Research Article

Group structure of Guiana dolphins, *Sotalia guianensis* (Cetacea, Delphinidae) in Ilha Grande Bay, Rio de Janeiro, southeastern Brazil

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ABSTRACT. Cetaceans present a group structure of great complexity and display a wide behavioral plasticity. Many efforts have been made to understand the group structures of the various species, however, this type of information is still lacking for some species. Therefore, our objectives were to 1) characterize the structure of the Sotalia guianensis groups in Ilha Grande Bay, Rio de Janeiro, Brazil, and 2) investigate how both behavior and season influence the group structure of this population. This species is considered "data deficient" by the IUCN. We conducted 28 boat trips using group focal procedures, and a total of 1,314 groups were observed. Of these groups, 1,268 (94.4%) contained calves, the largest percentage ever reported for the species. Groups with calves were larger than those without them, suggesting a strategy to protect these individuals with underdeveloped physiology. The mean group sizes reached 17.6 ± 18.3 individuals. Within these groups, we observed that both behavior (H = 112.5, d.f. = 2, P < 0.05) and season (number of simulations: 10,000; sample size of fall-winter = 544; sample size of spring-summer = 684; P < 0.05), demonstrated a statistically significant influence. The most common degree of cohesion was mixed, and cohesion also varied with behavior ($\chi^2 = 10.1$, P < 0.05) and season ($\chi^2 = 31.0$, P < 0.05). This paper contributes towards understanding the highly variable nature of S. guianensis group dynamics. These data may be important in understanding the structure of groups in a site that is being increasingly impacted by different human activities. Moreover, this area contains the largest aggregation ever observed for this species and may therefore represent an important source of genetic diversity for the species as a whole.

Keywords: Sotalia guianensis, Guiana dolphin, group structure, Ilha Grande Bay, southeastern Brazil.

Estructura grupal en delfines Guyana, *Sotalia guianensis* (Cetacea, Delphinidae), en la bahía de Ilha Grande, Río de Janeiro, sureste de Brasil

RESUMEN. Los cetáceos muestran una complejidad en la estructura de grupos, caracterizado por una gran plasticidad en su comportamiento. Se han efectuado numerosos esfuerzos para comprender las estructuras de grupos de muchas especies, pero para algunas estos datos son desconocidos. Los objetivos de este estudio fueron: 1) caracterizar la estructura de grupos de *Sotalia guianensis* en la Baía da Ilha Grande, Rio de Janeiro, Brasil, y 2) investigar como el comportamiento y las estaciones del año afectan la estructura de grupos de esta población. Esta especie es considerada con "datos deficientes" por la IUCN. Se efectuaron 28 salidas en bote en la Baía da Ilha Grande, usando el procedimiento de grupo focal y se observó un total de 1.315 grupos. De estos grupos, 1.268 (94,4%) contenían infantes, el mayor porcentaje registrado para esta especie. Los grupos con infantes fueron más grandes que los sin infantes, sugiriendo una estrategia para proteger estos individuos con fisiología menos desarrollada. El tamaño medio de los grupos observados fue de 17,6 ± 18,3 individuos. Dentro de estos grupos, se observó que ambos, comportamiento (H = 112,5; d.f. = 2; P < 0,05) y estación del año (número de simulaciones: 10.000; tamaño de muestra en otoño-invierno = 544; tamaño de muestra en primavera-verano = 684; P < 0,05), fueron estadísticamente significativos. El grado más común de cohesión fue mixto y varió con el comportamiento ($\chi^2 = 10,1$; P < 0,05) y estaciones del año ($\chi^2 = 31,0$; P < 0,05). Este

estudio contribuye a la comprensión de la naturaleza altamente variable de la dinámica de grupos de *S. guianensis*. Estos datos pueden ser importantes para comprender la estructura de grupos en un área que ha sido impactada crecientemente por diferentes actividades humanas. Además, esta área contiene la mayor agregación de individuos observada para esta especie y representa una importante fuente de su diversidad genética.

Palabras clave: *Sotalia guianensis*, delfín de Guyana, estructura de grupo, bahía da Ilha Grande, sureste de Brasil.

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INTRODUCTION

In general, most vertebrates show some degree of gregariousness. They tend to form different levels of group structure, such as shoals, flocks, herds, packs, parties or colonies of conspecific individuals (Reicziegel *et al.*, 2008). Conspecifics may influence different aspects of their lives, such as foraging success, sexual selection, predation pressure and aggression (Krause & Ruxton, 2002). Consequently, a wide range of behavioral, morphological and life history traits may be affected by sociality (Krause & Ruxton, 2002).

