had 26 to 48 ( $\bar{x} =$ 43.9 ± 4.8) associates; no significant differences (p = 0.87) were found between sexes. However, comparisons within sexes gave different results upon standardization to an unbiased sex ratio that is, F-F affiliates ranged from 22 to 36 ( $\bar{x} =$ 33.1 ± 3.3) (Figure 3) decreasing to 7 to 10 ( $\bar{x} = 8.8 \pm$ ± 1.1) when individuals were randomly removed to match M-M sample size, whereas M-M associates ranged from 4 to 10 ( $\bar{x} = 6.0 \pm 2.8$ ) (p = 0.03).

Computation of paired COA values showed that overall association patterns did not change significantly between years, and this was true for all possible dyads (Mantel's test, p < 0.01 in all cases). Both sexes showed a small number of moderate and strong associations (M-M = 7%; F-F = 2%) and a large number of infrequent and casual associations (M-M = 85%; F-F = 89%); thus, from all the possible paired combinations, most bottlenose dolphins did not associate consistently. However, since the significance of the Mantel's test may be biased when most paired comparisons

have singular values (i.e., infrequent and casual), a new test was performed using only COA values from fair to strong; in this case, we found temporal consistency in F-F associations, and only M-M annual matrices were not correlated (p = 0.4), thus being significantly different between years.

Females and putative females had a larger social network with weaker associations since they were less likely to form discrete small and consistent groups. Conversely, male and putative male associations were stronger and involved fewer partners. Few females had a higher number of moderate or strong associates that changed (although non-significantly) between years (i.e., F2, F4, F5, F6, F22, F23, F30, F36, and F37) (Figure 3). On the other hand, most males and putative males were involved in dyads that were very stable (Figure 3). However, male dyads also associated with other male individuals or pairs, but the latter associations were mostly moderate and inconsistent across years; for instance, dyad M1-M2 was associated with M5-M11 in the first year but switched to M6-M8 the following period (Figure 3). Moreover, some individuals constituted a third partner whether or not they were involved in other dyads (i.e., M6 and M10). Females were never the top ranked associates of males; however, some males (45%) showed moderate COAs towards some females (32%). The latter trends were evident from visual inspection of sociograms upon removal of infrequent and casual COA values (Table 2; Figure 3); thus, most

**Table 1.** Site fidelity index and residency parameters (*sensu* Ballance, 1990) for individuals sighted five or more times; range values are followed by average and standard deviation in parenthesis. F = females and putative females, M = males and putative males, and (S) = simulated. The F vs M column shows the significance\* of the comparisons.

	All	F	М	p (F vs M)
Site fidelity	0.12-0.61 (0.26 ± 0.12)	0.12-0.61 (0.28 ± 0.13)	0.12-0.39 (0.21 ± 0.07)	0.08
Occurrence	5-25 (10.8 ± 5.0)	5-25 (11.4 ± 5.3)	5-16 (8.5 ± 2.9)	0.08
Permanence	$217-700(554 \pm 132)$	$217-700(534 \pm 143)$	$334-700(557 \pm 83)$	0.99
Periodicity	18-175 (69 ± 33)	18-175 (65 ± 33)	34-132 (83 ± 30)	0.05
Site fidelity (S)	0.11-0.63 (0.28 ± 0.10)	0.11-0.63 (0.31 ± 0.11)	0.13-0.36 (0.20 ± 0.05)	0.04*
Occurrence (S)	83-429 (186 ± 81)	83-429 (204 ± 81)	84-270 (139 ± 40)	0.03*
Permanence (S)	353-700 (641 ± 173)	428-700 (674 ± 199)	353-700 (607 ± 158)	0.91
Periodicity (S)	2-24 (7 ± 4)	2-24 (6 ± 3)	10-21 (12 ± 3)	0.02*



Figure 3. Annual sociograms for sexed dolphins photographed five or more times off the Alvarado coast (n = 49); females and putative females (n = 38) are shown above, whereas males and putative males (n = 11) are shown below. Strength of associations is presented by line thickness: thin = fair (0.4 to 0.6), regular = moderate (0.6 to 0.8), and thick = strong (0.8 to 1.0).

