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ASSOCIATION PATTERNS OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN GALVESTON BAY, TEXAS

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Resightings of photographically identified bottlenose dolphins (*Tursiops truncatus*) were used to calculate association indices for a population of free-ranging individuals occurring in the Galveston Bay system, Texas, and the adjacent Gulf of Mexico. Thirty-five individual dolphins with four or more sightings per year were included in the analyses to ensure likelihood of identification and comparability in 1990 and 1991. The patterns of association were weak, with few strong associations between individuals. The average association indices for 1990 and 1991 were similar; however, the magnitude of individual association indices changed drastically between the years. The low number of detectable, long-term affiliations indicates high group fluidity.

Key words: bottlenose dolphins, *Tursiops truncatus*, association patterns, association index, social affiliations, group structure

Many social mammals live in groups of varying composition that facilitate such important aspects of life as feeding, reproduction, communication, learning, defense, and adequate response to environmental cycles (Alexander, 1974; Axelrod and Hamilton, 1981; Hamilton, 1964; Norris and Schilt, 1988). Social groups in which members know each other (individualized groups) allow for a choice of partners and for long-term fidelity. Terrestrial examples of such groups are known from carnivores (Bekoff, 1978; Kruuk, 1972; Mech, 1970, 1988; Schaller, 1972), ungulates (Clutton-Brock et al., 1982; Klingel, 1969), bats (Wilkinson, 1984, 1988), and primates (Altmann, 1980; Clutton-Brock, 1974; de Waal, 1982; Ghiglieri, 1985; Goodall, 1986; Tayler and Saayman, 1972).

In cetaceans, group stability varies from the stable family pods of orcas (*Orcinus orca*—Bigg et al., 1987; Heimlich-Boran, 1986) to the fluid fission-fusion society of spinner dolphins (*Stenella longirostris*—K. S. Norris et al., in litt.). The bottlenose dolphin (*Tursiops truncatus*) seems to be intermediate between these extremes of group

stability (Ballance, 1990; Bräger, 1992; Harzen, 1989; Weller, 1991; Wells, 1986, 1991; Wells et al., 1987; Würsig, 1978; Würsig and Harris, 1990). Bottlenose dolphins also have populations or subpopulations that are either migratory, resident to an area, or an incompletely understood combination of residency and seasonal shift in movements (Hansen, 1990; Scott and Chivers, 1990; Wells et al., 1990). Degrees of residency and associations between individuals are linked, and both may be related to physical and biological factors of the environment. We expect, for example, more pronounced seasonal migrations where temperatures and preferred prey vary strongly in seasonal manner (Kenney, 1990; Wells et al., 1990). If only part of a population migrates, there are shifts in affiliations between many individuals.

The present study seeks to explore association patterns of bottlenose dolphins in a shallow bay system in the northern section of coastal Texas. To describe interyear residency, it compares 2 subsequent years. However, the present analysis only presents basic association data that must be com-

pared by season as well as abiotic and biological factors as more long-term data are gathered in this ongoing study.

MATERIALS AND METHODS

Boat-based, photo-identification surveys were conducted May–October 1990 and February–December 1991 (217 trips) in the bay and coastal gulf waters around the northeastern end of Galveston Island, Texas (29°18'N, 94°48'W), with research vessels ranging in size from 5.0 to 6.5 m to cover an area of ca. 100 km². Over 1,000 individual bottlenose dolphins were identified in this area (Bräger, 1992, 1993; Henningsen, 1991) by distinctive markings on their dorsal fins (Würsig and Jefferson, 1990; Würsig and Würsig, 1977). However, the majority of these recognized dolphins were sighted only once, and it was concluded (Henningsen, 1991) that many dolphins merely pass through the area of Galveston Bay. Only a core of ca. 200 individuals use the area for longer term.