The group structure of cetaceans presents a wide behavioral plasticity, in which some species may form stable pods (Baird, 2000), fission-fusion groups (Connor, 2000), mother-calf groups (Clapham *et al.*, 2000) or groups formed only by males (Whitehead & Weilgart, 2000). Despite the great effort of various researchers, the group structure of cetaceans is not fully understood, especially for some species like the Guiana dolphin (*Sotalia guianensis*), which are considered "data deficient" by the IUCN (Van Bénéden, 1864).

The Guiana dolphin is a small delphinid, which can be found from northern Honduras to southern Brazil. and inhabits estuaries and bays (Simões-Lopes, 1998; Carr & Bonde, 2000). The diet of Guiana dolphins along the Brazilian coast has been investigated in detail and has revealed an opportunistic and generalist feeding habit in which their main prey tends to form small or large schools with pelagic or demersal habits (Di Beneditto & Ramos, 2004). Distribution studies on the S. guianensis social structure have shown a variety of relationships between biological and environmental components. These studies have demonstrated a lack of influence of the seasons in Guanabara Bay, RJ (Azevedo et al., 2005), heterogeneity in group size during the day in Baia Norte, SC (Daura-Jorge et al., 2005), differences in group size based on behavior in Sepetiba Bay, RJ (Nery et al., 2010) and on different habitats in Paranaguá Estuarine Complex, SP (Santos et al., 2010). However, several aspects (e.g., the relationship between composition and group size, cohesion and seasonality), of Guiana dolphin behavior, remain unknown, as is the case in Ilha Grande Bay. Our first objective was to characterize the structure of S. guianensis groups in Ilha Grande Bay, RJ, Brazil. Nerv et al. (2010) has shown that the S. guianensis population in Sepetiba Bay, a similar and adjacent area to Ilha Grande Bay, demonstrates large group sizes and a high percentage of calf group members. Our hypothesis is that these components of group structure will show the same pattern in Ilha Grande Bay. Our second objective was to investigate how behavior and season influence the group structure of this population. Our hypothesis is that behavior and season will be the main factors in determining S. guianensis group size, as the number of dolphins engaged in each group may be a better indicator of ecological variability because fish schools may consequently be responding to specific habitat features and to differences in seasons.

MATERIALS AND METHODS

Study area

Ilha Grande Bay (Fig. 1) is a large area encompassing 653 km², and is divided into the eastern, central and western zones. The western zone, where we conducted boat trips (23°02'S, 44°26'W), is of shallower depth (<10 m), contains approximately 31 islands and has a sandy/muddy bottom (Lodi, 2003b). The central zone of the bay behaves as a transition area between the land and sea (Nogara, 2000), receiving organic matter from river drainage and mangrove production (Signorini, 1980). From the sea, this bay receives deep waters rich in nutrients derived from the South Atlantic Central Waters (SACW) (Signorini, 1980). This zone is preferentially used by the S. guianensis population (Lodi, 2003b), and is surrounded by an outer region with depths between 20 and 40 m, and a smaller proportion of land mass than the inner region (DHN, 2011). The S. guianensis population in Ilha Grande Bay represents the largest aggregation of individuals ever seen at once (approximately 450



Figure 1. Study area, located in Ilha Grande Bay, southeastern Brazil.

animals) (Lodi & Hetzel, 1998), the highest abundance ever reported [1,311 individuals (95% CI 1,232-1,389 individuals) (Espécie, 2011) and fluid degree of residence patterns with individuals presenting different degrees of residence to the area (Espécie *et al.*, 2010).

Procedures

We carried out focal-group observations with continuous sampling (Lehner, 1996), from May 2007 to March 2010, onboard a 7.5 m vessel. A digital Sony DCRTRV 120 handycam was used to capture spatiotemporal behavior, which increased the analysis efficiency, as observations of dolphins in the wild are brief and many details can be lost. A group was defined according to the 10 m chain rule of Smolker et al. (1992), calves and juveniles were defined according to Geise et al. (1999) and the definition of cohesion was the same as that described by Shane (1990). We collected data for the three behavioral states of feeding, traveling as defined by Karczmarski et al. (2000) and socializing as defined by Slooten (1994). Table 1 summarizes all the definitions used in this work. Every time we spotted a group of dolphins, we recorded their behavior until they disappeared. Like some other delphinids, such as the bottlenose dolphin (*Tursiops truncatus*), *S. guianensis* presents fission-fusion dynamics (Connor, 2000) with groups changing in composition and members over short periods of time. Therefore, we believe that pseudo-replication is not an issue.