M-M associations were significantly higher than all other relationships (Table 2).

Finally, the randomization test using the routine in *Socprog* showed that many paired associations (53%) were either stronger or weaker than expected by chance (p < 0.05), indicating preferred and avoided partnerships. Such associations were rare in mixed sex (M-F) pairs (38%) and F-F dyads (45%), and common (86%) in M-M associations, thus accounting for missing links (i.e., avoidance) between individuals and indicating nonreciprocal associations (i.e., preferred) between dyad members (Figure 3).

## Discussion

Our results are deemed to adequately reflect the individual trends at least in the portion of the dolphin community under study, given the high rate of successfully identified bottlenose dolphins per sighting (77% of all groups). However, we acknowledge the potential for misinterpretation that may arise from combining data from positive and tentative sexing of the animals. The methods for sexing females described herein have been extensively used in other studies; moreover, additional considerations such as the exclusion of physically immature animals in the analyses and the extended search of photographic records from 8.5 y (2002 to 2010) may have increased the probabilities

**Table 2.** Summary of half-weight coefficients of association (COA) for dolphin dyads; parameters marked (H) summarize results using only the fair to strong associations (> 0.4). M = males and putative males, F = Females and putative females, and \* = significant value (p < 0.05).

	0 11	14 11	F 11		<b>P P</b>	
	Overall	M vs all	F vs all	M-M	F-F	M-F
Mean	0.24	0.22	0.24	0.27	0.25	0.19
SD	0.12	0.13	0.12	0.17	0.13	0.12
Median	0.22	0.20	0.23	0.22	0.24	0.18
Mean (H)	0.44	0.44	0.44	0.60*	0.45	0.45
SD (H)	0.13	0.11	0.09	0.14	0.10	0.06
Median (H)	0.42	0.40	0.41	0.58	0.42	0.44

that females have produced at least one calf, and, thus, the chances of being photographed with it. Nevertheless, there is still a slight chance of misclassifying females since long calving intervals and senesce may occur (Wells, 2003, 2009). On the other hand, the determination of males was difficult at best (Connor et al., 2000; Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Rogers et al., 2004); thus, the number of positively sexed males (64% of all males) understandably raises concerns regarding our ability to classify these animals correctly. Nevertheless, we believe that our classification is acceptable since all but one of the positively sexed males fulfilled our criteria (i.e., that individual appeared in one sighting next to a calf, which was photographed four times more frequently with its mother during the same sighting)-that is, dolphins classified as putative males were generally not recorded in close association with small animals, and no positive or potential male was recorded swimming in apparent synchrony with any of the known females (even when these were more easily and frequently spotted and were sometimes moderately associated to male dolphins).

As we are well aware that our sexing protocol and therefore some of our results are yet to be validated (hence, attempts to use biological samples for molecular sexing are already in place), it is fair to state that the high frequency of small aggregations (32% with one or two individuals) in spite of our inclusive definition of group is noteworthy, illustrating that the community may in fact be divided into small and likely single sexed social units. For instance, 50% of the sightings with sexed individuals identified over five times were composed of either males or females that join in common activities (such as socialization and feeding) (Campbell et al., 2002), establishing larger sex-mixed aggregations (Smolker et al., 1992; Bräger et al., 1994; Felix, 1997; Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Rogers et al., 2004). The latter unveils the possibility for sexual segregation in this community, which could be masked by a highly dynamic social structure that must be taken into account while interpreting the results.

# Residency and Site Fidelity

The criteria and methodology used for the estimation of site fidelity and residency patterns are often inconsistent across studies; thus, comparisons must be made with caution (Morteo et al., 2012a). However, field and laboratory methods used here are the same as those from Del Castillo (2010); hence, results are fully comparable. Site fidelity and residency patterns for the 232 individuals identified in this community since 2002 have been classified as either transient (31% of all individuals), seasonal visitors (41%), or year-round residents (27%) (Del Castillo, 2010; Morteo, 2011). Moreover, some of these animals (41%) have also been re-sighted for over 7 y, thus having strong site fidelity and long-term residency.

