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Social interactions between tucuxis and bottlenose dolphins in Gandoca-Manzanillo, Costa Rica

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Abstract: Studies measuring the extent of interspecific interactions between dolphin species are rare. We observed free-ranging tucuxis (*Sotalia fluviatilis*) and bottlenose dolphins (*Tursiops truncatus*) to document the frequency of occurrence of interspecific interactions relative to group size and behavioral state. We conducted opportunistic surveys in Gandoca- Manzanillo (9º36'N, 82º35'W), Costa Rica. Of the 71 groups analyzed, 46.5% were comprised only of tucuxis, 21.1% of bottlenose dolphins, and 32.4% of the two species. Social behavior was more frequent in mixed-species groups and in groups larger than four dolphins; foraging was more frequent in single-species groups and in groups smaller than five dolphins. Photographic documentation and sightings of putative hybrids suggest the occurrence of hybridization between both dolphin species. Results indicate that tucuxis and bottlenose dolphins interacted frequently and that these interactions were predominantly social in nature. Future studies will discern whether these interactions result in the development of hybrids.

Resumen: Los estudios que estiman la extensión de las interacciones interespecíficas entre delfines son raros. Nosotros realizamos observaciones de tucuxis (*Sotalia fluviatilis*) y toninas (*Tursiops truncatus*) en estado libre para estimar la frecuencia con la que ambas especies interactúan en relación al tamaño de grupo y el comportamiento. Las observaciones se realizaron en oportunidad desde una embarcación con motor fuera de borda en Gandoca-Manzanillo (9º36'N, 82º35'W), Costa Rica. Analizamos datos de 71 grupos de delfines, de los cuales 46.5% estuvieron formados solamente por tucuxis, 21.2% solamente por toninas y 32.4% por ambas especies. El comportamiento social fue más frecuente en grupos mixtos y en grupos de más de cuatro delfines; el comportamiento alimenticio fue más común en grupos uniespecíficos y en grupos menores a cinco delfines. Evidencia fotográfica y avistamientos de posibles híbridos sugieren que individuos de ambas especies producen híbridos. Los resultados indican que el tucuxi y la tonina interactuaron frecuentemente y que dichas interacciones fueron predominantemente sociales. Futuros estudios resolverán la cuestión de si dichas interacciones producen híbridos.

Keywords: Interspecific interactions, social behavior, *Sotalia fluviatilis*, tucuxi, *Tursiops truncatus*, bottlenose dolphin.

Theoretical and observational evidence suggest that social interactions between different species are uncommon (Arnold and Hodges, 1995). We define social interactions as those in which individuals engage in physical contact of any kind, including in and around the genital area. This broad definition comprises copulation and thus sexual behavior. Although different toothed whale species are often seen associated with each other, the most frequently observed interactions are non-sexual in nature (Corkeron, 1990; Ross and Wilson, 1996; Herzing and Johnson 1997). Yet, sightings of putative hybrids in the wild (Reyes 1996) and the confirmed presence of free-ranging hybrids (Árnason *et al.*, 1991; Baird *et al.*, 1998; Willis *et al.*, 2004) suggest that cetaceans at least occasionally engage in interspecific sexual behavior. Along the Costa Rican shore, tucuxi dolphins (*Sotalia fluviatilis*) occur frequently in and around Gandoca-Manzanillo Wildlife Refuge, where they have been observed interacting with bottlenose dolphins (DiBerardinis *et al.*, 1997). However, the nature of these interactions has not been quantified. Here we document observations indicating that free-ranging tucuxis and bottlenose dolphins (*Tursiops truncatus*) interact frequently and that these interactions are predominantly social in nature.

Gandoca-Manzanillo is an indentation of the southern Caribbean coast of Costa Rica (center at 9º36'N, 82º35'W) that belongs to the Gandoca-Manzanillo Wildlife Refuge (Figure 1). The study site is a partial bay delineated by Punta Mona, a promontory formed by old coral reefs, and the Sixaola River, which marks the border with Panamá and which turbid runoff enters the bay. The 25km^2 study area extends approximately 4km offshore and is characterized by sloping underwater sand shelves on either side of a deep underwater canyon in the center of the area, opposite Gandoca Lagoon.