For the purpose of analysis, we divided our data into two sampling periods: fall-winter (20th March-22th September) and spring-summer (23th September-19th March) (CPTEC-INPE, 2011).

To reach our first objective, we counted the number of groups and individuals in each group, the degree of cohesion between them and quantified the number of calves. For the second objective, we correlated all these variables with the behavior and sampling period.

Statistical analyses

To determine if the number of groups displaying a behavior category was more than expected, we ran a chi-square test for one sample. To test for differences between this variable and the sampling periods, we created the following index:

$G_i = N/n*100$

where G_i = standardized proportion of the number of groups observed in sampling period I; N = number of

Variable	Definition			
Group size	Dolphins 10 m apart from each other Smolker et al. (1992).			
Age classes	Calves were individuals presenting $1/4$ of adults body size and juveniles $1/2$ to $2/3$ of adults body size Geise <i>et al.</i> (1999).			
Feeding	Dolphins presented an absence of directional movements, diving frequently in asynchronous fashion Karcsmarski <i>et al.</i> (2000).			
Travelling	Dolphins presented directional and constant movements Karcsmarski et al. (2000).			
Socializing	Dolphins interacted with each others, displaying socio-sexual behavior. It was usual to observe sexual interactions such as the "belly-to-belly" position, in which there is a joint union of dolphins' genital region Slooten <i>et al.</i> (1994).			

Table 1. Definitions of all variables considered in this paper.

groups observed in sampling period i; and n = number of seconds of observation for each sampling period.

This index was created to standardize the differences in the amount of observation time for each sampling period.

To investigate differences between group size and behavior, we used a Kruskal-Wallis test. For group size and sampling periods, we used the bootstrap t-test for two samples as suggested by Reiczigel *et al.* (2008) using ten thousand simulations. As the group size data almost never reach parametric assumptions, the data were log transformed for this purpose.

Due to the heterogeneity and the typical nonnormal group size distributions, we used bootstrap bias corrected and accelerated procedure to estimate the confidence interval using Flocker 1.1® as described in Efron & Tibishirani (1993).

To determine if there were differences between age classes and group size, we used the Kruskal-Wallis test. When batching all age classes in only one category (offspring), we used the Mood's median test to quantify differences in group size between groups with offspring and groups without offspring. To investigate differences between the composition and behavior, we used a partition chi-square test. For the composition and sampling periods, we used a chisquared test for two samples. To evaluate the influence of behavior and sampling period on the degree of cohesion, we performed a partition chisquare test.

RESULTS

Twenty-eight boat trips were conducted for a total of 42.4 h of direct observation (75.5 h of effort). No

solitary individual was spotted during the entire study period.

Number of groups

We observed a total of 1.314 groups. A chi-squared test showed significant differences for behavioral influences (N_{feeding} = 783; N_{traveling} = 470; N_{socializing} = 61; χ^2 = 589.2; *P* < 0.05). The G*i* values were higher for the spring-summer period (G*i* = 3.08) than for the fall-winter period (G*i* = 1.31).

Group size

The mean group size was 17.6 ± 18.3 individuals (modal value = 15), and the group size ranged from 2 to 200 individuals. The bootstrap bias corrected and accelerated confidence interval ranged from 16.7 to 18.7. The most common group size was 2 to 10 animals (44.8%). Other group sizes included 11 to 20 (28.0%), 21 to 30 (17.2%), 31 to 40 (2.8%), 41 to 50 (2.2%) and more than 50 animals (5.0%).

Traveling groups ranged from 2 to 200 individuals (mean = 21.1 ± 24.7 , BCa CI = 19.4 to 23.8), feeding groups ranged from to 2 to 100 individuals (mean = 14.9 ± 13.5 , BCa CI = 14.1 to 15.8) and socializing groups ranged from 2 to 15 individuals (mean = 5.7 ± 3.1 , BCa CI = 5.2 to 6.6) (Fig. 2).

The Kruskal-Wallis test showed significant differences between group size and behavior (N = 1,345, H = 112.5, d.f. = 2, P < 0.05). The *post-hoc* multiple comparison of mean ranks test showed that the differences found occur among all behaviors (P < 0.05).

