



Fission-fusion dynamics of Guiana dolphin (*Sotalia guianensis*) groups at Pipa Bay, Rio Grande do Norte, Brazil

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ABSTRACT

Fission-fusion dynamics seem to reflect individual decisions as well as temporal and spatial variations in the organization of groups of the same species. To understand the group dynamics of the Guiana dolphin, *Sotalia guianensis*, at Pipa Bay, Brazil, we investigated the three dimensions of a fission-fusion social system: (1) variation in spatial cohesion, (2) variation in party size, and (3) variation in party composition. Sampling took place from December 2007 to February 2009 over 176 d and we analyzed the behavioral patterns of 658 groups. Within subgroups, animals remained cohesive, particularly in groups of adults and calves. Greater cohesion was also observed during resting and fission-fusion rates were higher during milling and feeding. Groups composed of adults and juveniles showed a higher dynamics index (group size variation as a function of time) than groups composed only of adults and the fission-fusion rate was higher during dry periods. Guiana dolphin groups frequently changed their group size and composition every 20 min on average. Taking these factors into consideration, we suggest that the Guiana dolphin demonstrates fission-fusion dynamics, a pattern of behavior similar to what has been observed in other coastal odontocete species, such as *Tursiops* spp. and *Lagenorhynchus obscurus*.

Key words: fission-fusion, Guiana dolphin, party composition, party size, social dynamics, social group, *Sotalia guianensis*, spatial cohesion.

In models that investigate animal groupings, interindividual distance can be interpreted as a result of the attractive and repulsive forces between individuals, which reflect the costs and benefits of close association between conspecifics (Krause and Ruxton 2005, Giraldeau 2008). Optimal group size, composition, and interindividual spacing do not always favor all individuals of the group in the same way. The resulting group may not be optimal for any of its members (Ranta *et al.* 1993, Conradt and Roper 2000). However, if the change in group composition has a low energy cost (due to either low predation risk, high food abundance, or low movement costs), the group may have fluidity of size and composition, with individuals constantly moving and groups constantly being created, changed, or dissolved (Ranta *et al.* 1993).

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Animal social groups characterized by high fluidity in subgroup (smaller social units) composition and size are labeled fission-fusion societies. Fission-fusion reflects variation of a group's spatial and individual cohesion over time. Seasonal availability of food can influence fission-fusion dynamics, with larger groups being formed during periods of or in areas of high food availability and smaller groups during periods of low food availability (Aureli *et al.* 2008). Recently, it has been argued that fission-fusion societies should be interpreted not in categorical terms, but on a continuous scale, with all social groups displaying some degree of fission-fusion (Aureli *et al.* 2008). This proposal allows many animal groups to be characterized by their degree of fission-fusion dynamics, and incorporates the degree of spatiotemporal cohesion in the social system. For such an analysis, Aureli *et al.* (2008) proposed a structure with three dimensions for the evaluation of the social system in a given environment: (1) variation in spatial cohesion, (2) variation in party size, and (3) variation in party composition among group members. This type of three-dimensional analysis allows classifying species or populations of a single species according to their degree of fission-fusion. Characterizing societies by their degree of fission-fusion dynamics is a good indicator of individual decisions about association patterns, in accordance with the cost-benefit balance associated with group life (Pearson 2009, Tsai and Mann 2013). Among mammals, fission-fusion social systems have been described for a few species including: primates (*e.g.*, *Pan troglodytes*, *Ateles paniscus*: Symington 1990, and *Pongo pygmaeus*: van Schaik 1999), bats (*e.g.*, Kerth and König 1999), deer (*e.g.*, Conradt and Roper 2000), elephants (*e.g.*, Couzin 2006), hyenas (*e.g.*, Smith *et al.* 2008) and dolphins (*e.g.*, *Stenella longirostris*: Norris *et al.* 1994; *Cephalorhynchus bectori*: Slooten 1994; *Tursiops* sp.: Connor *et al.* 2000; *Delphinus* spp.: Bruno *et al.* 2004; *Lagenorhynchus obscurus*: Pearson 2009; *Orcaella heinsobni* and *Sousa chinensis*: Parra *et al.* 2011).

Fission-fusion dynamics may reflect, among other factors, a necessary requirement for reducing competition for food and predation risk (*e.g.*, Connor *et al.* 2000, Heithaus and Dill 2002). For example, *Tursiops aduncus* in Shark Bay, Australia, form small groups while foraging, probably to reduce competition between them, and form large groups while resting to reduce the risk of predation (Heithaus and Dill 2002). However, *L. obscurus*, in Admiralty Bay, New Zealand, form larger groups during foraging, and more dolphins joined groups during this behavior. While resting, socializing, and traveling, dolphins showed a different degree of fission-fusion dynamics, with large temporal variation in group size and spatial cohesion (Pearson 2009).

