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SOCIAL ORGANIZATION OF MARINE TUCUXI DOLPHINS, *SOTALIA GUIANENSIS*, IN THE CANANÉIA ESTUARY OF SOUTHEASTERN BRAZIL

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Social organization is an important component of the population biology of a species that influences gene flow, the spatial pattern and scale of movements, and the effects of predation or exploitation by humans. An important element of social structure in mammals is group fidelity, which can be quantified through association indices. To describe the social organization of marine tucuxi dolphins (*Sotalia guianensis*) found in the Cananéia estuary, southeastern Brazil, association indices were applied to photo-identification data to characterize the temporal stability of relationships among members of this population. Eighty-seven days of fieldwork were conducted from May 2000 to July 2003, resulting in direct observations of 374 distinct groups. A total of 138 dolphins were identified on 1–38 distinct field days. Lone dolphins were rarely seen, whereas groups were composed of up to 60 individuals (mean $\pm$ 1 SD = 12.4 $\pm$ 11.4 individuals per group). A total of 29,327 photographs were analyzed, of which 6,312 (21.5%) were considered useful for identifying individuals. Half-weight and simple ratio indices were used to investigate associations among *S. guianensis* as revealed by the entire data set, data from the core study site, and data from groups composed of $\leq$10 individuals. Monte Carlo methods indicated that only 3 (9.3%) of 32 association matrices differed significantly from expectations based on random association. Thus, our study suggests that stable associations are not characteristic of *S. guianensis* in the Cananéia estuary.

Key words: association indices, photo-identification, social organization, *Sotalia guianensis*

Studies of social organization assume that the content, quality, and temporal patterning of interactions between a pair of individuals describe their relationship and that the patterning of relationships among multiple pairs of conspecifics defines the social structure of the population (Hinde 1976). Consequently, an important factor used to characterize social structure is group fidelity, which can be quantified through association indices (Whitehead and Dufault 1999). Such indices serve as an important tool for providing insight into mammal societies (Whitehead 1997; Whitehead and Dufault 1999), as evidenced by studies of vampire bats (*Desmodus rotundus*—Wilkinson 1985), bison (*Bison bison*—Green et al. 1989), and orangutans (*Pongo pygmaeus*—Mitani et al. 1991), each of which employed association indices to describe novel aspects of social relationships among conspecifics.

Despite the difficulties of observing aquatic mammals (Connor et al. 1998), numerous investigations of cetacean social bonds have been conducted over the last 20 years. Most species of odontocetes are considered highly social, with individuals spending a considerable amount of time in close proximity to congeners (Bräger 1999). The degree of stability of these social bonds varies from the enduring matrilineal relationships in pods of killer whales (*Orcinus orca*—Baird and Whitehead 2000; Bigg et al. 1990; Ford et al. 2000) to the fission–fusion dynamics of groups of spinner dolphins (*Stenella longirostris*—Östman 1994). Other odontocetes that have been the subject of long-term investigations of social relationships include Hector's dolphins (*Cephalorhynchus hectori*—Slooten et al. 1993), Atlantic spotted dolphins (*Stenella frontalis*—Herzing and Brunnick 1997), and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*—Chilvers and Corkeron 2002; Connor et al. 1992; Smolker et al. 1992). In particular, analyses of association indices in common bottlenose dolphins

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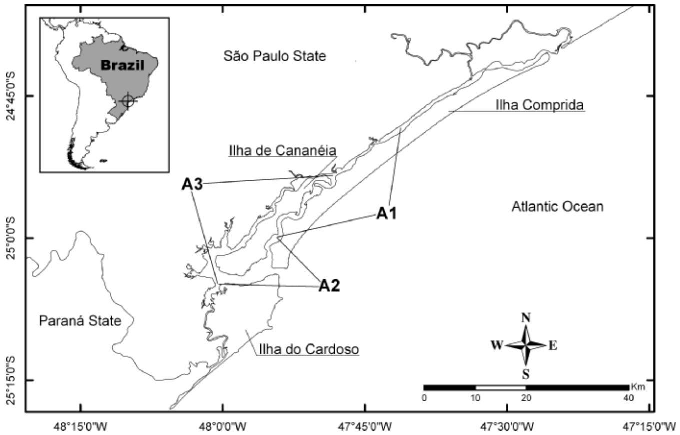

FIG. 1.—Map of the study area. The study population of marine tucuxi dolphins (*Sotalia guianensis*) was located in the Cananéia estuary, São Paulo State, Brazil. Subareas 1, 2, and 3 of the study site are indicated.