Temporal variations in the movements of coastal bottlenose dolphins have been related to environmental changes (Ballance, 1990; Simões-Lopes & Fabian, 1999; Lusseau, 2004; Morteo et al., 2004; Morteo, 2011). On the other hand, sex-related dispersal patterns are commonly attributed to differences in reproductive requirements and as a strategy to prevent inbreeding (Möller et al., 2001; Parsons et al., 2003; Krützen et al., 2004; Rogers et al., 2004). Both explanations seem plausible for the animals described herein since expected overall temporal patterns for this community are concurrent with seasonal shifts in local environmental conditions (Morteo, 2011) and also because females were significantly more resident than males (Table 1). Such arguments are supported when considering that the 11 males and 6 of the females analyzed here correspond to 19.5% of the seasonal visitors, and the 32 remaining females represent 56% of year-round residents described by Del Castillo (2010) and Morteo (2011).

The different movement patterns between sex classes may determine to some extent the number and availability of group partners and also possible mates, reinforcing the potential for sexual segregation (Whitehead et al., 2000); but more importantly, it suggests that males may be primarily responsible for gene flow among adjacent locations as found in at least some other dolphin communities (Wells, 2003; Natoli et al., 2004; Islas, 2005).

The use of simulated data to resolve the marginal sexual differences in site fidelity and residency deserves special attention; such differences were striking despite the limitations of our sex determination protocols (discussed above). Morteo et al. (2012a) analyzed the applicability of such simulations to account for potential biases derived from insufficient field effort. Even though their method was not developed for open populations, the high identification rate (Morteo, 2011), use of the most frequently sighted individuals, and short sampling period of this study allowed this part of the community to be treated as hypothetically closed (see Zolman, 2002).

### Associations

Bottlenose dolphins in Alvarado showed few high-level (COA > 0.6) and many low-level (COA < 0.4) associations, supporting a highly dynamic group membership. These values and the overall number of affiliates ranged within the reported values for other coastal communities of this species (Wells et al., 1987; Smolker et al., 1992; Bräger et al., 1994; Felix, 1997; Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002; Rogers et al., 2004). Females generally associated within a network, whereas males and putative males usually formed discrete sets of paired associations or triads (Figure 3). Each female was associated more consistently with other females in particular, but these associations were generally less stable than M-M associations. Such patterns have been described elsewhere (Smolker et al., 1992; Bräger et al., 1994; Felix, 1997; Maze-Foley & Würsig, 2002) and are considered evidence of sexual segregation, which seems a general rule for bottlenose dolphin communities in the wild (Quintana-Rizzo & Wells, 2001; Wells, 2003; Rogers et al., 2004). Although some males and putative males (45%) of the sex class) showed fair to moderate COAs towards a few females (32%), it is likely that such associations may respond to genetic (i.e., young but physically mature males sharing part of the range of their mothers) (Quintana-Rizzo & Wells, 2001; Maze-Foley & Würsig, 2002) or reproductive issues (i.e., persistent attempts to copulate with selected individuals) (Smolker et al., 1992; Connor et al., 2000) rather than actual social relations such as deliberate, frequent, and persistent encounters through which a broad range of cooperative or reciprocal activities take place, including but not limited to feeding, playing, mating, resting, and traveling.

As stated by Smolker et al. (1992), the sexrelated differences in temporal individual patterns (i.e., residency) may be part of the affiliation arrays observed between and within sexes; however, the significance of pair-wise associations observed for this community partially supports the latter. For instance, if social partnerships are dictated mainly by the temporal-spatial concurrence of individuals within a given area (i.e., similar patterns of site fidelity or residency), most of the observed association coefficients would not be different from those expected by chance (Connor et al., 2000). Moreover, since our inclusive definition of group may have somewhat overestimated the individual associations, the fact that slightly over one-half (53%) of these were stronger than expected by chance suggests the existence of underlying mechanisms driving partnership preferences (Bräger et al., 1994; Connor et al., 2000). For instance, whereas 62% of mixed sex pairs and 55% of F-F associations may have been chance encounters, most M-M associations (86%) were not.