The Guiana dolphin, *Sotalia guianensis*, is a coastal species commonly associated with bays and estuaries. Based on analyses of photo-identified individuals, two recent papers convincingly argue that these animals do not form stable associations, with most dyads presenting association indices indicative of casual acquaintances (*i.e.*, individuals associate longer than time lag d but disassociate and might reassociate) (Santos and Rosso 2008, Cantor *et al.* 2012). This lack of preferred associates seems to differ from the pattern observed in bottlenose dolphins, *Tursiops* spp., in which males and females present preferred partners, although limited in different ways: adult males forming long-term associates regardless of behavioral context and adult females forming behavior specific associations (Gero *et al.* 2005).

To understand the group dynamics of the Guiana dolphin, we investigated the three dimensions of the fission-fusion social system proposed by Aureli *et al.* (2008): spatial cohesion, temporal variation in group size, and temporal variation in group composition using short time span observations and taking into account the

behavioral context. Based on the patterns described for bottlenose dolphins (Gero *et al.* 2005) and ungulates (Conradt 1998), a close relative of cetaceans (*e.g.*, Lusseau 2003a), we predicted that: (1) spatial cohesion will be greater in adult-calf groups, due to offspring dependency, and while resting, due to the vulnerable state of the animals; (2) the fission-fusion rate will be greater during milling and feeding, due to interference or exploitation competition; (3) the fission-fusion rate will be greater in adult-juvenile groups due to the higher cost of behavioral synchronization between them than between same size animals; and finally (4) the fission-fusion rate will differ between seasons as a response to environmental changes and fluctuating food availability.

MATERIALS AND METHODS

Study Site

The study area is located at Madeiro Beach ($\sim 4 \text{ km} \times 0.6 \text{ km}$, 240 ha), Pipa Bay ($6^{\circ}13'S$, $35^{\circ}04'W$), on the southern coast of Rio Grande do Norte, Brazil, in a reserve protected for sustainable use (see Lunardi and Ferreira 2013). It is directly influenced by tidal variations and reaches depths of about 6 m. The region is characterized by two distinct seasons: dry season, September to February, and rainy season, March to August.

Data Collection

Systematic observations of the Guiana dolphin were made from an observatory located on cliffs about 25 m above sea level that surround Madeiro Beach. Sampling occurred from December 2007 to February 2009 between 0600 and 1600, under favorable observation conditions (clear sky or partially cleared, low intensity wind and no rain) with the help of Bushnell binoculars (7×50), a palmtop computer, and a stopwatch.

When the Guiana dolphins are in this bay, they form subgroups that are easily observed by the naked eye: subsets of individuals cluster together and remain apart from other clusters of individuals usually by more than 200 m. These clusters of individuals commonly engage in different behaviors and follow different routes within the bay (see Tosi and Ferreira 2008, 2010). We considered "a focal group" to be a number of dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same behavior (Shane 1990), in a maximum radius of 20 m from each other. Groups were only investigated when they were visually isolated from other groups by at least 200 m. We used known measurements of boats ($\sim 7 \text{ m}$, 12 m, 16 m), kayaks (3.7 m), and surfboards ($\sim 2 \text{ m}$) to get an estimate of intra- and intergroup distances.

Using focal groups and 2 min scan sampling method (Mann 1999), predominant group behavior ($\geq 50\%$ of the individuals at the surface) was recorded as one of five mutually exclusive states (Lunardi and Ferreira 2013): (1) milling: nondirectional swimming inside the bay; (2) feeding: pursuit, lunging, handling and/or ingestion of prey, group members move in various directions, without apparent cooperation, or they corner the prey, directing it toward shallow water; (3) traveling: uniform and directional movement, resulting from the animal's change of position from one area to another; (4) socializing: high levels of activity and intense physical contact between

individuals, animals spend more time at the surface; and (5) resting: slow traveling or no traveling, with, in most cases, synchronized intervals between dives.

The 2 min interval is the minimal interval that ensures safe characterization of the behavioral state (because it normally comprises three breathing bouts) and also ensures sampling independency for statistical analyses (Queiroz and Ferreira 2009). We recorded the behavior of the focal group closest to the observatory. When a dolphin group separated during a focal observation, we continued to record the behavior of the subgroup with the higher number of individuals. Sampling was discontinued when the animals left the field of vision of the observer. Three age-size classes were used: adult (~170 cm, see Rosas and Monteiro-Filho 2002), juvenile, and calf (about 3/4 and 1/2 of the body length of an adult animal, respectively). A prior test of reliability (Kappa test = 0.95, $n = 60$, CI 95% = 1.0–0.8, $P < 0.001$) was performed between an observer on the cliff top and an observer on the boat to test the reliability of the estimates of the three size classes. For each data sample, groups were classified into five types based on composition: adults only; juveniles only; adults and juveniles; adults and calves; and adults, juveniles, and calves.

To determine spatial cohesion, estimates of the distance (d) for each dyad, in each focal group, were classified into three categories (modified from Bejder *et al.* 2006) based on the approximate length of an adult animal: ≤ 2 m (~ up to one adult body), $2 \text{ m} < d \leq 10 \text{ m}$ (~>1 and up to 5 adult bodies), and $10 \text{ m} < d \leq 20 \text{ m}$ (~>5 and up to 10 adult bodies). As a reference, we used the group's center to estimate the distance between individuals in each focal group. When the estimated distance between individuals in a large group (>5 dolphins) became difficult to observe, the group was not sampled.