(*T. truncatus*—Wells 1991; Wells et al. 1987) revealed that some adult males, often not genetically related, form long-term, stable pair-bonds that may last for the duration of a male's life (Duffield and Wells 2002). Collectively, these studies indicate that analyses of association indices can provide critical insights into the social structures of marine mammals.

Despite the considerable increase in studies of cetacean societies in recent decades, numerous species remain poorly known. One example is the marine tucuxi dolphin (*Sotalia guianensis*), which is endemic to coastal Atlantic waters of South and Central America (Carr and Bonde 2000; Da Silva and Best 1996; Flores 2002). These animals have been the focus of recent taxonomic studies, which indicate that marine (*S. guianensis*) and riverine (*S. fluviatilis*) tucuxi dolphins are separate species (Caballero et al. 2007; Cunha et al. 2005; Monteiro-Filho et al. 2001). *S. guianensis* is listed as ''insufficiently known'' by the World Conservation Union, IUCN (Reeves and Leatherwood 1994; Reeves et al. 2003) and has been the focus of recent studies of the ecology of the Cananéia estuary (25°S, 48°W), São Paulo State, southeastern Brazil. During the last 10 years, the growth of uncontrolled tourism to watch dolphins, the destruction of mangrove areas for housing, and the installation of facilities to grow exotic species of shrimp and oysters have created significant concerns regarding preservation of the estuary and its inhabitants (Santos 2004). Thus, understanding the behavior of ecologically important species such as *S. guianensis* can be an important tool for management and conservation of this region.

Previous studies of marine tucuxi dolphins in the Cananéia estuary used photo-identification (photo-ID) to trace the origin of the distinctive use of sloping beaches for foraging to several individuals in the population (Santos et al. 2000, 2001), thereby providing possible evidence of cultural transmission in cetacean societies (see Krützen et al. 2005; Whitehead et al. 2004). With regard to social structure, Santos et al. (2001) showed evidence of site fidelity by known individuals. Although several studies have explored other aspects of the demography (Acuña 2002) and ecology (Santos et al. 2002, 2003; Yogui et al. 2003) of these animals, no other research on social interactions has been conducted. Thus, the nature and duration of social relationships in this species remain unknown.

The purpose of this study is to investigate social relationships among marine tucuxi dolphins in the Cananéia estuary via association indices applied to photo-ID data. This study is part of an ongoing monitoring program begun in 1996 that is based on photo-ID data from *S. guianensis*. Several factors, including recent studies of other small-bodied cetaceans, the presence of abundant year-round food resources in the Cananéia estuary, the lack of potential predators in the core, protected inshore portion of the study site, and the lack of sexual dimorphism in *S. guianensis*, suggest that associations among marine tucuxis are fluid. Although previous research (Monteiro-Filho 2000) suggests that *S. guianensis* in the Cananéia estuary forms stable family groups, this conclusion was not based on association indices or other rigorous quantitative analyses of social relationships. Therefore, a detailed investigation of the characteristics of associations among *S. guianensis* in the Cananéia estuary is warranted.

MATERIALS AND METHODS

Study area.—The Cananéia estuary is located at the southern tip of São Paulo State, Brazil (25°01′S, 47°55′W) and is part of a 180-km-long estuarine system that extends from Iguape, São Paulo State, to Paranaguá, Paraná State (Fig. 1). The estuary contains a muddy bottom and shallow waters (depth $\leq$23 m) that can be relatively turbid year-round (Schaeffer-Novelli et al. 1990). It is surrounded by large mangrove forests and is connected to coastal waters through 6 different channels. The area surveyed was approximately 132 km^2 and was split into 3 smaller subareas to allow all portions of the estuary to be surveyed within a 3-day period (Fig. 1). Subarea 1 was approximately 45 km^2 and was located in the northern section of the estuary. Subarea 2 was approximately 33 km^2 and was located close to the main estuary entrance. Subarea 3, which included western inner estuarine waters, was approximately 54 km^2. Boundaries and sizes were determined through previous surveys conducted between 1996 and 1999, when investigators made the 1st attempts to search for dolphins in the estuary. There were no physical barriers between the 3 subareas and no apparent reasons why dolphins would use these areas differentially.

