Temporal Determinants of Indo-Pacific Bottlenose Dolphin (*Tursiops aduncus*) Activity in the Port River Estuary (Adelaide, South Australia)

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Abstract

Activity budgets are a useful means of investigating an animal's relationship with its environment and can provide important conservation information. This study investigated the activity budgets of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Port River estuary in Adelaide, South Australia. A total of 106 d on the water provided 235.9 h of observation via individual follows with continuous sampling. Six categories (travelling, foraging, feeding, socializing, resting, and other) were recorded. There were statistically significant changes to daily activity budgets for resting, foraging, travelling, and feeding. There were no seasonal variations to the activity budgets, but foraging increased between December and March, which is the breeding period for these animals. These results were compared to bottlenose dolphin activity budgets in other parts of the world. These data provide a useful baseline against which to compare future impacts on this highly urbanized population.

Key Words: seasonal variation, Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, daily activity, activity budget, Port River estuary, South Australia

Introduction

The way an animal distributes its time among various activities is important in understanding the relationships between its behavior and its environment. Measurements of activity budgets over time have provided a valuable source of hypotheses concerning factors influencing behavior in a large variety of animal species (e.g., insects: Perrard et al., 2009; reptiles: Goodman, 2007; birds: Fasola & Biddau, 1997; bats, Burnett & August, 1981; cetaceans: Daura-Jorge et al., 2005; primates: Isbell & Young, 1993; Ménard, 2002; Hill et al., 2003; Ding & Zhao, 2004).

Activity budgets of bottlenose dolphins have revealed variations in activity patterns on a seasonal and daily basis in most areas studied, and these patterns are highly variable across sites. Würsig (1978), Shane (1990a), Hanson & Defran (1993), and Hart (1997), studying bottlenose dolphins in different parts of the world (Argentina, Florida and Texas, San Diego, and Florida, respectively), found a variety of seasonal differences in behaviors, while Lynn (1995) found no seasonal nor diurnal trends in Matagorda Bay, Texas. Most authors reported a daily pattern (Shane, 1990a; Hanson & Defran, 1993; Harzen, 1995; Hart, 1997; Allen et al., 2001), which differed according to regions. This literature overview indicates that bottlenose dolphins adapt their behavior to local ecological conditions, leading to highly variable activity patterns across regions. The behavioral flexibility shown by this species necessitates site-specific investigations.

The aim of the present study was to investigate the influence of temporal factors on the behavior of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from the Port River estuary in Adelaide, South Australia. Activity budgets were prepared according to time of day, season, and reproductive cycle, and the possible relations to biological and environmental factors influencing the activity patterns are discussed.