A group was defined as any number of dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity (Shane, 1990). Members of the same group were regarded as being associated. Sizes of groups were estimated, usually with a range of numbers (e.g., 8–12 animals in one group) assigned to a sighting. A “mean maximum” value was calculated from the mean of the larger number of this range. For this study of association patterns, individuals of groups were analyzed regardless of behavior. However, there is a correlation between behavioral pattern and group size (Bräger, 1992; Smolker et al., 1992).

To describe and quantify the level of association between two different dolphins, the half-weight index (HWI) as used by Dice (1945) was calculated, where the coefficient of association (HWI) = $2N/(n_1 + n_2)$; $2N$ = the total number of joint sightings scored once for each occurrence of both individuals together, n_1 = the total number of sightings for the first individual, and n_2 = the total number of sightings for the second individual.

The HWI can range from 0.0 for two individuals never seen together to 1.0 for two individuals always seen together. This index has been used extensively to describe terrestrial mammalian associations (e.g., Schaller, 1972). It also has been employed to describe associations of

bottlenose dolphins in Florida (Wells, 1986; Wells et al., 1987), Portugal (Harzen, 1989), California (Weller, 1991), and Australia (Connor et al., 1992; Smolker et al., 1992).

To minimize the potential error of not identifying an individual when present within an observed group and to be able to compare results from 1990 to results from 1991, only associations of the 35 most frequently identified individuals were analyzed (595 possible association indices/year). All 35 individuals were identified four or more times in each of the two sampling periods (n_1 and $n_2 \geq 4$). These individuals generally were easy to photograph and to identify, increasing the likelihood that they were identified when present. The resulting indices were grouped into six size classes, following Wells et al. (1987): 1) 0; 2) 0.01–0.19; 3) 0.20–0.39; 4) 0.40–0.59; 5) 0.60–0.79; 6) 0.80–0.99. The HWI was calculated separately for 1990 and for 1991 for all pairwise combinations for each of the 35 individuals. Because HWIs are not distributed parametrically, medians were calculated. However, to facilitate comparisons with published data, the less correct means and standard deviations also were presented.

RESULTS

Galveston dolphins occurred in groups of up to 30 individuals (Table 1). The mean group size consisted of 4.4 ± 3.56 (*SD*) individuals ($n = 552$). In both sampling periods, there was a small number of relatively strong associations and a large number of relatively weak associations (Fig. 1). The median association level of 0.154 in 1990 ($n = 165$ associations) decreased to 0.125 in 1991 ($n = 216$ associations), probably due to additional low-level associations being discovered. The arithmetic mean levels of the association for the two sampling periods were 0.19 ± 0.128 (*SD*) for 1990 and 0.17 ± 0.125 (*SD*) for 1991. From 1990 to 1991, 119 association indices decreased in magnitude, 177 increased in magnitude, and 26 indices did not change (Fig. 2).

Since the HWI only describes association patterns of two animals at a time, the group size in which an individual was identified was used as a measure to describe the stability of group composition. If the size of

an individual's group changed over time, its composition and associates must have changed simultaneously. Group sizes for each of these individuals varied greatly, as shown by the extreme ranges (Table 1). The total number of identified associates for each of the 21 individuals in this analysis always exceeded the respective mean group size (Table 1). The mean of the largest group size was 16.5 individuals (excluding the reference dolphin), which is smaller than the average number of associates identified in all groups (39.3 individuals). On average, the maximum group size encompassed 42% of all associates. Therefore, it is likely that no bottlenose dolphin was ever seen together with all of its associates in a single group.