The temporal variation in group composition was investigated according to an index proposed in this study (group size variation as a function of time), here named "dynamics index." For analysis of temporal variation in group composition, we evaluated only groups that did not change their composition during the period of focal observation.

The dynamics index was calculated using the following formula:

$$DI = \frac{En + Ex}{t}$$

where DI is the dynamics index, $En + Ex$ is the number of 2 min samples during which there was individual's entry into and/or exit (dolphin moved beyond the 20 m exclusion) of the focal group, and t is the number of consecutive sampling intervals.

This index indicates the degree of variation in group size at every sampling interval (2 min), and it ranges from 0 (focal groups with no individual entrances or exits) to 1 (focal groups with an entrance and/or exit every 2 min). In this study, we termed "stable groups" groups with no entrances or exits of dolphins during the period of observation ($DI = 0$) and "unstable groups" groups with at least one entrance and/or exit of dolphins during the period of observation ($0 < DI \leq 1$).

Analysis

We included in the analysis only sampling periods ≥ 10 min (minimum of five samples) per group. Because the normality assumption of group size, spacing distance, and dynamics index classes data was rejected, nonparametric (Zar 1999) or statistics based on bootstrap (Adams and Anthony 1996) were also used for the

analysis. The level of statistical significance was defined at $P < 0.05$. To test prediction 1 (spatial cohesion will be greater in adult-calf groups, and while resting) and prediction 2 (fission-fusion rate will be greater during milling and feeding) we used a straightforward chi-square analysis and the adjusted residual (AR). To test prediction 3 (fission-fusion rate will be greater in adult-juvenile groups) we also used chi-square analysis and the adjusted residual (AR) and one-factor analysis of variance in which the dynamics index was the dependent variable and the factor was group composition (based on 1,000 bootstrap samples). Additionally, we used a two-factor analysis of variance (independent measures) in which the dynamics index was the dependent variable, while the factors were composition and predominant group behavior during the observation period (homogeneity of the variances: Levene's, $F = 1.443$, $P = 0.14$). However, prediction 3 (fission-fusion rate will be greater in adult-juvenile groups) was not investigated for groups of juveniles ($n = 1$) and for groups of adults, juveniles, and calves ($n = 24$) due to the small sample sizes. Finally, to test prediction 4 (fission-fusion rate will differ between seasons), the Spearman correlation test was conducted between the dynamics index and the number of individuals in the group, as well as between the feeding and rainfall. The Parametric t test (based on 1,000 bootstrap samples) was used to test differences in group size and in the dynamics index for dry *vs.* rainy seasons (we took a data sample of the same size for each month). Details about the sample sizes used in these analyzes are shown in Table 1.

Table 1. Statistical tests and description of sample sizes used in the analysis of fission-fusion dynamics of Guiana dolphin at Pipa Bay, Brazil.

Analysis	Sample size	Description of the sample size	Statistical test
Composition group frequency	$n = 27,928$	Total number of 2 min time samples	–
Spatial cohesion, group composition, and behavioral context	$n = 93,552$	Total number of dolphins in the three distance ranges every 2 min	Chi-square
Correlation: dynamics index <i>vs.</i> number of dolphins in the group	$n = 658$	Total number of groups observed	Spearman
Fission-fusion <i>vs.</i> behavior state	$n = 4,826$	2 min time samples when there were individual's entry into and/or exit of the focal group	Chi-square
Fission-fusion <i>vs.</i> group composition	$n = 254$	Number of groups that did not change their composition during the period of focal observation	Chi-square
Group median size <i>vs.</i> dry and rainy seasons	$n = 12,357$	Total number of dolphins every 2 min	t -test
Correlation: feeding behavior <i>vs.</i> annual rainfall	$n = 12$	Months of the year	Spearman
Dynamics index <i>vs.</i> dry and rainy seasons	$n = 156$	Number of groups (to validate the comparison between the dry and rainy seasons, we took samples of equal size for each month at each station [$n = 26$ groups \times 6 mo = 156 groups])	t -test

RESULTS

A total of 658 groups was observed over 176 sampling days for a period of 933 h at Madeiro Beach. Mean focal observation duration $\bar{x} \pm SD$ was 84.9 ± 76.8 min (range 10–240 min, $n = 658$). Group sizes ranged from 2 to 19 individuals ($\bar{x} \pm SE = 3.4 \pm 0.01$, mode = 2). With regard to group composition, 42% ($n = 11,732$ time samples) contained adults and juveniles; 21.6% ($n = 6,038$), adults and calves; 18.8% ($n = 5,244$), adults, juveniles, and calves; 17% ($n = 4,742$), only adults; and 0.6% ($n = 172$), only juveniles.