We conducted 29 opportunistic boat surveys from April through May 2000 and 42 from March through May 2001, totaling 71 observations. Surveys were conducted from a 6m outboard-powered skiff. Each group of dolphins sighted was considered a focal group and followed for a minimum of 15 minutes. Group-follows ended when dolphins were lost or weather conditions prevented data collection. A group was defined as those animals close enough together to be potentially confused with each other by the observer (Mann, 1999). Groups that changed species composition during the sighting were rare (<5%), so we excluded them from analysis. To identify individual dolphins (Würsig and Würsig, 1977), we took photographs of dorsal fins with a reflex camera, a 100-300mm zoom lens, and a film speed of 100-400, depending on light conditions. However, the

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percentage of individuals in a group that we were able to identify was fairly low (<25%). Thus, to avoid pseudo-replication we only analyzed data from the group first sighted during each survey day.

The same person (AB) made the behavioral observations from the boat. We recorded group size, species composition of the group and predominant group activity (Mann, 1999). Predominant group activity was determined based on an assessment of the behaviors in which the majority of the group was engaged (Table 1). These behavioral states were defined after previous experience observing the animals (DiBerardinis *et al*., 1997). Due to the turbidity of the water all observations were made at the surface, based on the assumption that surface behavior was an unbiased sample of below-water activities (Acevedo-Gutiérrez and Parker, 2000). We only analyzed groups for which behavioral state, species composition, and size of groups were stable during the observation period (>90% of total groups observed). The frequency of occurrence of behavioral states was analyzed according to species with a maximum-likelihood test and according to group composition and group size with a log-linear model; group size was analyzed in relation to behavioral state and group composition (mixed-groups and single-species groups) with a two-way ANOVA (Zar, 1996). Given the distribution and average values of group sizes, we classified groups as small (≤4 dolphins), medium (5-8 dolphins), and large (≥9 dolphins).

Tucuxis and bottlenose dolphins were continuously observed in Gandoca-Manzanillo close to shore (<2km; Figure 1). Single-species groups and mixed-species groups were sighted throughout the two study periods. We analyzed data from 71 groups, of which 46.5% were comprised only of tucuxis, 21.1% of bottlenose dolphins, and 32.4% of the two species.

Group sizes of single-species were similar, averaging 5.9 ± 1.00 individuals in bottlenose dolphins and 6.7 ± 0.58 individuals in tucuxis (*t*-test: $t_{40} = -0.67$, $p = 0.505$). The number of dolphins in mixed-groups averaged 10.5± 1.01 individuals, which was significantly larger than the average number of 6.4 ± 0.49 dolphins found in single-species groups (*t*-test: $t_{62} = 4.15$, $p < 0.001$). However, in mixed-species groups the number of bottlenose dolphins was only 3.3 ± 0.34 individuals compared to 6.8 ± 0.73 tucuxi individuals (paired *t*-test: $t_{21} = -4.10$, $p < 0.001$).