DISCUSSION

This study of association patterns of bottlenose dolphins ultimately is based on the premise that being in close physical proximity is a sign of social affiliation. These patterns have been used to suggest long-term bonds and even elements of mating strategies (Norris and Dohl, 1980; Wells, 1986, 1991; Wells et al., 1987). This may not be correct, as a broad human example shows: office workers in close affiliation all day are not necessarily social partners. Association indices may not always give an indication of the quality or importance of an association for the dolphins involved. Low indices ($HWI < 0.40$) in a large population such as that in waters by Galveston do not necessarily indicate the lack of important associations, because they could be related only with certain behaviors or certain areas. For example, the average group size of bottlenose dolphins at Galveston was significantly larger when socializing than when feeding or traveling (Mann-Whitney U test: $P < 0.001$, $n = 103$ socializing and 430 feeding-traveling; Bräger, 1992). These groups are not stable, and are characterized by frequent changes in composition, as evidenced by the large number of small association indices and their asso-

TABLE 1.—Mean group size, standard error, range of group size, and total number of associates for 21 bottlenose dolphins most frequently identified in 1991 (20 or more observations) in comparison to the total number of identified accompanying dolphins, or associates.

Identification number (number of analyzed groups)	$\bar{X} \pm SE$	Range	Total number of associates in 1991
657 (32)	6.9 \pm 0.74	1–23	73
233 (28)	5.4 \pm 0.53	1–10	45
227 (29)	3.5 \pm 0.58	1–13	38
1,011 (15)	7.3 \pm 1.49	2–23	42
16 (14)	7.3 \pm 1.70	2–23	61
1,016 (16)	7.1 \pm 1.13	3–18	45
2 (16)	12.5 \pm 1.84	2–26	78
3 (11)	11.1 \pm 2.20	4–26	58
580 (10)	5.4 \pm 1.61	1–18	23
393 (11)	7.1 \pm 0.95	3–13	29
24 (6)	3.5 \pm 0.56	2–5	8
27 (8)	8.9 \pm 2.24	2–23	34
982 (11)	9.4 \pm 1.22	5–18	40
1,013 (11)	5.7 \pm 0.93	1–10	32
1,014 (10)	7.4 \pm 0.97	3–13	29
790 (7)	5.9 \pm 1.37	2–10	12
1,028 (5)	12.4 \pm 3.22	3–23	54
1,020 (4)	11.3 \pm 1.75	6–13	29
6 (7)	5.4 \pm 1.43	1–10	18
19 (12)	10.5 \pm 2.41	3–30	47
1,010 (9)	10.3 \pm 1.92	3–20	30

ciated changes in magnitude between sampling periods.

Bottlenose dolphins in waters by Galveston show few high-level ($HWI > 0.60$) affiliations. Most association patterns consist of low-level associations, which seem to vary in intensity between years. The structure of these dolphin groups is characterized by a high exchange rate of members. This group fluidity is similar to the association patterns of bottlenose dolphins along the Pacific coast of California (Weller, 1991) and in the Gulf of California (Balance, 1990). Group fluidity was apparent in the different group sizes in which a given individual was found, as different size groups require different associations between individuals. The few high-level affil-

