Diurnal and Seasonal Variation in the Behaviour of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina

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Abstract

Diurnal and seasonal patterns in the behaviour of a small population of bottlenose dolphins were assessed in Bahía San Antonio (BSA), Patagonia, Argentina, between 2006 and 2011. Results indicated that dolphins used the study area mainly to rest, travel, and forage, with a marked diurnal and seasonal pattern in their activity. During the early morning, most dolphin groups were resting, while towards the afternoon and evening, surface feeding and social activities peaked. During winter, social activities and surface feeding increased notably; during summer, diving behaviour reached its peak, presumably associated with a tail-out/peduncle-dive foraging strategy. The observed seasonal variation in foraging strategies is hypothesised to be related to the seasonal behavioural changes of prey species in the area that are linked to spawning. The variation in group size further appears to reflect the regulation of feeding competition while reconfirming the low predation risk within the study area. Results of this study indicate the behavioural and social flexibility of bottlenose dolphins in BSA and suggest a link to the seasonal variations in prey availability. Considering the general bottlenose dolphin population declines in Argentina presumably related to prey depletion, it could be argued that the temporal occurrence of spawning shoals and a general low presence of other top predators directly and indirectly make this a favourable area for this population. Additional information is required to more comprehensively address this hypothesis. The information presented herein serves as vital baseline data for future conservation management protocols.

Key Words: activity budget, foraging strategy, group size, intraspecific competition, seasonal patterns

Introduction

Many animals display daily and seasonal variations in their behaviour patterns (Bräger, 1993), which are presumed to balance costs and benefits of expending energy (Boness, 1984). As this balance changes, activity patterns may also change, reaching a complex compromise between needs related to feeding, resting, reproduction (Nielsen, 1983), and avoidance of predators (Mann et al., 2000). The more time animals spend in one behavioural state will decrease the amount of time devoted to other behaviours that may nonetheless be crucial to their survival. This highlights the importance of determining the activity patterns of an animal and the main factors affecting them.

The quantitative description of dolphin behaviour, however, can often be ambiguous as they are visible at the surface only during a small proportion of their time (Bearzi et al., 1999). For bottlenose dolphins (*Tursiops* sp.), it can be even more challenging as they show great behavioural flexibility in response to different ecological constraints which will vary depending on the habitat in which they live (Shane, 1990a), a feature that has contributed greatly to the survival success of this species (Shane et al., 1986; Bearzi et al., 1997; Reynolds et al., 2000).

In Argentina, bottlenose dolphins live in coastal waters from the province of Buenos Aires in the north to the province of Chubut in the south (also possibly in offshore waters; Bastida & Rodríguez, 2003). Infrequent records have been made as far south as the provinces of Santa Cruz and Tierra del Fuego (Goodall et al., 2011). Most behavioural studies conducted on bottlenose dolphins in Argentina (e.g., Würsig & Würsig, 1979) were discontinued in the 1980s because of noted population declines and the subsequent lack of sightings (Bastida & Rodríguez, 2003). One of the last remaining resident populations of the country is

suggested to reside in BSA (Río Negro province; Vermeulen & Cammareri, 2009). Research conducted in this area described this population as small, essentially closed, declining (Vermeulen & Bräger, 2015), and highly resident to the study area, indicating this bay as the core region within the larger home range of this population (Vermeulen & Cammareri, 2009). This study aims to provide a better understanding of the activity patterns of this vulnerable population of bottlenose dolphins. We aim to detect potential diurnal and seasonal patterns and form suggestions related to the main factors that influence these patterns. Our results will serve as vital baseline information for future monitoring of the impact of increasing anthropogenic pressures such as commercial and recreational fishing, and a recently initiated dolphin-based tourism.

Methods

Study Area

The study area of Bahía San Antonio (BSA) (40° 45' S, 64° 54' W; Figure 1) is a shallow bay with a maximum depth of no more than 30 m, located to the north of the Golfo San Matías, Patagonia, Argentina. With a surface area of approximately 655 km², the bay is known for its large fluctuations in sea surface temperature (SST), with differences reaching 16° C between summer (maximum 24° C) and winter (minimum 8° C), its relative high salinity (> 35 ppm year-round) compared to the waters south of the gulf (Gagliardini & Rivas, 2004), and its large tidal fluctuation of up to 9.5 m (Servicio de Hidrografia Naval, Argentina).