Data collection.—Fieldwork was conducted from May 2000 to July 2003. In the 1st year, emphasis was given to subarea 2. Since 2001, subareas 1 and 3 also have been surveyed. Field efforts in all subareas consisted of 2 days of fieldwork per season (e.g., spring and summer) for 3 consecutive years (n = 24 days of sampling per subarea). To avoid biasing observations, the subarea to be surveyed on a given day was chosen randomly. Small motor-powered boats (15 and 30 horsepower) were used to survey subareas in random zigzag movements to find as many groups as possible. Surveys were conducted in sea states ranging from 0 to 2 (relatively calm water) on the Beaufort scale.

When a group of dolphins was found, the boat approached the animals in a parallel orientation and the photo-ID effort began. A group of tucuxi dolphins was defined as any aggregation of 2 or more individuals, including female–calf pairs, observed within an area with a radius of approximately 100 m (sensu Wells et al. 1999). Members of an aggregation were generally, but not necessarily, engaged in similar activities. Observations of each group lasted from 20 to 240 min, depending on the size of the group. On most occasions, all individuals in a group, including calves, were photographed using a 35-mm reflex camera with a 300-mm zoom lens and ISO-400 color film. Photographs were taken at distances ranging from 2 to 10 m. In the main estuary entrance, aggregations of groups of tucuxi dolphins were sometimes composed of up to 60 individuals engaged in feeding activities. These aggregations were generally composed of smaller subgroups; distinct subgroups were selected randomly and then followed for the purpose of photo-ID. Once all individuals in a given subgroup had been photographed, we switched efforts to a different subgroup. This procedure was adopted in order to include all individuals from large aggregations in photographs while retaining information about potential social structure within such aggregations.

Photo analyses.—Individuals were identified by dorsal fin shape and the presence of distinctive notches on that fin using the photo-ID technique of Würsig and Würsig (1977) and following the recommendations of Würsig and Jefferson (1990). Photographs were analyzed with the help of 10× eyecup lenses; identifications were made by 2 investigators on 3 different occasions after each sampling period. To include an individual in our catalog of reference photos, both investigators had to agree on the animal identification; the same was true for resightings of previously identified animals. Photos were sorted into 4 categories according to focus, contrast, and dorsal fin size in relation to distance from the photographer. Photos were categorized as follows: 0—photographs that were taken just after a dolphin's dive and contained no image of the individual; 1—photographs without adequate quality to identify individuals in the frame; 2—photographs with good quality and dolphins at distances ranging from 5 to 10 m; and 3—photographs with quality that allowed individuals to be identified at distances ranging from 2 to approximately 4 m from the photographer. Photos placed in category 2 contained the individual's dorsal fin, as well as the right or the left side of the body. Photographs in which most of the frame showed the individual's dorsal fin were placed in category 3.

Individuals were included in the reference catalog only when they presented distinct and conspicuous notches along their dorsal fin borders, as determined following the procedure described by Karckzmarski and Cockcroft (1998). If an individual with a distinct notch along the border of its dorsal fin was photographed, it received the index "n," meaning "notch." If a dorsal fin of an individual did not have any conspicuous marks, the photograph received the index "w," meaning "without notches." The number of photographs in categories 2 and 3 with the "n" designation (2n + 3n) was divided by the total number of useful photographs (with and without notches in categories 2 and 3; 2n + 2w + 3n + 3w) in order to estimate the proportion of known individuals in the study population. The authors also estimated the number of known individuals in the population using the method of Chilvers and Corkeron (2002). Specifically, from a random sample of 500 photographs considered useful for identification purposes, the proportion of individuals with notched dorsal fins (proportion of "n" photos) was estimated. No calves were included in the photo catalog because notches were rarely found in this age class; an individual was considered a calf when it was less than two-thirds of adult size and remained close to an adult in the infant position (Mann and Smuts 1999; Mann et al. 2000).

Determination of sex.—Members of the study population were identified as females based on long-term observations ($\geq$5 identifications in different months) during which they were in close companionship with calves (echelon position sensu Mann and Smuts [1999]) yet isolated from other individuals. In contrast, animals were identified as "possible males" after long-term observations ($\geq$5 identifications in different months over a 3-year period) during which they were not observed with calves. The sexes of 16 animals, 6 of which were known from photo-IDs, were determined using molecular genetic procedures. Between October 2002 and July 2003, tissue samples from these individuals were obtained using an 80-pound crossbow adapted to collect skin samples from small cetaceans. DNA was extracted from these tissues following the method described by Bruford et al. (1992) and the sex of each animal was determined by polymerase chain reaction and electrophoresis in 1.5% agarose gels following the procedures of Bérubé and Palsboll (1996).