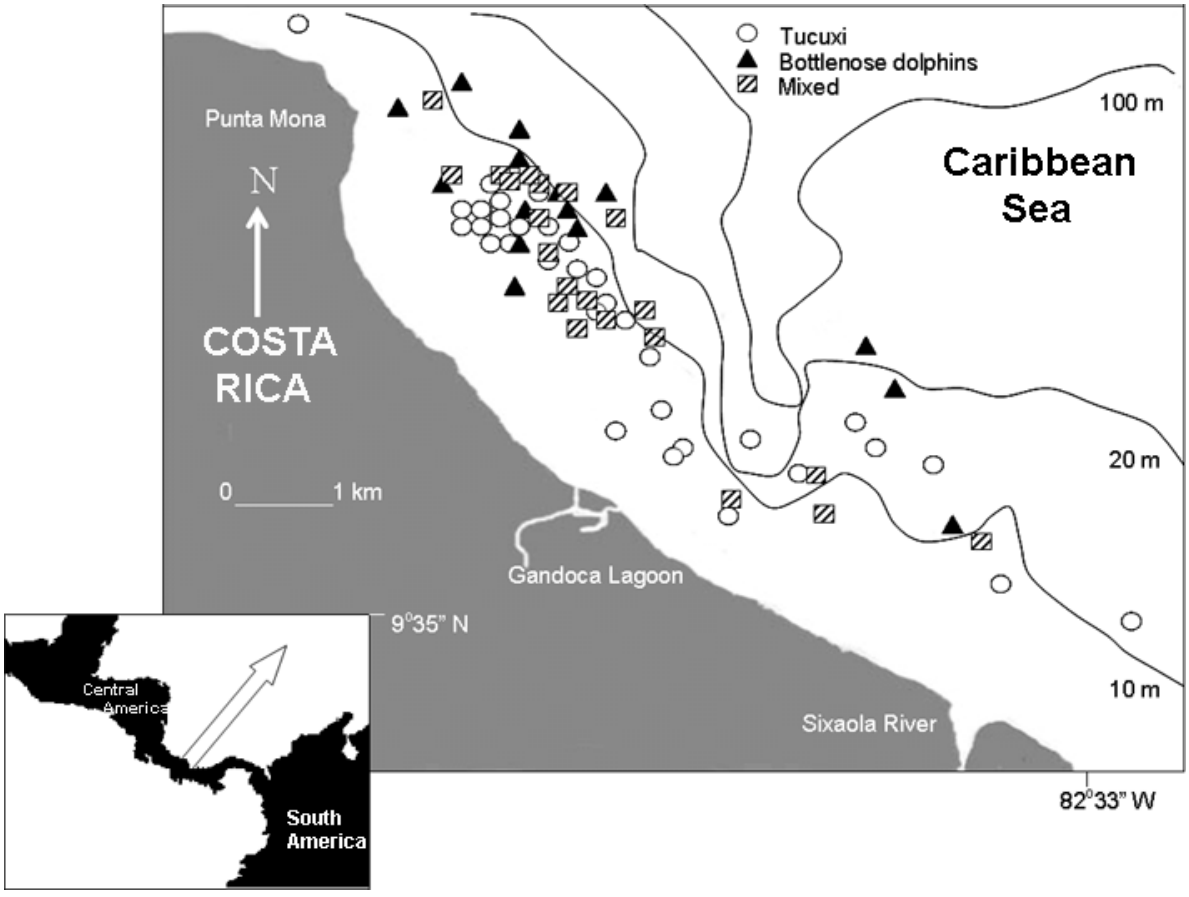

Figure 1. Map of the study site and locations of sightings of tucuxis, bottlenose dolphins, and mixed groups in Gandoca-Manzanillo, southern Caribbean coast of Costa Rica.

The most frequently observed behavioral states both in mixed-groups and single-species groups were foraging and social behaviors; 90.1% of the groups were engaged in one of these two behaviors. Due to low sample size in other states we only analyzed groups engaged in these two behaviors. Social behavior was more frequent in mixed-species groups (68.2%) whereas both tucuxis and bottlenose dolphins foraged more frequently in single-species groups, 93.1% and 69.2% respectively (Maximum-likelihood test: $G_2 = 22.88$, $p < 0.001$). We combined single-species groups of tucuxis and bottlenose dolphins into one category to analyze behavior in relation to group size. The frequency of occurrence of behavior was related to composition and to size of groups, social behavior was more frequently observed in medium and large groups and in mixed-species groups (Log-linear analysis: $\chi^2_4 = 18.97$, $p < 0.001$; Figure 2).

The relationship between group size, behavioral state and species group composition varied between bottlenose dolphins and tucuxis (see details in Figure 3). The number of bottlenose dolphins in a group was related to behavioral state and the presence of tucuxis in the mixed-species group. Bottlenose dolphins were observed in slightly larger numbers when engaged in social behavior than when foraging (Two-way ANOVA: $F_{1,31} = 19.45$, $p < 0.001$). Bottlenose dolphins were also found in larger numbers in single-species groups than in mixed-species groups (Two-way ANOVA: $F_{1,31} = 29.24$, $p < 0.001$). In addition, the number of bottlenose dolphins in a group was related to the interaction between behavioral state and presence of tucuxis. The largest numbers were observed when bottlenose dolphins were socializing in single-species groups (Two-way ANOVA: $F_{1,31} = 14.81$, $p < 0.001$). In contrast, the number of tucuxis in a group was unrelated to behavioral state or presence of

Table 1. Pre-defined group activities of tucuxis and bottlenose dolphins in Gandoca-Manzanillo.