Fieldwork

All surveys were conducted under good weather conditions (Beaufort Sea State ≤ 3) and during daylight hours between 0800 and 1800 h (minimum length of each survey was 4 h). During land-based surveys, a continuous scan was performed from a fixed point (see Figure 1) using binoculars until dolphins were spotted (observation height varying between 2 and 12 m above sea level). Only dolphin groups close enough to shore were observed in order to ensure the quality of behavioural observations. During boat-based surveys, a steady speed (4 to 5 kts) was maintained with two to three observers (always the same observers) continuously searching visually (naked eye) for dolphins. The course of each survey was non-standardised; the area was surveyed at random (depending on weather conditions and fuel availability) until a dolphin group was found (Figure 1).

A dolphin group was followed until it was lost from view or until it became clear that the animals' normal behaviour was being disturbed (being attracted to or avoiding the research vessel). When the dolphin group split, we continued observing the largest portion of the group. When a dolphin group was lost from view, the survey continued at random until a minimum of 4 h fieldwork was completed or a new dolphin group was encountered (verified as a new group based on photo-identification data). Land- and boat-based surveys were separate from each other. Seasons were defined as (1) summer = January-March, (2) autumn = April-June, (3) winter = July-September, and (4) spring = October-December. Average SST measured in the field (using a water thermometer) for different seasons, winter = 9.5° C (SD = 1.5), spring = 12.8° C (SD = 0.4), summer = 20.4° C (SD = 1.2), and autumn = 12.0° C (SD = 0.8).
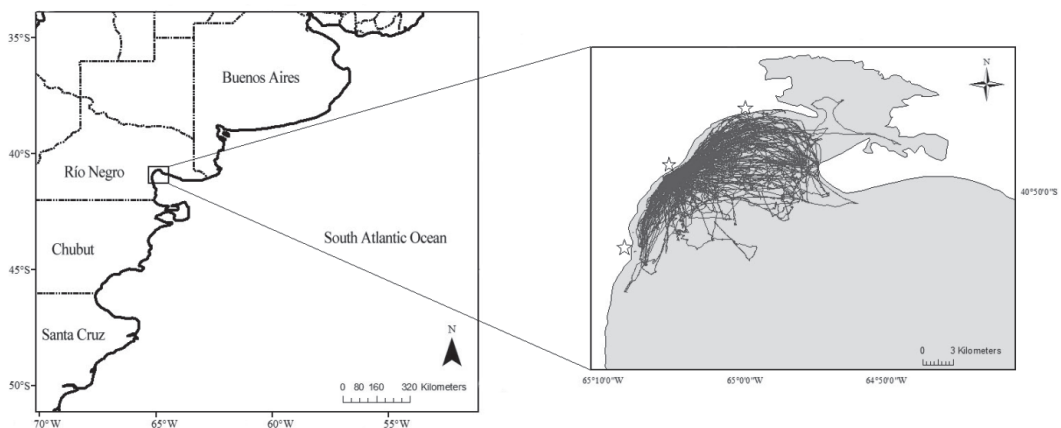

Figure 1. Map of the study area, Bahía San Antonio (BSA), indicating boat-based survey effort tracks; stars indicate the land-based observation points.

A *dolphin group* was defined as all individuals within a 100-m radius of each other, interacting or engaged in similar activities (Irvine et al., 1981; Wells et al., 1987; Wilson, 1995; Lusseau et al., 2005) and moving in the same direction. Once a bottlenose dolphin group was encountered, group size was determined, and each group was documented either as "with calves" or "without calves." Calves were defined as being up to $\frac{2}{3}$ the length of an adult, with or without foetal folds (Mann & Smuts, 1999), and commonly swimming in close association with an adult (Shane, 1990a). The group size and presence of calves was later verified through photo-identification analysis.

Data on the behaviour of dolphin groups were gathered using a focal group 5-min point sampling mode (Altmann, 1974; Mann, 1999). During each period, the predominant activities of the majority of the group (> 50%) were noted. The behavioural categories are summarised in Table 1. Dives longer than 30 s were categorised in the behavioural state diving as they were longer than the mean dive duration of 21.8 s measured for coastal bottlenose dolphins in Argentine waters (Würsig, 1978).

Analyses
As was observed in the field and subsequently indicated by Vermeulen (2014), dolphins showed a preference of the intertidal zone of the bay, and appeared to move in and out with the tide to remain in this area as long as possible. Behavioural samples from both land- and boat-based surveys were, therefore, gathered from the same region, ensuring little bias when pooling the samples from both survey methods together. Sightings of less than 30 min were discarded from analysis so as to comply with the definition of a group follow stated by Mann (1999). In order to obtain independent samples, only one behaviour sample from each dolphin group was selected at random to examine the activity patterns and inform subsequent statistical analyses. The obtained values, therefore, represent the frequencies of observed activities rather than time budgets.