Group sizes were larger in the spring-summer period (24.0 ± 21.6) than in the fall-winter period (14.4 ± 16.9) . The bootstrap t-test showed significant differences between mean group size and sampling



Figure 2. Variation of mean group size according to different behaviors.

period (number of simulations: 10,000; sample size of fall-winter = 544; sample size of spring-summer = 684; P < 0.05).

Group composition

Of all the groups observed, 1,268 of them contained offspring members (94.4%). After discriminating between age classes, 61.6% (N = 781) of the groups contained only adults and calves as their members, 34.1% (N = 433) contained calves, juveniles and adults as their members and 4.3% (N = 54) contained only adults and juveniles as their members. Groups with only calves and adults ranged from 2 to 200 individuals (mean = 13.0 ± 14.5 , BCa CI = 11.5 to 13.6), groups with only juveniles and adults ranged from 2 to 15 individuals (mean = 5.6 ± 3.4 , BCa CI = 4.8 to 6.5), groups with calves, juveniles and adults ranged from 3 to 200 individuals (mean = 16.7 ± 17.9 , BCa CI = 15.2 to 18.5) and groups with only adults ranged from 2 to 20 individuals (mean = 7.1 ± 3.5 , BCa CI = 6.6 to 7.8). The Kruskal-Wallis test showed a statistically significant difference between group size and different age classes (H = 78.6, N = 1,268, d.f. = 2, P < 0.05 (Fig. 3).

When grouping all age classes into a single category (*e.g.*, offspring), the Mood's median test also showed statistical significance ($\chi^2 = 78.1$, d.f. = 1, *P* < 0.05).

When analyzing the influence of the annual period on group structure, the chi-squared test for two samples showed no significant difference ($\chi^2 = 0.98$; *P* > 0.05).



Figure 3. Mean group size variation according to different age class groups.

Cohesion patterns

The most commonly observed cohesion pattern was mixed (Table 2). Chi-square tests showed significant differences between cohesion and behavior ($\chi^2 = 10.1$; mixed vs tight P < 0.05; mixed+tight vs loosely P > 0.05; mixed+tight+loosely vs widely dispersed (P > 0.05); total: P < 0.05), and cohesion and sampling periods ($\chi^2 = 31.0$; mixed vs tight P < 0.05; mixed+tight tight vs loosely P < 0.05; mixed+tight+loosely vs widely dispersed P < 0.05; mixed+tight+loosely vs widely dispersed P < 0.05; mixed+tight+loosely vs widely dispersed P < 0.05; total: P < 0.05; mixed+tight+loosely vs widely dispersed P < 0.05; mixed+tight+loosely vs widely dispersed P < 0.05; total: P < 0.05).

DISCUSSION

The structure and organization of groups of small cetaceans can be a result of several factors, which include biological (e.g., predation risk, abundance, distribution of prey and reproduction) and environmental (e.g., water depth, sea surface temperature, salinity, and bottom topography) components (Gygax, 2002). The group sizes, observed in Ilha Grande Bay, were among the largest in the entire distribution. The large aggregation of individuals in this location may be a result of the ecological functions of Ilha Grande Bay, including a site with shallow and protected waters for rearing calves, and an seasonable site for social learning, especially coordinated with feeding behavior (Tardin et al., 2011). In the Paranaguá Estuarine Complex (PR), Santos et al. (2010) reported that Guiana dolphin group sizes ranged from 2 to 90 individuals with mean group size of 11 individuals. In Guanabara Bay, the group size ranged from 1 to 40 individuals with a mean group size of 13 individuals (Azevedo et al., 2005). In Baía Norte (SC), the group

Behavior	Feeding	Travelling	Autumn-Winter	Spring-Summer
Tight	242	156	419	254
Mixed	365	167	337	183
Loosely	8	1	15	13
Widely dispersed	4	5	8	6

Table 2. Degrees of cohesion in different behaviors and sampling periods. Numbers inside cells are the number of groups observed.

size ranged from 1 to 59 individuals with a mean group size of 29 individuals. However, in Sepetiba Bay, an adjacent area of Ilha Grande Bay, the group size ranged from 2 to more than 50 individuals with a mean group size of 16 individuals (Nery et al., 2010). It is interesting to note that the number of individuals sighted, in a single day in Ilha Grande Bay, was the highest of all other estuaries, except Sepetiba Bay. Both bays are very similar in terms of oceanographic conditions, such as input of freshwater and the availability and seasonality of prey, which could be possible explanations for the high abundance of these two populations [Sepetiba abundance: 1,043 individuals (95% CI: 999-1115) (Nery, 2008); Ilha Grande Bay abundance: 1,311 individuals (95% CI 1,232-1,389 individuals) (Espécie, 2011)]. Therefore, the Sepetiba-Ilha Grande complex seems to be an important location for the species as it contains the two largest populations that demonstrate the largest group sizes.