Spatial Cohesion, Group Composition and Behavioral Context

Figure 1 shows the frequency of occurrence of three distance ranges (≤ 2 m, $2 \text{ m} < d \leq 10$ m, and $10 \text{ m} < d \leq 20$ m) kept between individuals, according to group composition. Regardless of composition type, in more than 50% of the time samples, all individuals within a focal group remained very cohesive, staying at a distance of up to 2 m apart from each other. Groups composed of adults and calves remained very cohesive (≤ 2 m) in 74% of the time samples, while groups composed only of adults or only of juveniles tended to spread more (total number of dolphins of the three distance ranges every 2 min = 93,552, $\chi^2 = 827.6$, $df = 8$, $-2.8 > AR > 2.8$, $P < 0.001$).

The frequencies of the three distance ranges kept between individuals during each behavioral state are shown in Figure 2. Greater cohesion (≤ 2 m) was observed between individuals while resting, traveling, and socializing. However, individuals tended to stay further apart during feeding (total number of dolphins of the three

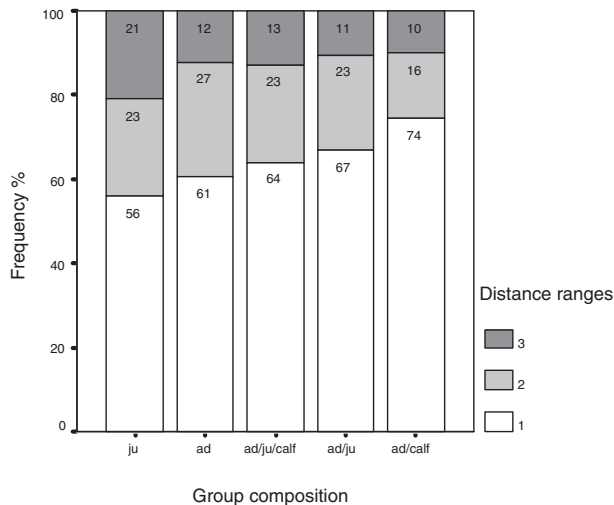


Figure 1. Frequency of occurrence of three distance ranges (1: ≤ 2 m, 2: $2 \text{ m} < d \leq 10$ m, and 3: $10 \text{ m} < d \leq 20$ m), kept between Guiana dolphins in the group, according to the following compositions: ju (juveniles), ad (adults), ad/ju/calf (adults, juveniles, and calves), ad/ju (adults and juveniles), and ad/calf (adults and calves) at Madeiro Beach, Brazil. The numbers inside the bars indicate the frequency of occurrence.

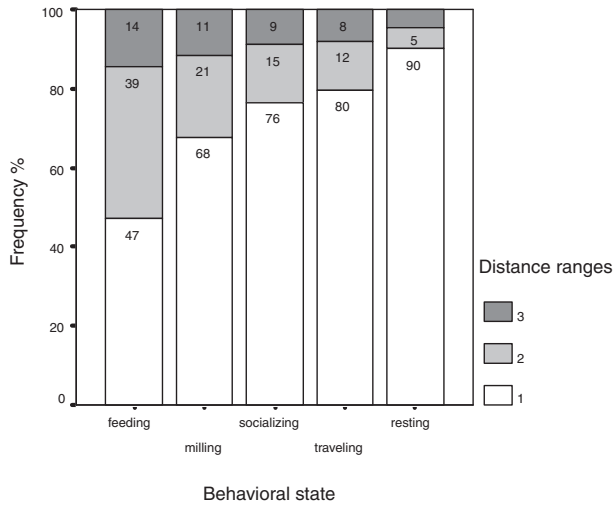


Figure 2. Frequency of occurrence of three distance ranges (1: ≤ 2 m, 2: $2 \text{ m} < d \leq 10$ m, and 3: $10 \text{ m} < d \leq 20$ m), kept between Guiana dolphins in a group, during the observation of five behavioral states: feeding, milling, socializing, traveling, and resting. The numbers inside the bars indicate the frequency of occurrence.

distance ranges every 2 min = 93,552, $\chi^2 = 3,967.8$, $df = 8$, $-2.8 > AR > 2.8$, $P < 0.001$).

Fission-fusion and Behavioral State

To assess the temporal variation in group size, we investigated the frequency of individuals that entered and/or exited the focal group during the observation period. New individuals joined the group mainly during feeding ($n = 4,826$ time samples, $\chi^2 = 117.9$, $df = 4$, $AR = 9.9$, $P < 0.001$), and left during milling ($AR = 8.4$) and resting ($AR = 3.3$; Fig. 3).

The dynamics indices ranged from 0 to 0.67, with $\bar{x} \pm SE = 0.14 \pm 0.004$. Although we obtained a statistically significant correlation between the dynamics index and number of individuals ($n = 658$ groups, Spearman $r = 0.078$, $P = 0.046$), the correlation coefficient was weak.