Considering that females were more resident, they were expected to be frequently found within the area and therefore to have higher rates of fleeing interactions with most of the other females given their dynamic social networks (Smolker et al., 1992). This, however, was not a general rule; some females had no interaction whatsoever with other females, while others were strong associates with only a few female partners, thus showing long-term associations. The latter constitutes the basis for what has been described as *female bands*, which may be composed of a wide mixture of individuals, where some may be genetically related (Wells et al., 1987; Möller et al., 2001; Quintana-Rizzo & Wells, 2001). F-F bonds in cetaceans have been thought to improve their protection against predators and male harassment, and to increase their competitive success for resources over other females, while associations of individuals of similar age or reproductive state may help them in calving and nursing their young (Whitehead et al., 2000; Rogers et al., 2004). Conversely, males and putative males aggregated only in strongly associated dyads or trios (Figure 3) and seemed to resemble "first-order alliances" (sensu Connor et al., 2000, p. 111); however, the bonds among such small units also resemble "second-order alliances" (sensu Connor et al., 2000, p. 111). Strong bonds between males have been reported in several locations (e.g., Sarasota Bay, Florida, by Wells et al., 1987; Guayaquil, Ecuador by Felix, 1997; San Luis Pass, Texas, by Maze-Foley & Würsig, 2002; Bahamas by Parsons et al., 2003; Cedar Keys by Quintana-Rizzo & Wells, 2001; and Port Stephens, Australia, by Möller

et al., 2001). However, second-order alliances and male trios are less common (Smolker et al., 1992; Connor et al., 2000; Möller et al., 2001). It is not clear whether such potential male alliances within the Alvarado waters have the same role as those from Shark Bay, where individuals work together to herd, steal, and protect females for reproductive purposes, and to defend against predators and other male alliances (Smolker et al., 1992; Connor et al., 2000). In Sarasota Bay, Florida, male pairs may guard receptive females to restrict their access to other males, while improving prey acquisition and protection from predation and aggressions from other males (Owen et al., 2002; Wells, 2003). Explanations for this behavior include improved fitness by means of kin selection (Krützen et al., 2003; Parsons et al., 2003), but such evidence is still controversial (Connor et al., 2000; Möller et al., 2001).

The function or true nature of associations in this study was limited by the lack of detailed ethological observations, which were prevented by extremely low underwater visibility (< 0.3 m) and some degree of evasive behavior (Morteo et al., 2012b). Further information on group affiliations, genetic relatedness, and detailed behavioral observations of these and other individuals will help to unravel the social dynamics of this bottlenose dolphin community, providing insight into their mating system and establishing the mechanisms of gene flow driving its evolutionary change. This information may also be of relevance for the conservation and management of the species in this particular location, where the animals face anthropogenic threats from artisanal fishing activities (Morteo, 2011; Morteo et al., 2012b).

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# Literature Cited

- Ballance, L. T. (1990). Residence patterns, group organization and surface association of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 267-284). San Diego: Academic Press. http:// dx.doi.org/10.1016/B978-0-12-440280-5.50017-2
- Bejder, L., & Dawson, S. (2001). Abundance, residency, and habitat utilization of Hector's dolphins (*Cephalorhynchus hectori*) in Porpoise Bay, New Zealand. New Zealand Journal of Marine and Freshwater Research, 35, 277-287. http://dx.doi.org/10.1080/00288330.2001.9516998
- Bejder, L., Fletcher, D., & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour*, 56, 719-725. http://dx.doi.org/10.1006/anbe.1998.0802
- Bräger, S., Würsig, B., Acevedo, A., & Henningsen, T. (1994). Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Galveston Bay, Texas. *Journal of Mammalogy*, 75, 431-437. http://dx.doi.org/ 10.2307/1382564
- Campbell, G. S., Bilgre, B. A., & Defran, R. H. (2002). Bottlenose dolphins (*Tursiops truncatus*) in Turneffe Atoll, Belize: Occurrence, site fidelity, group size, and abundance. *Aquatic Mammals*, 28(2), 170-180.
- Connor, R. C., Smolker, R. A., & Bejder, L. (2006). Synchrony, social behavior and alliance affiliations in Indian Ocean bottlenose dolphins (*Tursiops adun*cus). Animal Behavior, 72, 1371-1378. http://dx.doi. org/10.1016/j.anbehav.2006.03.014
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences*, 89, 987-990. http://dx.doi.org/ 10.1073/pnas.89.3.987
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. (2000). The bottlenose dolphin: Social relationships in a fissionfusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of whales and dolphins* (pp. 91-126). Chicago: University of Chicago Press.
- Del Castillo, V. (2010). Ecología poblacional del tursión (Tursiops truncatus) en la costa de Alvarado, Veracruz [Population ecology of bottlenose dolphins (Tursiops truncatus) off the coast of Alvarado, Veracruz] (Tesis de licenciatura). Benemérita Universidad Autónoma de Puebla, Puebla, México. 81 pp.
- Fazioli, K. L., Hofmann, S., & Wells, R. S. (2006). Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 32(2), 212-222. http://dx.doi.org/10.1578/AM.32.2.2006.212