Association index analyses.—Most studies of cetacean societies have been based on 2 association indices and hence we opted to use both the half-weight (HW) and the simple ratio (SR) indices (Cairns and Schwager 1987; Ginsberg and Young 1992) to examine social relationships in our study population. All dolphins photographed in the same group on the same day were recorded as being associated. Groups for which not all individuals were photographed were excluded from the analyses. In determining whether all individuals in a group were photographed both notches on the dorsal fin border and short-lasting marks along either side of the body (e.g., tooth rakes, scars, or white pigmentation) were used to distinguish group members. As outlined above, feeding aggregations composed of $\geq$20 individuals usually consisted of smaller subgroups of animals, each of which was photographed as completely as possible before moving to the next subgroup. To avoid biasing our data toward parent–offspring affiliations, observations of female–calf pairs were excluded from consideration; only observations of individually distinctive juveniles and adults were used in analyses of associations among individuals.

To better evaluate associations among tucuxi dolphins in the Cananéia estuary and to reduce the chances of bias in our results, 3 distinct analyses were conducted. First, data from all subareas of the study site were pooled for analysis. This procedure assumed that all individuals in the population had the same probability of being photographed in any part of the

TABLE 1.—Mean group sizes for marine tucuxi dolphins (*Sotalia guianensis*) in the Cananéia estuary. Group sizes were monitored from May 2000 to July 2003; a total of 374 groups, all members of which were identified, were included in these analyses. Data are presented for each subarea of the study site as well as for the entire site.

Subarea	$\bar{X} \pm SD$ group size	No. groups	Range (no. individuals)	Median group size
1	13.5 ± 11.9	71	2–60	11
2	12.9 ± 11.8	256	1–60	10
3	7.8 ± 6.9	47	2–45	6
Overall	12.4 ± 11.4	374	1–60	9

study area. A total of 178 groups were included in this analysis, with sample sizes for each year as follows: 2000 ($n = 35$), 2001 ($n = 58$), 2002 ($n = 44$), and 2003 ($n = 41$). Both indices (HW and SR) were calculated for individuals for which ≥ 5 up to ≥ 10 distinct observations (photo-IDs) were obtained.

Second, data from subarea 2, the best-sampled subarea of the study site, were examined in detail. A total of 139 groups were included in this analysis, with sample sizes for each year as follows: 2000 ($n = 28$), 2001 ($n = 40$), 2002 ($n = 37$), and 2003 ($n = 34$). Both indices (HW and SR) were calculated for individuals for which ≥ 5 up to ≥ 10 distinct observations (photo-IDs) were obtained.

Third, data from small groups ($n = 2$–10 individuals) were examined. Typically, it is easier to photograph all members of smaller groups, providing more reliable data for smaller associations (Chilvers and Corkeron 2002). A total of 88 groups were included in this analysis, with sample sizes for each year as follows: 2000 ($n = 15$), 2001 ($n = 27$), 2002 ($n = 24$), and 2003 ($n = 22$). Both indices (HW and SR) were calculated for individuals for which ≥ 3 up to ≥ 6 distinct observations (photo-IDs) were obtained.

To analyze the association data, we attempted to maximize both the number of individuals observed (ensuring representative data) and the sighting frequencies for the individuals considered (ensuring reliability of data—Bejder et al. 1998). In order to conduct more comprehensive analyses, different selection criteria involving >1 class of sightings were adopted (see Chilvers and Corkeron 2002). To minimize autocorrelation of the data and to ensure independence of sampling procedures, groups composed of individuals identified previously in the same day were excluded from the analyses. To evaluate the significance of the results of repeated statistical tests, the Bonferroni correction (Zar 1996) was employed. *P*-values for each association index were obtained by dividing the fixed α-value (0.05) by the number of analyses run for each index.