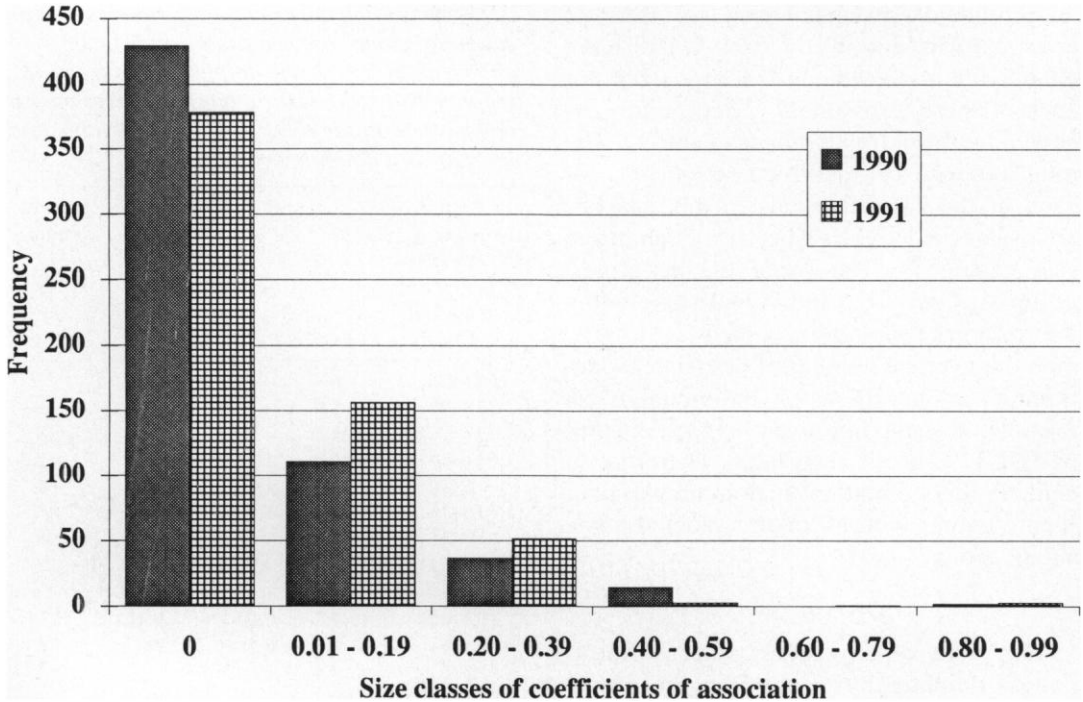


FIG. 1.—The distribution of associations ($n = 595$) of all bottlenose dolphins identified four or more times in both 1990 and 1991 ($n = 35$) over the size classes of the half-weight index. Note that these size classes, which follow Wells et al. (1987), are not all the same size.

iations are not understood. They could represent mothers and older offspring, as noted by Wells et al. (1987), or strong male-male bonds, as described by Connor et al. (1992), but this is not known.

The association patterns of bottlenose dolphins have been studied extensively in Sarasota, Florida (Wells et al., 1987). Wells et al. (1987) calculated association indices of 38 dolphins that consisted of juveniles, subadults, and adults from the population in Sarasota Bay for the years 1980–1984. The dolphins were on average associated with 60 different individuals (range of 25–91 associates), although Wells et al. (1987) pointed out that these numbers might be low because they were unable to identify ca. 18.5% of the sample that consisted of juveniles, subadults, and adults. Harzen (1989) used the same method to study the associations of 30 bottlenose dolphins in the Sado Estuary, Portugal, in 1986 and

1987; he found a large number of relatively strong associations (72% of the HWIs were ≥ 0.40). According to Wells et al. (1987) and Harzen (1989), dolphin societies in Florida and Portugal consisted of only a limited number of members (100 and 60 individuals, respectively) that were associated with each other often, therefore resulting in high indices.

Weller (1991) calculated association indices for 160 individuals observed near San Diego, California, between 1984 and 1989. Contrary to the results of the studies in Florida and Portugal, 95% of all coefficients in the study in California were < 0.40 , with a mean of 0.21. The most frequently sighted individual ($n = 24$) was seen with 259 different affiliates over the 6-year period (Weller, 1991). Weller's (1991) findings were similar to the results from Galveston.