Due to the limited number of samples per season for each year, the seasonal variation could not be compared within each of the different survey years (2006 through 2011). However, seasons were pooled together to test for seasonal variation across years. For analysis of daily variation in behaviour, the day was divided into five periods of equal duration: (1) early morning (0800 to 0959 h), (2) morning (1000 to 1159 h), (3) noon (1200 to 1359 h), (4) afternoon (1400 to 1559 h), and (5) evening (1600 to 1800 h). These time spans were chosen as a balance between reflecting detailed information vs confirming an acceptable sample size per category. To test for significance of both diurnal and seasonal variation (all same seasons pooled together) in behaviour, contingency tables were created, and a Chi-square test was applied. Kruskall-Wallis tests were used to test the variation in group sizes. Separate Mann-Whitney U tests with Bonferroni corrections were used to further understand individual differences. To investigate the relation between the number of calves in a group and group size, a linear regression analysis was performed. All statistical analyses were conducted using the software *STATISTICA 7.0* (StatSoft, Inc., 2004).

Table 1. Definitions of behavioural categories used in this study

Travelling	Moving steadily in one direction
Surface feeding	Obvious feeding activities (e.g., tossing fish) performed close to water surface; fast moving in circles at the surface by dolphins. Fish are often seen to jump out of the water. Usually, birds concentrate over the dolphins. No clear physical contact between individuals can be observed.
Diving	No steady directional movement at the surface; tail-out dives longer than 30 s occurring during the 5-min sample.
Socialising	At least some of the group members are in frequent physical contact, with no steady directional movement, displaying surface behaviours (e.g., rolling over each other, jumping towards each other). Playful behaviour defined as any activity involving a foreign object (e.g., kelp tossing was included in this category) (Shane et al., 1986).
Milling	Moving in varying directions in one general location, with no obvious surface behaviours and no apparent physical contact
Resting	Lying motionless or moving slowly at the surface
Not classified	When none of the above categories could be assigned to a group

Behavioural states adapted from Shane, 1990a; Bearzi et al., 1999; Bearzi, 2005.

Results

Fieldwork

In total, 356 systematic photo-identification surveys of bottlenose dolphins were conducted between 2006 and 2011. Of these surveys, 227 were land based and 129 were conducted from a small outboard-powered rigid-hull inflatable boat. The total effort equalled 1,470 h (885 h land-based and 586 h boat-based), resulting in 214.2 h of observation of 415 dolphin groups or 31 min on average spent with each dolphin group. The behavioural observations of 265 dolphin groups (DGs) were included in analyses (Table 2), with the distribution of effort and observations of

different DGs over the seasons, and the number of DGs used in analyses summarised (group follows ≥ 30 min; Mann, 1999).

Diurnal and Seasonal Variations in Behaviour

Analysis of behavioural data showed that of all DGs ($n = 265$), most were resting (28%), followed by travelling (27%) and surface feeding (15%). Overall, fewer DGs were found diving (12%), milling (5%), and socialising (6%). The behaviour could not be accurately classified for 7% ($n = 19$) of the observed DGs.

The relative frequencies of observed behavioural patterns varied significantly among different periods of the day ($\chi^2 = 40.8, df = 24, p < 0.02$).

Table 2. Field effort, amount of time of dolphin observations, the number of observed dolphin groups (#DGs), and the number of observed DGs used in analyses (i.e., groups followed more than 30 min; Mann, 1999)