Analyses were performed using the SOCPROG 1.3 program (Whitehead 1995, 1999), as run in MATLAB 5.3 (The Math Works, Inc., Natick, Massachusetts). To evaluate whether associations in the study population were statistically different from random, the Monte Carlo method (Manly 2006) was used following the recommendations of Bejder et al. (1998) and Whitehead (1999). To test for both long- and short-term associations in all analyses conducted ($n = 32$), the Monte Carlo test was run 5 times, yielding 20,000 permutations of the original matrices. For each association analysis, the proportion of all association values (observed and randomly generated) that were greater than or equal to the observed value was used as the *P*-value for that analysis (Bejder et al. 1998). If this *P*-value was less than 0.05 (or the α-value indicated by Bonferroni correction), the null hypothesis of random association was rejected. However, as noted by Bejder et al. (1998), rejecting the null hypothesis does not indicate that associations are random, but rather that there is no evidence for stable associations among individuals.

RESULTS

Group size.—From May 2000 to July 2003, a total of 87 photo-ID survey days were conducted in the Cananéia estuary, resulting in observations of 374 distinct groups for which all members were identified. Group sizes ranged from 2 to 60 dolphins, although most groups contained 2–20 individuals (mean ± 1 $SD = 12.4 \pm 11.4$ individuals per group; Table 1). Lone dolphins were rarely seen ($n = 7$ occasions), reinforcing the supposition that tucuxis are highly sociable dolphins. Groups were significantly larger in subareas 1 and 2 compared to subarea 3 (Kruskal–Wallis *H*-test, $H = 12.65$, $d.f. = 2, 374$, $P = 0.0018$; Table 1).

Photo-ID and determination of sex.—A total of 29,327 photographs were analyzed, from which 6,312 (21.5%) were considered useful for identification purposes, meaning that the dorsal fin of any individual in those photos was clearly visible. Inspection of these photos revealed that 29.1% of individuals in the studied population could be identified based on the unique pattern of notches along the border of their dorsal fin. In a random selection of 500 useful photographs, 31.9% contained individuals with distinctive dorsal fin notches.

Based on these analyses, a total of 138 distinct dolphins were observed on 1–38 occasions per animal (mean ± 1 $SD = 8.0 \pm 6.1$ occasions). Twenty-five (18.1%) of these individuals were categorized as females based on the constant presence of calves in the infant position. Eleven individuals (8.0%) were never observed in the close company of a calf over the 3-year duration of the study and were categorized as "possible males." Genetic assignment of sex confirmed that 4 of the animals observed with calves were females and that 2 of the animals identified as "possible males" were indeed males. Of the 10 remaining unknown individuals, 6 were females and 4 were males.

Association index analyses.—Sample sizes for the 3 association analyses conducted were 178 (whole study area), 139 (subarea 2), and 88 (groups of ≤ 10 individuals). Respectively, these represent 47.5%, 37.2%, and 23.5% of the 374 fully photographed groups in our data set. Based on the selection criteria employed for each analysis, the number of individuals used to generate association index values varied from 5 (3.6% of the photo-identified population) to 86 (62.3% of the identified population).

Overall, these analyses provided little evidence of long-term associations among adults in the study population. From 14% to 84% of the association index values generated equaled 0,

Table 2.—Association index analyses for marine tucuxi dolphins (*Sotalia guianensis*) in the Cananéia estuary, with data from all subareas of the study site pooled. Both simple ratio (SR) and half-weight (HW) indices were used to analyze data obtained from May 2000 to July 2003. Analyses were conducted for groups containing from ≥5 to ≥10 adults. For each size category, the sample size and percentage of associations with index values of 0 are shown. For each index, observed mean ± *SD* values are given, as are expected means based on random associations among individuals. *P*-values denote significant differences between observed and expected means.

Group size	Association index	No. individuals	% index values = 0	Index values		
				Observed ($\bar{X} \pm SD$)	Expected ($\bar{X} \pm SD$)	P[a]
$n \geq 5$	SR	86	48	0.06 ± 0.08	0.06 ± 0.08	0.87
	HW			0.10 ± 0.13	0.11 ± 0.11	0.16
$n \geq 6$	SR	76	42	0.06 ± 0.08	0.06 ± 0.07	0.58
	HW			0.11 ± 0.13	0.11 ± 0.11	0.004*
$n \geq 7$	SR	66	38	0.07 ± 0.08	0.07 ± 0.07	0.75
	HW			0.11 ± 0.13	0.11 ± 0.11	0.03
$n \geq 8$	SR	52	30	0.08 ± 0.09	0.08 ± 0.08	0.52
	HW			0.13 ± 0.13	0.13 ± 0.12	0.008*
$n \geq 9$	SR	47	26	0.08 ± 0.08	0.08 ± 0.07	0.81
	HW			0.13 ± 0.12	0.13 ± 0.11	0.11
$n \geq 10$	SR	32	24	0.09 ± 0.09	0.09 ± 0.08	0.66
	HW			0.15 ± 0.13	0.15 ± 0.12	0.02