With regard to the environmental influences *S. guianensis* group formation, some studies have shown that environmental data do not influence group formation (*e.g.*, Azevedo *et al.*, 2005 (group size *vs* water depth), Santos *et al.*, 2010 (group size *vs* temperature, water depth, transparency and salinity). However, others authors did find a relationship, *e.g.*, dos Santos *et al.*, 2010 (group size *vs* water depth), Cremer *et al.* 2010 (group size *vs* season), Daura-Jorge *et al.*, 2005 (group size *vs* daylight h). Our study area contains similar conditions throughout (*i.e.*, sandy/muddy bottom, large number of islands, and input of freshwater and similar depth); therefore, there is no large environmental variation.

This study did not tested whether group structure varied with environmental data. However, our results show that implementation of future research about how group structure changes with non-biological components can be important to better understand the population dynamic of *S. guianensis* in Ilha Grande bay.

Our data showed that the number of groups was higher during the fall-winter period than during the

spring-summer period. However, the number of individuals in each group during the fall-winter period was smaller than compared with the spring-summer period. This result may suggest a differential distribution of food resources during the spring-summer period that could support larger groups without enhancing the competition between individuals. As a result, these larger groups would enhance prey capture success. In fact, the Social Foraging Theory suggests that animals should maximize individual intake and thus aggregate to exploit available food resources (Giraldeau & Caraco, 2000). During the springsummer period in Ilha Grande Bay, fish that form large schools such as Sardinella brasiliensis and Harengula clupeola are observed and reported to spawn (Matsuura, 1978). These fishes are part of the S. guianensis diet (Di Beneditto & Ramos, 2004) and may therefore be driving the fission-fusion dynamics of dolphins to adapt to prey schooling patterns. Interestingly, Tardin et al. (2011) reported that the number of individuals engaged in coordinated feeding tactics in this population was higher during the springsummer period than during the fall-winter period.

The mean group size was greater in traveling groups than in groups performing other behaviors. This result can be explained by the observation that the groups were often traveling toward the outer part of the bay, which represents deeper and unprotected waters, requiring the gathering of more individuals (group sizes of 100-200 individuals). As most of the groups had offspring among their members, the aggregation of individuals while traveling to the outer areas of the bay may represent a strategy to protect the offspring from predators. During feeding, group size might be limited by intraspecific competition, during which individuals would aggregate in larger groups only when the net individual intake would be higher than when feeding in smaller groups. In terms of socializing, this study analyzed only socio-sexual behavior, and the observed group sizes were smaller given that only a few individuals were performing sexual activities. This behavior, of a very intense nature, occurs in a smaller percentage of the population than traveling or feeding behavior (Tardin, *pers. comm.*). During this time, it is easy to observe individuals constantly slapping water and each other, lifting water, and swimming belly-to-belly.

Different behavioral influences on group size may be found in the literature. While observing the same species, Daura-Jorge et al. (2005) in Baía Norte (SC) reported that the largest group sizes were seen during feeding behavior. In Sepetiba Bay (RJ), Nerv et al. (2010), reported that the largest group sizes occurred during socializing behavior. One hypothesis, which may be derived from these interpopulation comparisons, is that these differences represent different ecological conditions that each habitat provides for each population. The high behavioral plasticity of the Delphinidae family may be reflected in an interspecies comparison. May-Collado & Ramirez (2005), reported that the spotted dolphin (Stenella attenuata) aggregated in larger groups during feeding, whereas the Atlantic white-sided dolphin (Lagenorhynchus acutus) in New England (Weinrich et al., 2007), and the Dusky dolphin Golfo (Lagenorhynchus obscurus) in Nuevo. Argentina (Degrati et al., 2008), demonstrated the largest group sizes when in traveling behavior.