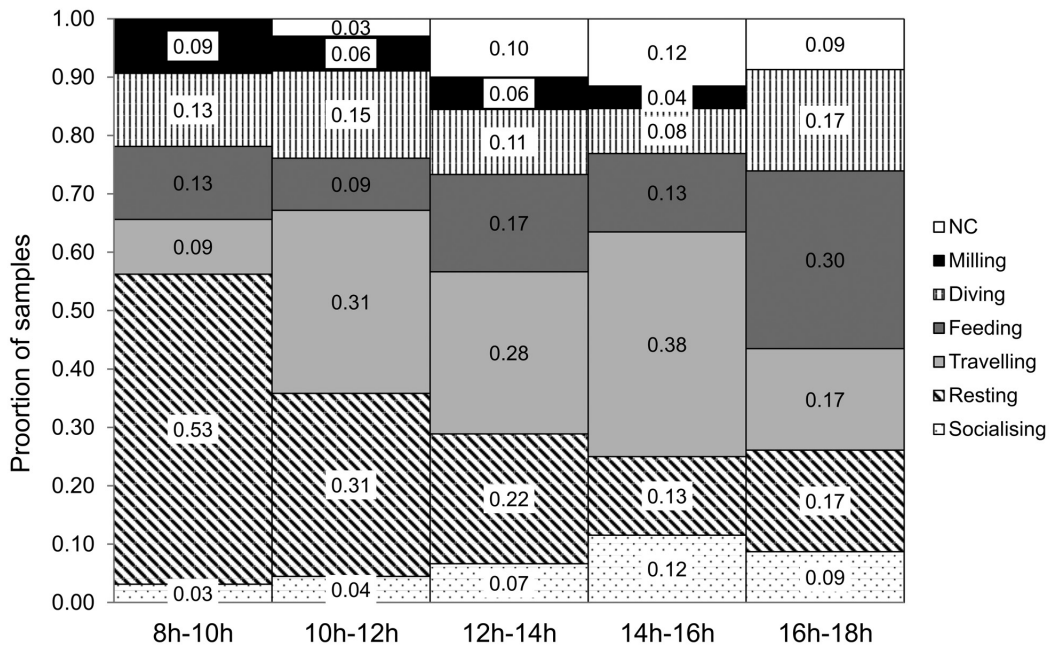|	Effort (h)			Amount of time of dolphin observations (h)				
	Total	Land-based	Boat-based	Total	Land-based	Boat-based	Total # DGs	#DGs used in analyses
Summer (15 mo)	400.8	224.6	176.2	60.8	23.2	37.6	117	98
Autumn (15 mo)	386.9	300.8	86.9	32.8	20.4	12.4	128	49
Winter (18 mo)	531.7	301.3	230.4	99.9	37.3	62.6	134	89
Spring (12 mo)	150.7	58.7	92.0	20.7	12.4	8.3	36	29
Total	**1,470.0**	**884.6**	**585.5**	**214.2**	**93.3**	**120.9**	**415**	**265**

Figure 2. Diurnal variation in relative frequencies of activities performed by bottlenose dolphin (*Tursiops truncatus*) groups in BSA (total: $n = 265$; 8 to 10 h: $n = 33$; 10 to 12 h: $n = 67$; 12 to 14 h: $n = 90$; 14 to 16 h: $n = 52$; 16 to 18 h: $n = 23$). Numbers in each block indicate each specific proportion of samples.

Resting clearly occurred mostly in the early morning, decreasing during the day, and then slowly increasing again in the evening (Figure 2). Social activity was observed more during the afternoon and evening periods; whereas, surface feeding seemed to peak in the evening hours (Figure 2). This diurnal trend did not seem to vary significantly across the surveyed years ($\chi^2 = 76.2$, $df = 114$, $p = 0.5$; data not shown).

The relative frequencies of observed behavioural patterns varied significantly among the different seasons ($\chi^2 = 83.7$, $df = 18$, $p < 0.01$). Socialising and surface feeding clearly peaked during winter and spring. Diving behaviour was observed during summer months after which it declined drastically into autumn and was not observed during winter or spring (Figure 3).

Group Size
Median dolphin group size ($\overline{X}$) was 4 (lower quartile value = 2, upper quartile value = 8, $n = 265$) and ranged from 1 to 50 individuals. The most frequently observed group size was 4 to 6 individuals (20%), followed by groups of 7 to 10 individuals (18%), pairs (16%), trios (12%), groups of 11 to 20 individuals (11%), and larger groups (8%). Lone individuals ($n = 40$) accounted for 15% of the sightings. Group sizes did not seem to vary across years (K-W H = 24.9, $df = 4$, $p = 0.7$) nor

over the various periods of any day (K-W H = 0.64, $df = 4$, $p = 0.4$). Group size did vary significantly across seasons (K-W H = 36.8, $df = 3$, $p < 0.01$), with groups being significantly larger in winter ($\overline{X} = 7$, $n = 89$) than during spring ($\overline{X} = 4$, $n = 29$), summer ($\overline{X} = 3$, $n = 98$), and autumn ($\overline{X} = 3$, $n = 49$) (separate Mann-Whitney U tests with Bonferroni correction $\alpha = 0.0125$: summer-autumn, U = 2,249, $p = 0.5$; summer-winter, U = 7,367, $p < 0.01$; summer-spring, U = 1,133, $p = 0.09$; autumn-winter, U = 1,142, $p < 0.01$; autumn-spring, U = 1,747.5, $p < 0.05$; winter-spring, U = 957.5, $p < 0.01$).