GROUP ACTIVITY	DESCRIPTION
Foraging	Dolphins moving in a multi-directional or circular pattern and occurrence of any of the following: fish scraps on surface, birds circling and diving or catching fish near dolphins, schools of fish on surface near dolphins, or fish jumping out of water in front of dolphins.
Social	Intense physical activity and contact between animals, including rubbing, touching, leaps, genital contact, mounting, body rolling, tail walking.
Resting	Dolphins motionless at surface and group rising up slowly and synchronously to breath and sinking back down. Group members usually surface within 3m of each other, without touching.
Traveling	Dolphins moving in the same direction at a consistent speed over a period of time.
Milling active	Dolphins moving faster than when resting, in a multi-directional or circular pattern, with no sign of foraging or physical contact.

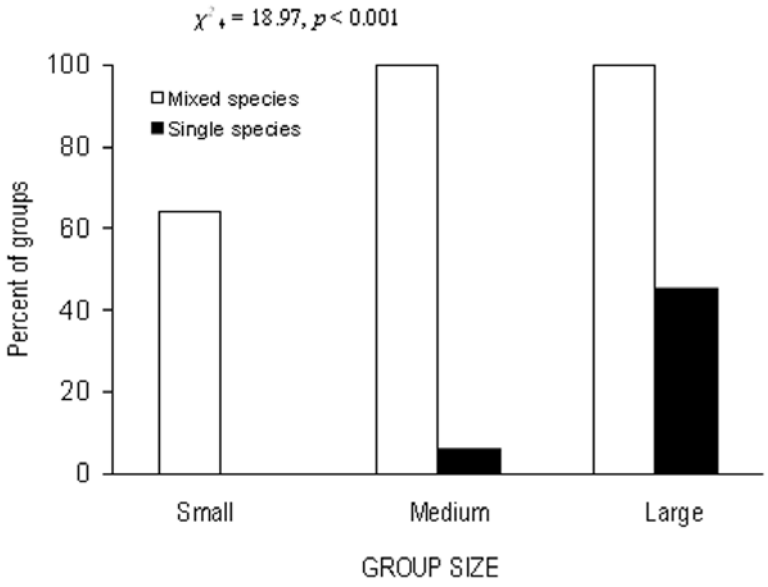

Figure 2. Percentage of occurrence of social behavior relative to group composition and group size. The analysis was conducted on observed frequencies of groups engaged in social and foraging behaviors. Groups were classified as small (≤4 dolphins), medium (5-8 dolphins), and large (≥9 dolphins).

bottlenose dolphins (Behavior, Two-way ANOVA: $F_{1,47} = 0.00$, $p = 0.958$; Group composition, Two-way ANOVA: $F_{1,47} = 0.01$, $p = 0.927$). The number of tucuxis in a group was also unrelated to the interaction between behavioral state and the presence of bottlenose dolphins (Two-way ANOVA: $F_{1,47} = 0.32$, $p = 0.577$).

Tucuxis interacted with bottlenose dolphins throughout the study period and close to a third of the dolphin groups we encountered were comprised of both tucuxis and bottlenose dolphins. This frequency of occurrence is over twice as large as that reported for mixed-species groups of bottlenose dolphins and Atlantic spotted dolphins in Bahamas (Herzing and Johnson, 1997), which is another region where inter-specific dolphin interactions have been regularly observed.