[a] After Bonferroni correction, critical $P = 0.008$ ($\alpha = 0.05$ divided by 6).
* $P < 0.008$.

indicating no consistent relationship among the individuals included in these analyses (Tables 2–4). Across all analyses, mean values for the SR association indices ranged from 0.03 to 0.11 (Tables 2–4); these values are considered "low," or indicative of little association between individuals (Quintana-Rizzo and Wells 2001). Similarly, mean values for the HW association indices were low, ranging from 0.04 to 0.15 (Tables 2–4). Association index values for specific pairs of animals rarely (<4%) reached "moderately high" levels (0.61–0.80) and no "high" levels of association (0.81–1.00) were detected among members of the study population.

Of the 32 mean association index values generated, only 3 (9.3%) differed significantly from random estimates of association among members of the same data set (Tables 2 and 3). In each of these cases, differences between the standard deviations for actual and randomly simulated groups indicated the existence of several stable relationships among members of the study population (see Whitehead 1995, 1999). Stable dyads revealed by these analyses consisted of pairs of unknown sex, 2 males with females, females with other females, and a pair of males. These dyads represented 0.8–2.5% of all possible dyads in our 32 matrices with nonzero association values. These individuals also were observed associating with other members of the population, including unidentified individuals. Although the latter interactions could not be included in our analyses because we could not reliably identify all participants, these observations suggest that even stable associations between individuals are not exclusive.

Table 3.—Association index analyses for marine tucuxi dolphins (*Sotalia guianensis*) in the Cananéia estuary, with data from subarea 2. Both simple ratio (SR) and half-weight (HW) indices were used to analyze data obtained from May 2000 to July 2003. Analyses were conducted for groups containing from ≥5 to ≥10 adults. For each size category, the sample size and percentage of associations with index values of 0 are shown. For each index, observed mean ± *SD* values are given, as are expected means based on random associations among individuals. *P*-values denote significant differences between observed and expected means.

Group size	Association index	No. individuals	% index values = 0	Index values		
				Observed ($\bar{X} \pm SD$)	Expected ($\bar{X} \pm SD$)	P[a]
$n \geq 5$	SR	73	39	0.07 ± 0.08	0.07 ± 0.08	0.68
	HW			0.13 ± 0.14	0.13 ± 0.12	0.14
$n \geq 6$	SR	64	35	0.08 ± 0.09	0.08 ± 0.08	0.59
	HW			0.13 ± 0.14	0.14 ± 0.12	0.05
$n \geq 7$	SR	53	32	0.09 ± 0.09	0.09 ± 0.08	0.48
	HW			0.14 ± 0.14	0.14 ± 0.12	0.001*
$n \geq 8$	SR	43	25	0.09 ± 0.09	0.09 ± 0.08	0.68
	HW			0.15 ± 0.14	0.15 ± 0.12	0.09
$n \geq 9$	SR	33	17	0.11 ± 0.09	0.11 ± 0.08	0.33
	HW			0.18 ± 0.14	0.18 ± 0.12	0.04
$n \geq 10$	SR	26	14	0.11 ± 0.08	0.11 ± 0.07	0.16
	HW			0.18 ± 0.13	0.18 ± 0.12	0.02

[a] After Bonferroni correction, critical $P = 0.008$ ($\alpha = 0.05$ divided by 6).
* $P < 0.008$.

TABLE 4.—Association index analyses for marine tucuxi dolphins (*Sotalia guianensis*) in the Cananéia estuary, with data from groups of ≤10 individuals from all subareas. Both simple ratio (SR) and half-weight (HW) indices were used to analyze data obtained from May 2000 to July 2003. Analyses were conducted for groups containing from ≥5 to ≥10 adults. For each size category, the sample size and percentage of associations with index values of 0 are shown. For each index, observed mean ± *SD* values are given, as are expected means based on random associations among individuals. *P*-values denote significant differences between observed and expected means.