Fission-fusion and Group Composition

More than 50% of all groups of adults and adults and calves remained stable ($DI = 0$, *i.e.*, no entry or exit event), while only 33.3% of groups composed of adults and juveniles showed $DI = 0$ ($AR = -3$; Fig. 4). However, these group compositions did not show statistically significant differences between other DI classes ($n = 254$ groups, $\chi^2 = 14.6$, $df = 10$, $P > 0.05$). Groups composed only of adults showed a lower DI (mean $DI \pm SE = 0.05 \pm 0.01$) than groups composed of adults and juveniles ($n = 254$ groups, mean $DI \pm SE = 0.09 \pm 0.01$, $F = 4.58$, $df = 2$, $P = 0.006$). However, the DI of groups composed of adults and calves did not differ from that of groups composed only of adults or of adults and juveniles (mean $DI \pm SE = 0.06 \pm 0.01$, $P > 0.05$).

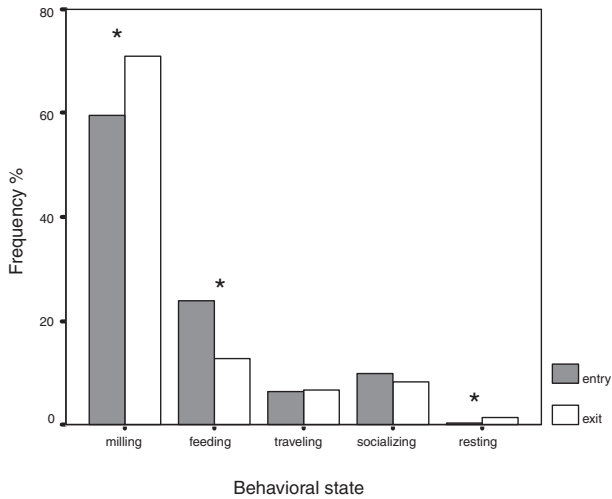


Figure 3. Frequency of occurrence of Guiana dolphin individuals' entry and exit events in the groups, during the observation of five behavioral states. Asterisk indicates the statistically significant differences between entry and exit of dolphins in the focal group.

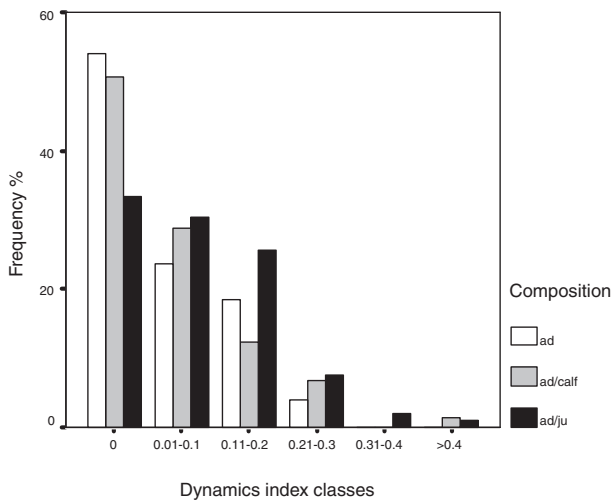


Figure 4. Frequency of occurrence of dynamics index (group size variation as a function of time) classes in three different Guiana dolphin compositions: ad (adults), ad/calf (adults and calves), and ad/ju (adults and juveniles).

We recorded a weak, but statistically significant, interaction between group composition and behavior regarding the *DI* ($n = 254$ groups, adjusted $r^2 = 0.086$, $F = 2.528$, $df = 7$, $P = 0.016$; Fig. 5). Higher *DI*s were observed in groups of adults and juveniles, especially during socializing and milling, while groups of adults presented lower *DI*s for all behaviors except feeding. In this analysis, statistically significant

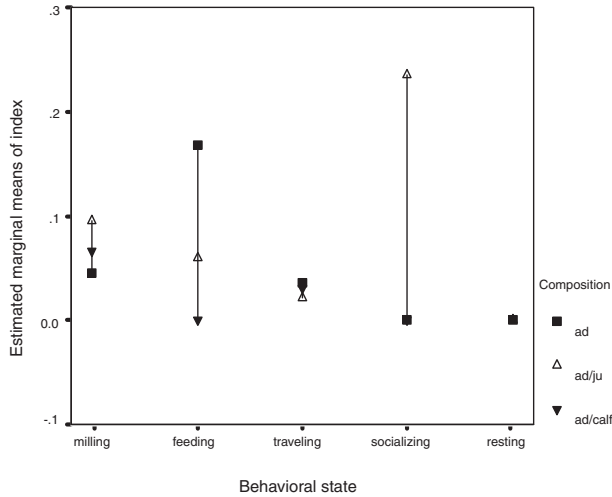


Figure 5. Estimated marginal means of the dynamics index (group size variation as a function of time) according to the predominant behavioral state of the group and the three composition types: ad (adults), ad/ju (adults and juveniles), and ad/calf (adults and calves). Statistically significant differences were found between groups of adults and of adults and juveniles and between milling and feeding and milling and resting.

differences were found between groups of adults and of adults and juveniles, with respect to the *DI* (Tamhane *post hoc* test, $P = 0.006$). Groups of juveniles and of adults, juveniles, and calves were not assessed due to small sample sizes.