Tucuxis and bottlenose dolphins were predominantly engaged in foraging activities when in single-species groups (Figures 1 and 2), in a place where outflow from the Sixaola river and the steep slope near shore apparently provides a rich feeding ground for either dolphin species, as well as for a variety of birds. Consequently, the overlapping ranges of the tucuxis and bottlenose dolphins may be due to their mutual use of a small, localized coastal area as a feeding ground. However, it is currently unclear if tucuxis and bottlenose dolphins exploit different prey types or sizes in the study area. When in single-species groups, tucuxis spent a larger proportion of their time foraging than did bottlenose dolphins (Figure 2). Group size of bottlenose dolphins was related to behavioral activity and to presence of members of the other species, but such variation was not observed for tucuxis (Figure 3). Since the number of bottlenose dolphins engaged in social behavior was smaller in mixed groups than in single-species groups, it appears that only a few bottlenose dolphin individuals departed their group to join mixed groups whereas the entire tucuxi group joined mixed groups. Focal follows of individual tucuxis and bottlenose dolphins will assist in clarifying this question.

Tucuxis and bottlenose dolphins also interact in southern Brazil, the southern limit of tucuxi distribution (M.C.Santos[4], pers. comm.). Gandoca-Manzanillo and southern Brazil are

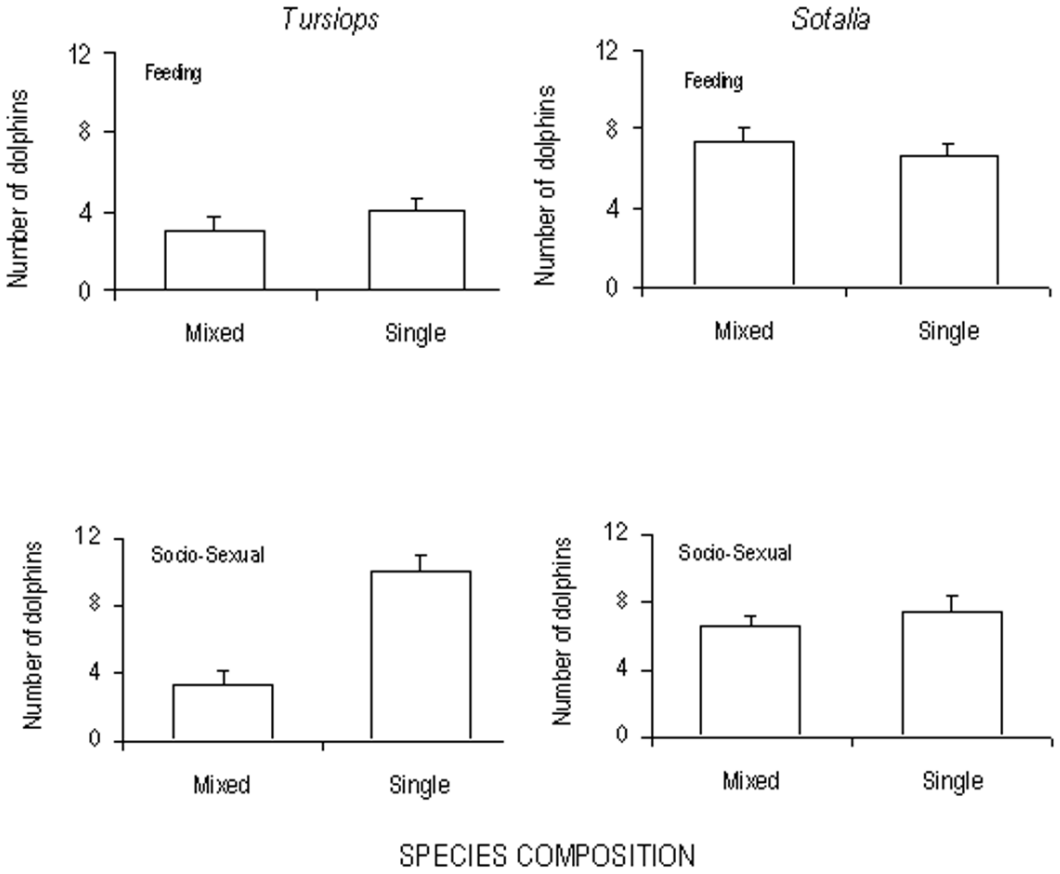

Figure 3. Number of dolphins of each species relative to behavior and species composition. Error bars indicate SEM. See text for statistical results.