- Felix, F. (1997). Organization and social structure of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf de Guayaquil, Ecuador. *Aquatic Mammals*, 23(1), 1-16.
- García, R. (1995). Presencia de la tonina Tursiops truncatus (Montagu, 1821), en la zona de pesca de camarón de Alvarado, Ver., México (Cetacea: Delphinidae) [Presence of bottlenose dolphins Tursiops truncatus (Montagu, 1821), in the shrimp fishing area off Alvarado, Ver., Mexico] (Tesis de licenciatura). Universidad Nacional Autónoma de México, DF, México. 47 pp.
- Islas, V. (2005). Genética de poblaciones y filogeografía de toninas Tursiops truncatus en el sur del Golfo de México y el Caribe [Population genetics and philogeography of bottlenose dolphins Tursiops truncatus in the Southern Gulf of Mexico and Caribbean] (Tesis de maestría). Universidad Nacional Autónoma de México, DF, México. 90 pp.
- Krützen, M., Sherwin, W. B., Berggren, P., & Gales, N. J. (2004). Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Marine Mammal Science*, 20, 28-47. http://dx.doi.org/10.1111/j.1748-7692.2004.tb01139.x
- Krützen, M., Sherwin, W. B., Connor, R. C., Barre, L. M., Van De Casteele, T., Mann, J., & Brooks, R. (2003). Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society B: Biological Sciences*, 270, 497-502. http://dx.doi.org/10.1098/rspb.2002.2229
- Lusseau, D. (2004). The hidden cost of tourism: Detecting long-term effects of tourism using behavioral information. *Ecology and Society*, 9(1), 2.
- Maze-Foley, K., & Würsig, B. (2002). Patterns of social affiliation and group composition for bottlenose dolphins (*Tursiops truncatus*) in San Luis Pass, Texas. *Gulf* of Mexico Science, 2, 122-134.
- Möller, L. M., & Beheregaray, L. B. (2004). Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, *13*, 1607-1612. http://dx.doi.org/10.1111/j.1365-294X.2004.02137.x
- Möller, L. M., Beheregaray, L. B., Harcourt, R., & Krützen, M. (2001). Kinship and alliance formation in wild male bottlenose dolphins. *Proceedings of the Royal Society* of London, Series B, 268, 1756-1762. http://dx.doi. org/10.1098/rspb.2001.1756
- Morteo, E. (2011). Ecología social de delfines Tursiops truncatus en aguas costeras de Alvarado, Veracruz, México [The social ecology of bottlenose dolphins Tursiops truncatus in the coastal waters off Alvarado, Veracruz, Mexico] (Tesis de doctorado). Universidad Veracruzana, Boca del Río, México. 129 pp.
- Morteo, E., Rocha-Olivares, A., & Morteo, R. (2012a). Sensitivity analysis of residency and site fidelity estimations to variations in sampling effort and individual catchability. *Revista Mexicana de Biodiversidad*, 83(2), 487-495.