Dolphin group sizes were also analysed according to group behaviour. Groups were significantly larger when surface feeding ($\overline{X} = 10$, $n = 37$) and socialising ($\overline{X} = 8$, $n = 18$) than during all other classified behaviours (Figure 4; diving: $\overline{X} = 2$, $n = 32$; resting: $\overline{X} = 4$, $n = 74$; travelling: $\overline{X} = 4$, $n = 71$; milling: $\overline{X} = 3.5$, $n = 14$; K-W H = 54.4, $df = 6$, $p < 0.01$). More specifically, dolphin groups engaged in surface feeding during winter ($\overline{X} = 27.5$) were significantly larger than dolphin groups engaged in surface feeding during all other seasons (spring: $\overline{X} = 8$, summer: $\overline{X} = 4$, autumn: $\overline{X} = 7$; K-W H = 16.8, $df = 3$, $p < 0.01$). Groups for which the behaviour could not be classified had a median size of two individuals ($n = 19$, min. = 1, max. = 20).
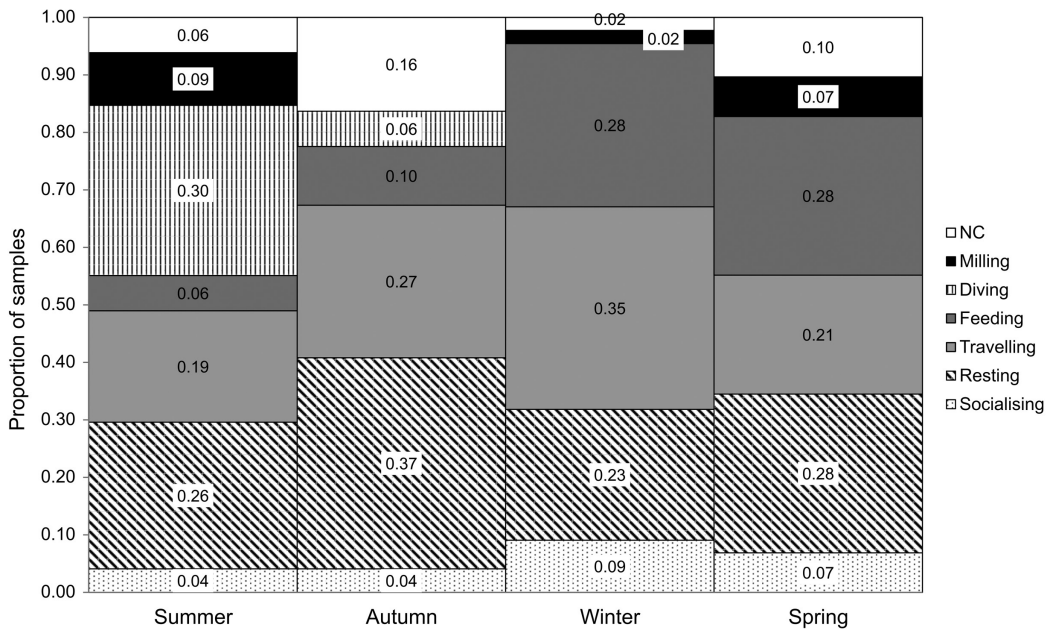