Fission-fusion and Seasonal Fluctuations

The number of individuals in the groups differed between the two seasons. Group median size was greater in the rainy season and lower during the dry season ($n_{\text{rainy}} = n_{\text{dry}} = \text{total number of dolphins every 2 min} = 12,357$, $t = -13.77$, $df = 24,712$, $95\% CI_{\text{rainy}} = 3.6\text{--}3.7$, $95\% CI_{\text{dry}} = 3.3\text{--}3.4$, $P < 0.001$; Fig. 6). Only the frequency of feeding and socializing behaviors differed between the seasons. Feeding was most common during the dry season ($n_{\text{dry}} = n_{\text{rainy}} = 12,357$, $\chi^2 = 93$, $df = 1$, $P < 0.001$; Fig. 7) and we obtained a statistically significant negative correlation between the sum of the feeding sample and the annual rainfall ($n = 12$, Spearman $r = -0.74$, $P < 0.001$). Socializing was most common during the rainy season ($n_{\text{dry}} = n_{\text{rainy}} = 12,357$, $\chi^2 = 60.8$, $df = 1$, $P < 0.001$; Fig. 7). The *DI* also differed between the seasons ($n_{\text{dry}} = n_{\text{rainy}} = 156$ groups, $t = 2.66$, $df = 310$, $P = 0.008$), with a higher *DI* for the dry season ($95\% CI = 0.15\text{--}0.19$), than for the rainy season ($95\% CI = 0.12\text{--}0.15$).

DISCUSSION

Spatial Cohesion, Group Composition and Behavioral Context

According to our data, in over 50% of the sampling periods of focal groups, Guiana dolphins tended to be cohesive; individuals, for the most part, remained up

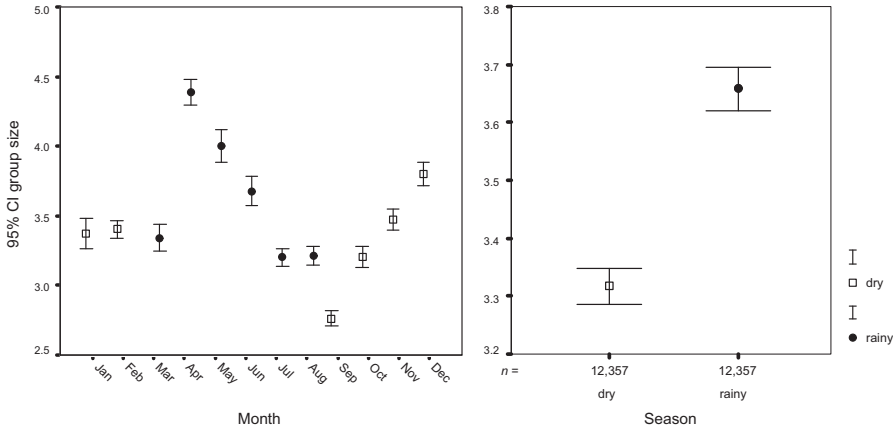


Figure 6. Groups size mean of Guiana dolphin during sampling intervals of 2 min during two seasons, dry and rainy, from January to December 2008. Group size mean was higher during the rainy season than dry season.

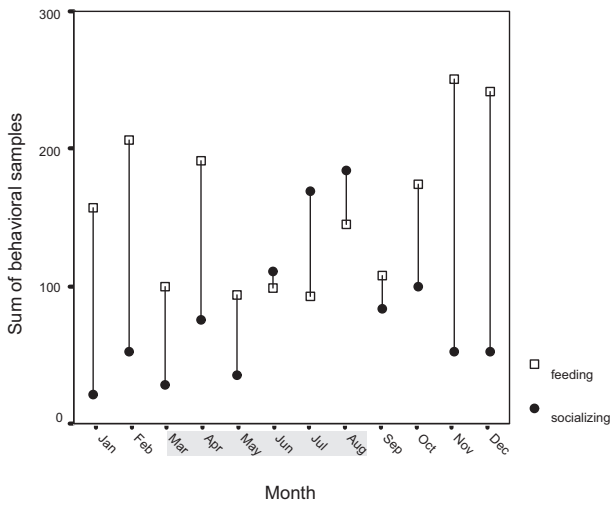


Figure 7. The sum of feeding and socializing sampling during 2 min intervals in two seasons, dry (shaded field) and rainy (unshaded field), from January to December 2008. Feeding was more common in the dry season, while socializing was more common in the rainy season.

to 2 m apart. These data confirm and refine what has already been described about the Guiana dolphin. Individuals present at Madeiro Beach can form up to six subgroups with more than 100 m between them and while in the subgroups, 80% of the individuals remain within 20 m from each other (Tosi and Ferreira 2010).

Confirming our first prediction, adults and calves remained the most cohesive compared to other group compositions investigated. Several authors have described a prolonged nursing period, strong adult-calf bond and infant position in dolphins as

an important mechanism for survival of calves (*e.g.*, Smolker *et al.* 1993, Gubbins *et al.* 1999). Therefore, we expected that, due to the strong dependence of calves on adults, they would remain close to each other most of the time.