[4] Dr. Marcos César de Oliveira Santos, personal communication, June 2005. Projeto Atlantis – Universidade de São Paulo, Instituto de Biociências, Departamento de Ecologia Geral, São Paulo, Brazil

unique in this regard since tucuxis in other regions appear not to interact with other cetacean species foraging in the same or adjoining areas (Vidal *et al*., 1997; Santos *et al*., 2000; Edwards and Schnell, 2001). Because single-species groups engaged predominantly in feeding activities while mixed-species groups engaged predominantly in socializing (Figure 2), we assume that there was a switch in behavior when groups comprised of tucuxis and bottlenose dolphins formed. Because socializing also increased with group size (Figure 2), it is possible that this switch in behavior was partly related to the increased number of individuals in the newly formed groups.

We were unable to determine the specific instances in which social interactions between tucuxis and bottlenose dolphins were either aggressive or amicable. However, we observed multiple instances of aggressive behavior, including biting, body slams, and fast speed pursuits, which have also been reported in other studies of odontocetes (Corkeron, 1990; Ross and Wilson, 1996; Herzing and Johnson, 1997). These observations suggest that the interactions between tucuxis and bottlenose dolphins could have been competitively- or aggressively-based, an explanation that fits within the aggressive behavior of tucuxis in captivity (Terry, 1983, 1986) and bottlenose dolphins in the wild (Connor *et al*., 1992; Ross and Wilson, 1996; Herzing and Johnson, 1997). It is unclear if one dolphin species dominates the interactions in Gandoca-Manzanillo. Body size would favor bottlenose dolphins, as it appears to occur in the interactions between bottlenose dolphins and Atlantic spotted dolphins (Herzing and Johnson, 1997), yet number of individuals would favor tucuxis. Observations of dolphin chases or displacement from a particular site, or photographic documentation of scars incurred before and after an interaction might clarify whether dominance occurs.

Currently there are not enough data on individual identification and behavioral transitions to determine the proximate mechanisms behind the social interactions between tucuxis and bottlenose dolphins, nor if these interactions are unique to a specific set of individuals or more widely distributed. Photographic documentation of two hybrids and sightings of close to six putative hybrids suggest that copulation and hybridization does occur in the study site (Figure 4). Because DNA studies are required to ascertain the conclusive existence of hybrids (Árnason *et al*., 1991; Baird *et al*., 1998; Willis *et al*., 2004), the existence of such individuals in Gandoca-Manzanillo requires further research.

Confirmed cetacean hybrids in the wild have been reported for several species, for example blue and fin whales (*Balaenoptera musculus* and *B. physalus*) (Árnason *et al*., 1991; Árnason and Gullberg, 1993) and harbor and Dall's porpoises (*Phocoena phocoena* and *Phocoenoides dalli*) (Rosel *et al*., 1995; Baird *et al*., 1998; Willis *et al*., 2004). Twenty-five dolphin hybrids have been reported in captivity, all of which involve bottlenose dolphins and six other dolphin species (Bérubé, 2002). Most hybrids do not survive to produce offspring, however a first-generation hybrid between a bottlenose dolphin and a false killer whale (*Pseudorca crassidens*) has given birth twice after mating with a bottlenose dolphin (Duffield, 1998), suggesting that dolphin species that are not closely related might produce viable and fertile hybrids. Instances of hybridization are more common between closely related taxa (Bérubé, 2002). However, among delphinids tucuxis only show affinity with rough-toothed dolphins (*Steno bredanensis*) and are distantly related to bottlenose dolphins (LeDuc *et al*., 1999). As a consequence, if the socio-sexual interactions between tucuxis and bottlenose dolphins result in hybridization, these two species will represent the most distantly related cetaceans in which hybrids occur in the wild.

Figure 4. Photograph of a putative tucuxi and bottlenose dolphin hybrid. Photo: Paul Forestell.

In conclusion, Gandoca-Manzanillo is a unique area in which tucuxis and bottlenose dolphins engage on a frequent basis in social interactions. Future studies will discern the proximate and ultimate mechanisms involved in these interactions as well as whether these interactions result in the development of hybrids.

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