Group size	Association index	No. individuals	% index values = 0	Index values		
				Observed ($\bar{X} \pm SD$)	Expected ($\bar{X} \pm SD$)	P[a]
$n \geq 3$	SR	29	84	0.03 ± 0.07	0.03 ± 0.06	0.22
	HW			0.04 ± 0.11	0.04 ± 0.10	0.35
$n \geq 4$	SR	13	71	0.04 ± 0.07	0.04 ± 0.07	0.35
	HW			0.07 ± 0.11	0.07 ± 0.11	0.12
$n \geq 5$	SR	8	61	0.04 ± 0.06	0.04 ± 0.06	0.55
	HW			0.08 ± 0.10	0.08 ± 0.10	0.05
$n \geq 6$	SR	5	30	0.08 ± 007	0.08 ± 0.07	0.50
	HW			0.14 ± 0.11	0.14 ± 0.12	0.51

[a] After Bonferroni correction, critical $P = 0.013$ ($\alpha = 0.05$ divided by 4).
* $P < 0.013$.

DISCUSSION

To minimize potential biases in our analyses of association indices, 2 precautions were taken. First, a large number of photographs were taken of each group of *S. guianensis* observed. This procedure was intended to identify as many naturally marked individuals per group as possible. Because tucuxi dolphins are small and shy, inhabit murky waters, and are not sexually dimorphic, it was not possible for observers to choose only known individuals. Indeed, most known individuals could not be detected by the naked eye from the research vessel. Therefore, any tucuxi dolphin that surfaced close to the boat was photographed. Second, a strict criterion was established to analyze photographs of dorsal fins. Specifically, only individuals with highly distinguishable dorsal fin notches were included in the catalog, which was reviewed extensively over time. The robustness of results obtained from analyses of association indices depends on the care invested in field efforts, in analyses of photographs, in defining the individuals to be included in the photo catalog, and the procedures chosen to analyze the data. Despite the difficulties imposed by this species' morphology and behavior and the characteristics of its habitat, it was possible to identify and reidentify a considerable number of individuals across time and space. Because most of the dolphins identified were photographed in successive seasons and years, they appear to be residents of the Cananéia estuary, as previously suggested by Santos et al. (2001). Therefore, the data collected during this study appear to be robust and representative of the composition of the population.

The association indices used in this study are the 2 most commonly employed methods for assessing social relationships in cetaceans. The SR index is considered the most accurate when there are no sampling biases and when individuals are identified throughout the study population (Ginsberg and Young 1992). However, factors such as individual variation in behavior, the nature of the habitat, and the abundance of the study species may influence the success of cetacean photo-ID surveys (Würsig and Jefferson 1990). For example, species such as the La Plata dolphin (*Pontoporia blainvillei*)—which has the same color patterns of its murky habitat, is usually found in dispersed small groups, and which spends from 1 to 4 s on the water surface while breathing—may not be good subjects for photo-ID studies. Sampling errors such as misidentifying individuals and including incompletely sampled (i.e., photographed) groups in the analyses can further bias association indices, providing an incomplete and inconsistent depiction of associations among individuals. When the proportion of identified individuals in the community is low, these errors tend to be compounded (Chilvers and Corkeron 2002). Under these conditions, it may be more appropriate to use the HW index, which, compared to the SR index, gives twice as much weight to the co-occurrence of individuals, thereby reducing the possible effects of biases in sampling (e.g., Rossbach and Herzing 1999; Slooten et al. 1993; Smolker et al. 1992). Interestingly, in the present study, the only significant departures from random expectations were detected using the HW index, suggesting the choice of index is important and that the use of multiple indices may reveal patterns not evident from a single analysis.

As indicated above, the proportion of identifiable animals in the population may play an important role in analyses of associations among individuals. In the present study, approximately 30% of the individuals surveyed were naturally marked with distinctive dorsal fins. This percentage is similar to those found in other studies of small cetaceans (e.g., Chilvers and Corkeron 2002; Slooten et al. 1993). Because analyses of association indices only include identifiable animals, the application of these indices to populations with a low proportion of known individuals may be conservative, with a large percentage of associations (i.e., those involving unidentified individuals) going undetected (Chilvers and Corkeron 2002; Slooten et al. 1993). Based on a photo-ID survey including freeze-branded and non–freeze-branded bottlenose dolphins, Owen et al. (2002) determined that unknown individuals probably associate in the same manner as identified animals. These authors argued that unidentified individuals probably included adult males and females, thereby representing both adult categories included in their study. Thus, Owen et al. (2002) concluded that the bias in their data set due to unidentified animals was probably negligible and should not have affected the results of their association analyses. Our results were based solely on known individuals; although our assumption that identifiable and unidentifiable animals behave similarly has not been tested, we have no reason to suspect that associations within the study population differed between these subsets of individuals.