Also according to the first prediction, a high degree of cohesion among individuals was observed while resting. Greater cohesion during resting may represent an important defense strategy because in this state the animals are more vulnerable to approaching boats (*e.g.*, Lusseau 2003*b*) and swimmers. However, we also recorded a high degree of cohesion among individuals during socializing and traveling. Greater cohesion during socializing may be due to the intrinsic characteristic of this behavior, which is the constant physical contact between group members. Traveling was mainly observed when dolphins entered and exited the bay. It is likely that outside the bay individuals are more vulnerable hence becoming more cohesive during travel. There are records of two potential predators in the area, the tiger shark (*Galeocerdo cuvier*) and the hammerhead shark (*Sphyrna lewini*) in Formosa Bay, only 20 km from Madeiro Beach, Pipa Bay (Garcia 2006). Groups were less cohesive during feeding. This behavior is frequent in Madeiro Beach, and is most common in solitary animals or in groups of two individuals (Tosi and Ferreira 2008). This pattern suggests that the proximity between individuals in a group, associated with prey availability and patch size, may influence feeding behavior and increase competition, in a pattern of proximity between individuals more similar to that described for *T. aduncus* (Heithaus and Dill 2002) than for *L. obscurus* (Pearson 2009).

Fission-fusion and Behavioral State

The Guiana dolphin groups observed at Madeiro Beach ranged from 2 to 19 individuals ($\bar{x} \pm \text{SE} = 3.4 \pm 0.01$). This is small compared to the average group size observed in other coastal areas in Brazil, such as Guanabara Bay, RJ (13, Azevedo *et al.* 2005); Cananéia, SP (12.4, Santos and Rosso 2008); and North Bay, SC (29, Daura-Jorge *et al.* 2005). Two factors may account for this group size difference between Guiana dolphin populations in Brazil: (1) differences in the definition of what a group would be (see Azevedo *et al.* 2009), and (2) the specific ecological conditions of the group's habitat. For example, Daura-Jorge *et al.* 2005 defined "group" as any aggregation of dolphins composed of smaller social units (called subgroups), while in this study "group" was defined as a number of dolphins observed in apparent association and moving in the same direction in a maximum radius of 20 m from each other (equivalent to one subgroup). Additionally, the presumed low resource availability (based on traditional knowledge of fishermen) and the bay's small size compared to other areas may be directly influencing group size at Madeiro Beach. The smaller group size observed for *T. truncatus* in Drowned Cayes, Belize, is likely due to the apparent low risk of predation, coupled with low density of food resources (Kerr *et al.* 2005). Small groups of *T. truncatus* in the Adriatic Sea have higher food intake rates as a result of limited prey availability and, therefore, better chances of prey capture (Bearzi *et al.* 1997). For transient killer whales the energy obtained varied with group size. Groups of three individuals had a higher energy rate per individual than a typical group of six individuals. The dispersal of individuals may be due to the energy benefit obtained by foraging in small groups (Baird and Dill 1996). Thus, we would expect smaller groups of Guiana dolphins in Madeiro Beach, where food, presumably, is not abundant enough to keep large groups and cooperative hunting is not essential. The small group sizes of Guiana dolphins at Madeiro Beach are, however, very similar to those described for other species that live in a fission-fusion

social system such as hyenas (*Crocuta crocuta*: $\bar{x} = 4$, Smith *et al.* 2008), spider monkeys (*Ateles geoffroyi*: $\bar{x} = 4$, Symington 1990), deer (*Cervus elaphus*: $\bar{x} = 3$, Conradt and Roper 2000), and bottlenose dolphins ($\bar{x} = 4$ and 6, Connor *et al.* 1999).

According to prediction 2, the analysis of variation in group size showed a tendency for new individuals to join the group during feeding and exit during milling and resting. The individual decision can be a combined result of both dependent and independent decisions on group density, the latter based on the influence of neighbors and resulting in repulsion or attraction between individuals (Gueron *et al.* 1996). The entry and exit of individuals during feeding may be due to recruiting outsiders for a cooperative hunting strategy or to individuals being attracted to successful hunters, thereby causing the group to deviate from its optimal size (Barnard and Sibly 1981, Giraldeau 2008). The fact that there is a high individual exit rate during milling and a high entrance rate during feeding, as well as the fact that larger groups have low hunting success, suggests that the second possibility could be correct. Thus, individuals that detect others feeding nearby may be drawn by this resource, although larger groups may have lower hunting success. Individuals that are already present can act as competitors by reducing the resources' availability: per scramble—reducing resource availability through exploitation, or per interference competition—competitors' presence scared the prey away more quickly (Giraldeau 2008).

We often observed respiratory synchrony between individuals while resting, and if there is energy cost associated with the respiratory synchrony, this could be one of the factors that influenced the exit of individuals during this behavior. Furthermore, there is no record of potential predators at Madeiro Beach, which may favor smaller group sizes during resting.