Figure 3. Seasonal variation in relative frequencies of activities performed by bottlenose dolphin groups in BSA (total: $n = 265$, summer: $n = 98$, autumn: $n = 49$, winter: $n = 89$, spring: $n = 29$); numbers in each block indicate each specific proportion of samples.
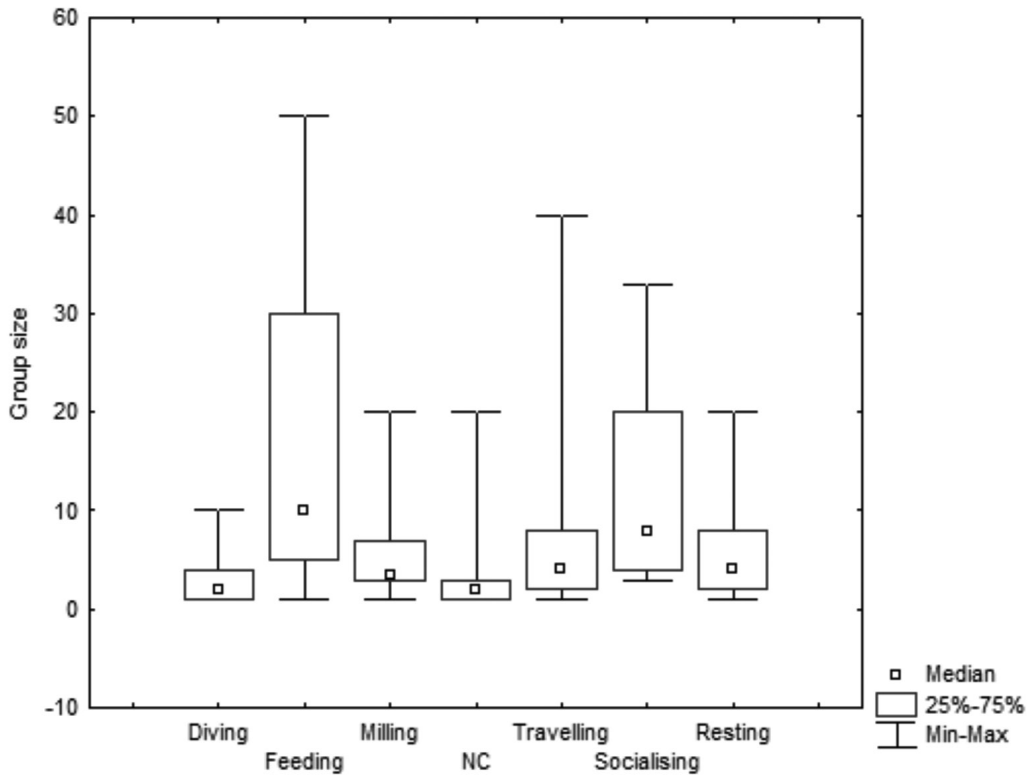
Figure 4. Median group size of bottlenose dolphins in BSA vs behaviour, indicating the median, quartile values, and non-outlier range (total: $n = 265$, socialising: $n = 18$, resting: $n = 74$, travelling: $n = 71$, surface feeding: $n = 37$, diving: $n = 32$, milling: $n = 14$, and not classified: $n = 19$)

Overall, 75% of the encountered DGs contained calves (between 1 to 8 calves per group). Excluding mother/calf pairs from analysis, group size seemed positively related to the presence of calves ($R^2 = 0.49$, $n = 72$, $p < 0.01$). Groups containing calves were significantly larger ($\overline{X} = 8$) than groups without calves ($\overline{X} = 3$; Mann-Whitney U-test: U = 1,756, $p < 0.05$).

Discussion

This study showed that bottlenose dolphins used the study area mainly to rest, travel, and feed. The frequencies of travelling and feeding activities are comparable to those found for other bottlenose dolphin populations inhabiting inshore waters (ranging between 15 to 36%; e.g., Shane, 1990b; Hanson & Defran, 1993; Lynn, 1995; Neumann, 2001) but varied on a diurnal and seasonal basis.

Resting has been defined as one of the most dangerous behaviours because of reduced vigilance (Würsig et al., 1994; Connor & Heithaus, 1996) and lack of seeming refuge from predators for aquatic mammals (Heithaus & Dill, 2002).

As dolphins have low travel costs (Williams et al., 1992), they will most likely rest in the safest habitats (Heithaus, 2001). Furthermore, in fission-fusion societies such as that of the bottlenose dolphin, one reason groups are believed to increase in size is to reduce predation risk (e.g., Heithaus & Dill, 2002). Therefore, the large amount of resting behaviour and the small median group size observed during resting behaviour seems to corroborate the low predation risk in the study area, reported previously by Vermeulen & Bräger (2015). This hypothesis seems further supported by the large number of dolphin groups with calves observed in the area.

Group size appeared to be positively related with the amount of calves in the group. This tendency has been reported for other bottlenose dolphin populations (dos Santos & Lacerda, 1987; Wells et al., 1987; Weigle, 1990; Weller, 1991; Bearzi et al., 1997) and was associated not only with better calf protection but also with increased calf assistance, reduced maternal investment, and the benefits of learning (Norris & Døhl, 1980; Johnson & Norris, 1986).

Diurnal Variation in Foraging Behaviour

It is believed that feeding habits have a large impact on shaping the behavioural patterns of bottlenose dolphins (Shane et al., 1986), a species that is known to have a range of feeding strategies and takes advantage of a number of prey items (Leatherwood, 1975; Barros & Odell, 1990). Therefore, a diurnal variation in their behaviour would be expected if available prey behaviour varies during the day.