- Morteo, E., Heckel, G., Defran, R. H., & Schramm, Y. (2004). Distribution, movements and group size of the bottlenose dolphin (*Tursiops truncatus*; Montagu, 1821) south of Bahía San Quintin, Baja California, México. *Ciencias Marinas*, 30(1A), 35-46.
- Morteo, E., Rocha-Olivares, A., Arceo-Briseño, P., & Abarca-Arenas, L. G. (2012b). Spatial analyses of bottlenose dolphin–fisheries interactions reveal human avoidance off a productive lagoon in the western Gulf of Mexico. Journal of the Marine Biological Association of the United Kingdom, 92(8), 1893-1900. http://dx.doi. org/10.1017/S0025315411000488
- Natoli, A., Peddemors, V. M., & Hoelzel, A. R. (2004). Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *Journal of Evolutionary Biology*, *17*, 363-375. http://dx.doi.org/10.1046/j.1420-9101.2003.00672.x
- Owen, E. C. G., Hofmann, S., & Wells, R. S. (2002). Ranging and social association patterns of paired and unpaired adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology*, 80, 2072-2089. http://dx.doi.org/10.1139/z02-195
- Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. E., & Thompson, P. M. (2003). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, 66, 185-194. http://dx.doi.org/10.1006/anbe.2003.2186
- Quintana-Rizzo, E., & Wells, R. S. (2001). Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: Insights into social organization. *Canadian Journal of Zoology*, 79, 447-456. http://dx.doi.org/10.1139/cjz-79-3-447; http:// dx.doi.org/10.1139/z00-223
- Rogers, C. A., Brunnick, B. J., Herzing, D. L., & Baldwin, J. D. (2004). The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science*, 20, 688-708. http://dx.doi. org/10.1111/j.1748-7692.2004.tb01188.x
- Simões-Lopes, P. C., & Fabian, M. E. (1999). Residence patterns and site fidelity in bottlenose dolphins, *Tursiops* truncatus (Montagu) (Cetacea, Delphinidae) off southern Brazil. Revista Brasileira de Zoologia, 16(4), 1017-1024. http://dx.doi.org/10.1590/S0101-81751999000400012
- Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, *123*, 38-69. http://dx.doi.org/10.1163/156853992X00101
- Urian, K. W., Hofmann, S., Wells, R. S., & Read, A. J. (2009). Fine-scale population structure of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida. *Marine Mammal Science*, 25, 619-638. http://dx.doi. org/10.1111/j.1748-7692.2009.00284.x
- Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199-225). Los Angeles: University of California Press.

- Wells, R. S. (2003). Dolphin social complexity: Lessons from long-term study and life history. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 32-56). Cambridge, MA: Harvard University Press. http://dx.doi.org/10.4159/harvard.9780674419131.c4
- Wells, R. S. (2009). Identification methods. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia* of marine mammals (pp. 593-599). San Diego: Elsevier. http://dx.doi.org/10.1016/B978-0-12-373553-9.00139-5
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* (pp. 247-305). New York: Plenum Press. http://dx.doi.org/10.1007/978-1-4757-9909-5\_7
- Whitehead, H. (2009). SOCPROG programs: Analyzing animal social structures. Behavioral Ecology and Sociobiology, 63, 765-778. http://dx.doi.org/10.1007/ s00265-008-0697-y
- Whitehead, H., Christal, J., & Tyack, P. L. (2000). Studying cetacean social structure in space and time. In J. Mann, R. C. Connor, P. L. Tyack, & H Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 65-87). Chicago: University of Chicago Press.
- Würsig, B., & Jefferson, T. A. (1990). Methods of photoidentification for small cetaceans. In P. S. Hammond, S. A. Mizroch, & G. P. Donovan (Eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Reports of the International Whaling Commission (Special Issue 12), 43-52.
- Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition and stability of coastal porpoises, *Tursiops truncatus. Science*, 198, 755-756. http://dx.doi.org/10.1126/science.198.4318.755
- Zolman, E. S. (2002). Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River Estuary, Charleston County, South Carolina, U.S.A. *Marine Mammal Science*, 18(4), 879-892. http://dx.doi. org/10.1111/j.1748-7692.2002.tb01079.x