The proposed dynamics index (*DI*) quantifies the variation in group size over time. The mean dynamics index obtained was $\bar{x} \pm \text{SE} = 0.14 \pm 0.004$, *i.e.*, for every 20 min of observation we recorded an individual entering or leaving the focal group. In this study we observed one fission or fusion event on 17% of 2 min sampling intervals. This result is similar to the result described in Admiralty Bay, New Zealand, to dusky dolphins (*L. obscurus*)—one fission or fusion event on 19.7% of 2 min sampling intervals (Pearson 2009). In Cananéia, Brazil, Guiana dolphins present unstable associations and the analysis of the association index revealed that only 9% of the associations were significantly different from random associations (Santos and Rosso 2008). Similarly, in the coastal zone of the Abrolhos Bank, Brazil, associations between Guiana dolphins seem to be brief (Cantor *et al.* 2012). In Admiralty Bay, groups of dusky dolphins were larger during feeding and new individuals were attracted during this behavior, suggesting that the groups are highly dynamic when searching for food (Pearson 2009). Coordinated foraging strategies influence fission-fusion dynamics and have a positive effect on group size and its fusion rate (Pearson 2009).

Fission-fusion and Group Composition

In agreement with prediction 3, groups of adults and of adults and calves presented lower dynamics indices than groups of adults and juveniles. More than 50% of all groups of adults and of adults and calves remained stable, with no individual entry or exit events, whereas groups of adults and juveniles showed, on average, an entry or exit event every 20 min. The dynamics index of adult-juvenile groups was greatest during milling and socializing, while groups of adults presented the highest dynamics index only while feeding. In Shark Bay, bottlenose dolphins showed preferred associations according to behavioral states and juveniles showed less stability in

preferred partnerships (Gero *et al.* 2005). Animals may compromise their time budgets when they synchronize their behavior with partners of different phenotypes (Conradt and Roper 2000). Thus, differences in the cost of behavioral synchrony may promote predominance in the population of groups of the same phenotype (Conradt and Roper 2000, Ruckstuhl and Neuhaus 2001).

Aggregation dynamics have been widely studied with mathematical modeling (*e.g.*, Conradt and Roper 2000) and these studies highlight the importance of phenotype homogeneity in the formation of subgroups. For example, groups composed of juveniles frequently differ in size, shape, structure, and cohesion from groups composed of adults because energy requirements and predation risks also differ (Laroche *et al.* 2008). In ungulates, the more dimorphic the individuals in a group (age/sex dimorphism), the less synchronous the group is, and the less efficient it is in foraging and traveling. Ungulates form subgroups of similar phenotype, with the exception of the mother-foal dyad, which tends to remain together (Conradt 1998). Phenotypic heterogeneous groups of Guiana dolphins, except for the adult-calf pair, seem to be more unstable than homogeneous groups, because both groups differ mainly in foraging skills and energy requirements and, possibly, in synchronization costs (Ruckstuhl and Neuhaus 2001).

Fission-fusion and Seasonal Fluctuations

In concordance with prediction 4, seasonal analysis of the group size, frequency of feeding and socializing and the dynamics index of the Guiana dolphin showed statistically significant differences between the dry and rainy seasons. During the dry period, groups were smaller and feeding behavior, as well as higher dynamics indices, were more common; during the rainy season, groups were larger and socialization as well as lower dynamics indices occurred more frequently. The seasonal behavioral variation of the Guiana dolphins appears to be similar to that of the bottlenose dolphins and consistent with the hypothesis of behavioral flexibility as a response to environmental changes and fluctuations in prey type and availability (Bearzi *et al.* 1999). The dolphin group size in Shark Bay also appears to be responsive to food availability. Foraging groups of *T. aduncus* had fewer individuals than resting groups, suggesting that dolphins form smaller groups during foraging to reduce competition (Heithaus and Dill 2002). In the Amazon and Orinoco Rivers, ecological factors such as aquatic productivity also influenced the group sizes of river dolphins, *Inia geoffrensis* and *S. fluviatilis* and the largest group size of river dolphins occurred when resources were concentrated (Gomez-Salazar *et al.* 2011).

Summary

Our analyses indicate that, in Madeiro Beach, Guiana dolphin groups are cohesive in space, but unstable through time, changing their group size and composition every 20 min on average. In other words, the individuals are cohesive when in the group, but group membership often changes. Greatest cohesion (≤ 2 m) was observed mainly between individuals while resting, and in groups composed of adults and calves. However, individuals tended to stay further apart during feeding likely due to interference or exploitation competition. Groups of adults and adults and calves remained more stable (changed less their group size) than groups of adults and juveniles. Fission-fusion seems to follow immediate behavioral demands, mainly for resting and feeding, probably in response to environmental changes. For example, feeding was

most common during the dry season, while socializing was most common during the rainy season. Finally, although our analyses did not focus on finding preferential partnerships or central individuals, our results indicate that the behavioral analysis in spatiotemporal scale can be effective to investigate the fission-fusion social system of animal groups.

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