The diurnal trend related to feeding activity showed remarkable similarities with another study conducted previously on this species in Peninsula Valdés, Argentina (Würsig & Würsig, 1979); however, our results differed from diurnal patterns found in Bahía Engaño, Argentina (Coscarella & Crespo, 2009); Galveston, Texas (Bräger, 1993); South Africa (Saayman et al., 1973); the north San Diego coast (Hanson & Defran, 1993); and Cardigan Bay, Wales (Bristow & Rees, 2001). These studies found a general but variable trend towards increased feeding activity in early morning and late afternoon. Still, some bottlenose dolphin populations show no diurnal cycle in their behavioural patterns—for example, in the Adriatic Sea (Bearzi et al., 1999) and in Sarasota Bay (Irvine et al., 1981; Scott et al., 1990). According to Bearzi et al. (1999), the lack of a diurnal pattern in his study population was linked to a large amount of time dedicated to foraging (82% of daily time budget), including searching for food in places with limited food resources. Nevertheless, as was indicated previously by Shane (1990b) and Bearzi et al. (1999), a direct comparison of behavioural patterns between regions is complicated. Dolphin behaviour will be influenced by a wide range of factors depending on the habitat in which they live. Furthermore, methodological differences in data collection and analyses, including, for example, the use of varying definitions for behavioural states, subjective interpretations of observed behaviour, and so on, can also make comparisons challenging.

Seasonal Variation in Foraging Behaviour and Group Size

In order to interpret the seasonal variation in foraging behaviour, it is important to consider the seasonal variation in prey availability and density within the study area. BSA is an important spawning and nursing area for many fish species like the South American silver porgy (*Diplodus argenteus*), Patagonian blenny (*Eleginops maclovinus*), Brazilian flounder (*Paralichthys brasiliensis*), silverside (*Odonthestes* sp.), Argentinean hake (*Mercluccius hubbsi*), and silver warehou (*Sironella porosa*) (DiGiácomo et al., 1993; Perier, 1994; Perier & DiGiácomo, 2002). All these species show a remarkable seasonal variation in their behaviour (Perier, 1994): during winter and early spring, they form dense shoals inside the bay to spawn near the coast; in summer, these species seek shelter near rocks and caves, although most leave the bay towards autumn. At the same time, Atlantic squid (*Loligo sanpaulensis*) enter the bay for spawning. Although very few data are available on the diet of bottlenose dolphins in Argentina, at least three of these species are confirmed prey–Patagonian blenny, Silverside, and South American silver porgy (Vermeulen, pers. obs., 2008).

Winter and Spring—Dolphins were more frequently engaged in surface feeding during winter and spring, which possibly indicates a higher energy demand during colder seasons caused by lower water temperatures (Shane, 1990a). Although possibly true for winter, this could not solely explain the variation in surface feeding in spring vs autumn when average water temperatures are similar. Bräger (1993) suggested that an increased amount of foraging might indicate more time is needed to obtain the required energy when less food is available. Bearzi et al. (1999) also related the large amount of foraging behaviour (82% of time budget) to a limited amount of prey species. On the other hand, Cornick & Horning (2003) showed that in some marine mammal species increased foraging time and efficiency were caused by an increase in prey encounter rate. McFadden (2003) indicated similar results for dusky dolphins (*Lagenorhynchus obscurus*) for which an increased feeding bout length was related to successful foraging in cooperative hunting groups.

The suggestion of increased prey availability during winter and spring in this study appears to be further supported by the clear increase in group size during surface feeding activities, especially in winter ($\overline{X}$ = 27.5), often related to increased food capture efficiencies when prey is abundant (e.g., Wells et al., 1980; Würsig & Würsig, 1980). Also, for spinner dolphins (*Stenella longirostris*), increased group size and cooperation were particularly evident when they were foraging in high prey densities (Benoit-Bird & Au, 2003). Indeed, the increased group size during foraging suggests a patchy prey distribution (Defran & Weller, 1999), and it might indicate dolphins were targeting the dense spawning shoals observed this time of year (Perier, 1994). Cooperative feeding in larger groups is expected to improve individual fitness when prey is aggregated and abundant (Wells et al., 1980; Defran et al., 1999; Wells & Scott, 2002).

Summer—Over the seasons, prey shifts may occur requiring more time to search for other

types of prey (Bräger, 1993), resulting in a shift of foraging strategy. As surfacing patterns characterised by long dives have been related to feeding activities (Gunter, 1954; Norris & Prescott, 1961; Hussenot, 1980; dos Santos & Lacerda, 1987; Bearzi et al., 1999), the diving behaviour observed during summer may be related to a "tail out/peduncle-dive" foraging strategy. In other regions, long dive durations have been related to resting (Lynn, 1995). Although no underwater observations were possible during this study to confirm our hypothesis, the very little amount of time dedicated to surface feeding behaviour in summer suggests that diving behaviour may be foraging related. We suggest this foraging strategy is related to the targeting of benthic species (i.e., spawning Atlantic squid [*Loligo sanpaulensis*]; Perier, 1994) and/or to the behavioural tendency of local prey species to seek shelter from predators under rocks and in caves, making them less easily accessible to the dolphins.