The differences in the social structure be-

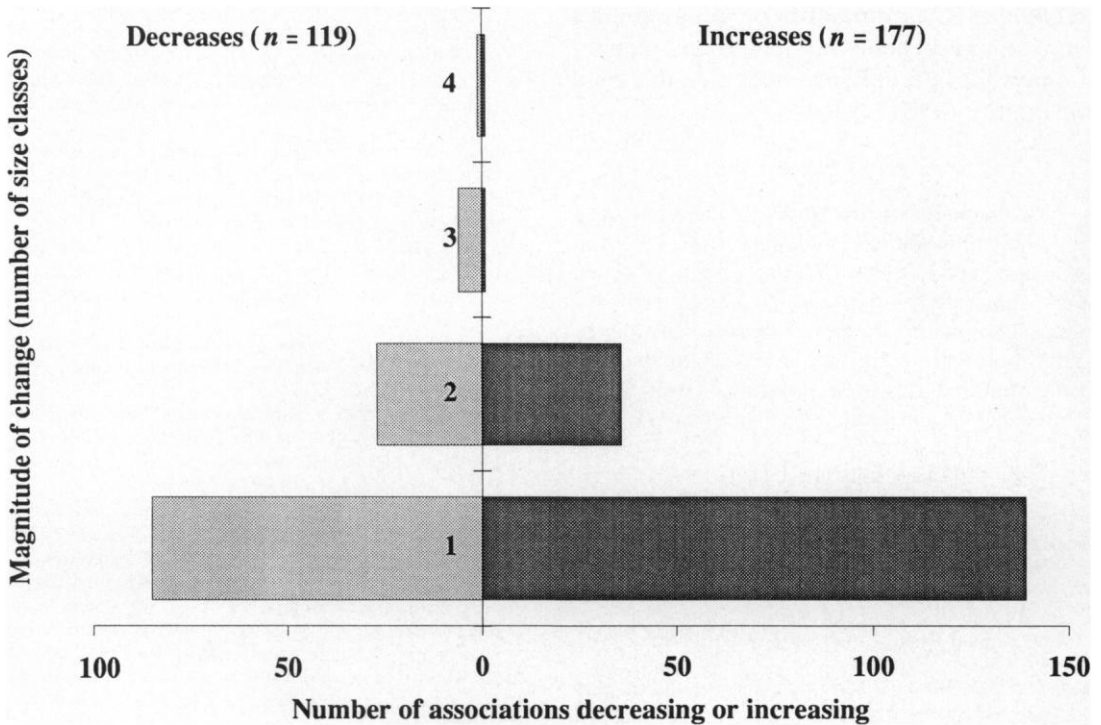


FIG. 2.—The number of associations between two individuals ($n = 322$) that decreased or increased by number of size classes between the two sampling periods in 1990 and in 1991. The six size classes are 0.00, 0.01–0.19, 0.20–0.39, 0.40–0.59, 0.60–0.79, and 0.80–0.99, following Wells et al. (1987). For example, a decrease of four size classes, which happened once, was due to a change from 0.93 to 0.11 (left side of top of figure). Twenty-six associations did not change in magnitude.

tween the communities of Sarasota and Sado and the communities of Galveston and the Southern California Bight are striking. The generally high level of the HWI in the first two communities probably depends on the small number of available associates in a rather confined area. In Texas and California, the number of associates for each individual probably is larger because of an overall larger population size.

The fluid structure of some odontocete groups has led to the speculation that reciprocal altruism might play an important role in social relationships of dolphins (Connor and Norris, 1982; Tyack, 1986). Individual association fluidity allows for rapid changes in group sizes and, therefore, may efficiently aggregate the appropriate number of dolphins for differing activities such as travel,

feeding, socializing, resting, mating, and caring for young. Dolphins who coordinate activities in these efficiently-sized groups presumably benefit by enhanced fitness to themselves and their offspring (Alexander and Borgia, 1978; Würsig, 1986). Individual recognition is a prerequisite for reciprocal altruism and facilitates relations in social groups. It is possible that social mammals such as bottlenose dolphins do not need to regularly associate with the same individuals, because they recognize and remember each other as affiliates over long periods of time. The high fluidity and short-term nature of associations in the present study suggest that individuals routinely leave one group to join another, an indication that individuals within the study area may know each other. The ability to

recognize a large number of other animals and strong benefits to reciprocal interactions would permit and encourage this kind of fluidity (Trivers, 1985).

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Occurrence and Group Organization of Atlantic Bottlenose Porpoises (*Tursiops truncatus*) in an Argentine bay

Bernd Würsig

Biological Bulletin, Vol. 154, No. 2. (Apr., 1978), pp. 348-359.

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The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*)

Bernd Würsig; Melany Würsig

Science, New Series, Vol. 198, No. 4318. (Nov. 18, 1977), pp. 755-756.

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