Our data also may have been biased with respect to the sexes of the animals monitored. Individuals were identified by the permanent notches on the border of their dorsal fin, notches that were probably received during social interactions. Odontocete cetaceans, particularly males, tend to use their teeth in aggressive interactions with conspecifics (Heyning 1984; McCann 1974). As a consequence, males may be more likely to acquire distinctive dorsal fin notches. MacLeod (1998) found that in sperm and beaked whales, males were indeed more likely than females to possess scars, a tendency that he attributed to male–male interactions. However, the same was not true for most delphinids, in which rates of scarring were similar for males and females (MacLeod 1998). In these species, the teeth are used primarily for grasping prey and wounds may occur in playful contexts as well as during sexual combat, suggesting that both males and females may acquire dorsal fin notches. Assuming that sources and patterns of scarring are similar in marine tucuxi dolphins, information from other dephinid species suggests that our sample of identified animals was likely not substantially biased toward either sex.

Our analyses of association indices revealed that only 9% of observed outcomes were significantly different from those expected if tucuxi dolphins associate randomly. This finding suggests a lack of consistency in group membership, with strong bonds among individuals other than female–calf pairs being uncommon. The same tendency has been described for several other small cetaceans; with the exception of alliances among males in bottlenose dolphins, all other species studied exhibit brief and variable associations (e.g., Chilvers and Corkeron 2002; Connor et al. 1992; Karczmarski 1999; Owen et al. 2002; Quintana-Rizzo and Wells 2001; Slooten et al. 1993; Smolker et al. 1992; Wells et al. 1987). In contrast, a previous study of *S. guianensis* in the Cananéia estuary described stable associations composed of families (e.g., father–mother–calf, father–pregnant female, father–calf, and mother–calf associations—Monteiro-Filho 2000). This study relied upon visual identification of individuals which, based upon our experiences with the Cananéia population, may have been less reliable than photo-ID of animals. The few stable associations detected during our study did not consist exclusively of family groups, suggesting that other types of relationships occur in this population. Finally, the subgroups comprising larger feeding aggregations varied over the course of this study, providing additional evidence that social relationships in this population may be fluid.

This is the 1st study of marine tucuxi dolphins to use photo-ID and analyses of association indices to characterize the social structure of this species. Our findings, which suggest that associations among *S. guianensis* in the Cananéia estuary may be fluid rather than stable, have potentially important implications for other aspects of the biology of these animals, including their response to increasing encroachment by human activity. A more detailed, longitudinal study of this population should yield additional insights into the nature and duration of social relationships in this species.

Resumo

A organização social é um importante componente da biologia populacional das espécies por influenciar no fluxo gênico, no padrão espacial do uso de área, e nos efeitos de predação ou exploração humana. Um fator importante utilizado como ponto de partida para investigar a estrutura social em mamíferos é a fidelidade de grupo, que por sua vez pode ser quantificada através de índices de associação. Para descrever a organização social de botos-tucuxi marinhos (*Sotalia guianensis*) encontrados no estuário de Cananéia (25°S, 48°W), sudeste do Brasil, índices de associação foram aplicados a dados obtidos com a aplicação da técnica de foto-identificação para caracterizar as relações entre membros desta população. Oitenta e sete dias de incursões foram conduzidos entre maio de 2000 e julho de 2003, resultando na observação direta de 374 grupos distintos. Um total de 138 indivíduos foram identificados entre 1 e 38 dias diferentes. Indivíduos solitários foram raramente observados, enquanto os grupos foram compostos por até 60 indivíduos (média = 12.4 indivíduos ± 11.4 *DP* por grupo). Um total de 29.327 fotografias foi analisado, das quais 6.312 (21.5%) foram consideradas úteis para propósitos de identificações individuais. Os índices de peso-médio (HW) e de razão simples (SR) foram utilizados para investigar as associações entre *S. guianensis* utilizando-se todo o banco de dados, apenas os dados coletados na principal subárea de estudos, e para os grupos compostos por até 10 indivíduos. O método de Monte Carlo foi utilizado para avaliar se as associações eram estatisticamente diferentes do acaso. Apenas 3 (9.3%) de 32 matrizes de associação diferiram significativamente de populações aleatórias. O presente estudo sugere que as associações estáveis não são características para *S. guianensis* no estuário de Cananéia.

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