The significantly smaller group sizes during observed diving behaviour further indicate that prey targeted while diving was not aggregated and probably limited (Würsig, 1986). Such very small group sizes related to foraging have previously been suggested as a strategy to reduce scramble competition in bottlenose dolphins (Pearson, 2009). This means individuals distribute themselves among patches of resources to minimise competition (Gowans et al., 2007) and lower their time travelling between patches of food (Pearson, 2009). This way intraspecific competition is reduced, and individual fitness is increased (Würsig, 1986). It is clear that if the benefit of foraging individually is greater than that of foraging in a group, social foraging will not be a stable strategy (Caraco, 1987). It is said that preying on schooling species is the most energetically profitable foraging tactic for a cooperative predator (Meynier et al., 2008), suggesting that during summer, fewer schooling prey species were available.

Ecological aspects (e.g., habitat characteristics, prey availability, and predation risk) are considered to be important in shaping the social interactions within cetacean communities (Lusseau et al., 2003). The apparent variations in group size in this study is a clear reflection of bottlenose dolphins' tendency to live in fission-fusion societies (Würsig & Würsig, 1977; Wells et al., 1987) in which group size and composition will change to maximize behaviourally specific benefits (Gero et al., 2005). According to various authors, the benefits of grouping (e.g., summarised in Gygax, 2002) are often so predictable that differences in group size are better explained by the costs of grouping (Chapman et al., 1995). It is generally stated that the largest cost of grouping is related

to a reduced foraging efficiency (Chapman et al., 1995). Fission-fusion societies are thus known to improve the regulation of feeding competition and offer greater flexibility in exploiting resources (Lehmann & Boesch, 2004). This indicates that group size and composition will be adapted to be optimal according to the variation in prey species, abundance, density, and availability.

Conclusion

The presented data reflect the behavioural and social flexibility of bottlenose dolphins which is most likely related to changes in prey availability and density throughout the year. We suggest this flexibility allows these dolphins to regulate their fluctuations in intraspecific feeding competition.

Although the carrying capacity of a population is known to be related to the productivity and quality of its home range (Macdonald & Rushton, 2003; Mitchell & Powell, 2004), it is also important to consider how a population can make use of these resources. For example, Lusseau (2005) argued that area avoidance induced by human disturbance or predation risk can lower the population's carrying capacity (Singer et al., 2001; Heithaus & Dill, 2002; Mitchell & Powell, 2004). Also, Bertram (1978) stated that predation pressure could interfere with a population's carrying capacity by acting as an opposing pressure on grouping, limiting the possibility to form small groups when needing to regulate intraspecific competition. As was stated by Lehman et al. (2007), reducing costs of group living through a fission-fusion society is only possible in species for which the advantages of living in large groups are not primarily driven by predation pressure. It could thus be argued that a combination of factors inherent to the species and the study area, such as low cost of locomotion and low predation pressure, may have ensured that separating into small foraging groups remained a viable ecological option to reduce intraspecific competition, allowing the animals to make full use of a limited amount of resources.

Although no concrete information is present on causal factors of the severe bottlenose dolphin population declines in Argentina, hypotheses have been formulated about the wide-ranging effects of increasing environmental pressures such as overfishing (Bastida & Rodríguez, 2003; Coscarella et al., 2012). This raises questions on what may have made BSA favourable for maintaining one of the last remaining resident populations (Vermeulen & Cammareri, 2009). The present data could argue that the temporal occurrence of spawning shoals and a general low presence of other top predators, such as large sharks and killer whales

(*Orcinus orca*), directly and indirectly increased the population's carrying capacity in BSA, delaying the effects of prey depletion when compared to other regions. It might also explain the relatively high degree of residency of the population within this area (Vermeulen & Cammareri, 2009). Nonetheless, as this population also recently has been reported as declining (Vermeulen & Bräger, 2015), further detailed studies on foraging behaviour, targeted prey species, and carrying capacity are essential. In terms of conservation management, the presented information seems crucial in the evaluation of the recently commenced tourism activities as any potential of area avoidance might lead to a sudden decrease in the population's carrying capacity (Lusseau, 2005) with potentially devastating effects.

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