To our knowledge, Ilha Grande Bay has the highest percentage of S. guianensis offspring ever reported in its entire distribution. These data reinforce the important ecological function that this bay may have for this population, especially containing shallow and warm waters that seems to be free of predators (W. Alcantara do Carmo, pers. comm.). These conditions seem to favor the aggregation of many groups with offspring. These groups provide the opportunity for both better physiological development and social learning for the offspring. Other S. guianensis habitats along its distribution may also serve as important sites for the care for offspring. For instance, in the Paranaguá Estuarine Complex, Santos et al. (2010), reported that groups with offspring represented 84.6% of all groups. These two ecologically similar areas may provide interesting insight about the costs and benefits of group formation in S. guianensis. Both areas are mainly shallow with a sandy/muddy bottom and a large number of microhabitats, such as islands, rocky coasts and mangroves, which increase biological diversity and can therefore minimize the individual costs of living in large groups, such as intraspecific competition.

Groups with offspring contained a larger number of individuals compared to groups without offspring. Our hypothesis is that mothers with offspring aggregate to protect against other conspecifics, which allows them to benefit from the dilution effect (Landeau & Terborgh, 1986), decreasing the calves' chances to be attacked and killed. In fact, a record of infanticide has been reported in the adjacent population of Sepetiba Bay (Nery & Simão, 2009) and therefore may be a source of injury to the offspring. Moreover, studies on the bottlenose dolphin demonstrated that offspring have an underdeveloped physiology, including less muscle mass (Dearolf et al., 2000) and limited aerobic (Noren et al., 2001) and anaerobic (Noren, 2004) capacities. Therefore, they are easily targeted by predators or conspecifics. When discriminating between age classes, our data showed that groups with only adults and juveniles demonstrated similar characteristics to groups with only adults (i.e., few groups with a smaller number of individuals). Groups with only adults and calves had up to 200 individuals and demonstrated higher mean values, possibly reinforcing the dilution effect for this specific age class.

While working with *Lagenorhynchus acutus* in New England and *L. obscurus* in Golfo Nuevo, Argentina, Weinrich *et al.* (2007) and Degrati *et al.* (2008), respectively, reported that groups containing offspring members were larger than those that did not, indicating a possible common strategy to avoid injuries to offspring.

Our data on group cohesion indicated that a mixed formation was most commonly observed. In this formation, individuals were spatially separated from each other to varying degrees. This result suggests that the social bonds connecting individuals may be different, and this difference is observed in the various degrees of cohesion that individuals share within the same group. For example, individuals with stronger bonds may stay closer to each other by spacing themselves one body length apart from each other, whereas others that may be casual acquaintances may distance themselves further apart. In Guanabara Bay, Azevedo et al. (2005) found that no degree of cohesion (called "spatial geometry" by the author) was predominant; however, group sizes were higher in the mixed formation. Feeding and traveling behaviors were most commonly observed to occur in mixed formation. The coordinated feeding behavior displayed by this population represents random and fluidic movements, which seems to overcome prey defenses (Tardin et al., 2011). In mixed formations, individuals are spaced at different degrees and may better coordinate their actions to herd prey from multiple locations. When traveling, social bonds may be the driving force causing individuals to space themselves at different degrees, as spatial proximity may influence the hydrodynamics of each individual. Interestingly, during socio-sexual behavior, all the observed groups were tightly spaced, which describes the nature of this behavior in which individuals engage in sexual and aggressive activities and are in constant physical contact. These groups contained only adult members, in contrast to the traveling and feeding groups, which contained both calves and adults. This relationship between cohesion and group composition may indicate that groups with and without calves may be a force that influences cohesion and, consequently, behavior.

This paper contributes to understand the highly variable nature of *S. guianensis* group dynamics. These data may be important in understanding the structure of groups in a site increasingly impacted by different human activities. Moreover, this area contains the largest aggregation of this species ever seen (Lodi & Hetzel, 1998) and, therefore, may represent an important source of genetic and social diversity for the species as a whole.

ACKNOWLEDGMENTS

We thank Sergio Moreira from Aqualie Institute, Dona Elza, Walcir Alcantara do Carmo (Tico) and Gilberto for their valuable help. Personnel for this study were partially supported by the Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) (R.H.O. Tardin, Grant number E-26/151.047/2007 y E-26/100.866/2011); Conselho Nacional de Pesquisa e Desenvolvimento (CNPq) (M.A. Espécie, Grant Number 111555/2008-6), and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (R.H.O. Tardin, and M.A. Espécie).

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Received: 16 May 2011; Accepted: 22 October 2012

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