Materials and Methods

Study Area

The Port River estuary is 15 km northwest of central Adelaide, South Australia (Figure 1). The "estuary" is in fact a tidal inlet as the outfall of the Port River was diverted directly to the gulf in the 1950s. Most of the inlet is shallow (< 3 m at low tide) with the deepest waters located in two dredged channels (5 to 12 m). The study area has been heavily influenced by human activity (Wade, 2002). The Government of South Australia proclaimed the area a dolphin sanctuary in June 2005 through the
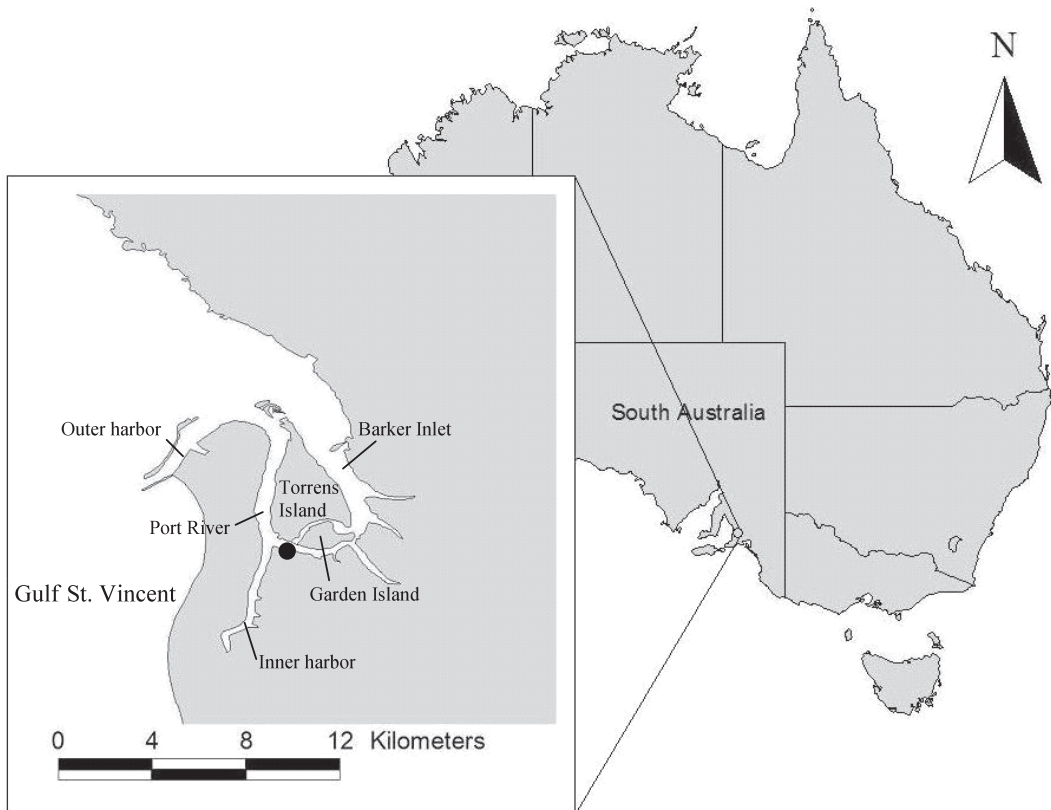
Figure 1. The Port River estuary is composed of the outer and inner harbors; the Port River, which is dredged to allow ships to reach the inner harbor; two islands (Torrens and Garden); and Barker Inlet, which, in turn, has several smaller inlets. Black dot = launch site.

Adelaide Dolphin Sanctuary Act in order to protect the bottlenose dolphins and their habitat.

Adelaide's climate is Mediterranean in character, with cold wet winters and warm dry summers. The median surface water temperature in the Port River estuary ranges from 12° C in July to 25.5° C in February (1997 to 2000; Wade, 2002). The seasons are defined as spring (September-November), summer (December-February), autumn (March-May), and winter (June-August).

Data Collection
Data were collected during daylight hours covering 19 mo, from October to November 2002, February to July 2003, and October 2003 to August 2004, in calm seas (sea state ≤ 3, Beaufort scale). The sampling method involved individual follows with a continuous sampling of behaviors (Altmann, 1974). The research vessel was launched in the north arm (Figure 1, black dot), and surveys were undertaken alternatively to the east or west of the launch site. When dolphins were encountered, a single individual was selected for the follow, with the choice being made to ensure that equal numbers of each age-class (only adults and subadults were followed) were represented in the data, as well as to ensure that as many individuals were included as possible. The selected dolphin was then followed as long as possible, and behavioral observations were continuously recorded into a handheld dictaphone, including the exact time of changes to behavior. The dolphin's location (i.e., estimated angle and distance from the boat via GPS coordinates) was noted every 3 min.

Adults were fully grown animals (estimated to be more than 1.8 m in length; Steiner & Bossley, 2008), all being individuals regularly seen in the area and known to be adults from a long-term photo-identification study ongoing in the estuary since 1989. Subadults were dolphins between 1.5 and 1.8 m that were not consistently accompanied by an adult. The distance between the boat and the dolphins was kept at approximately 50 m to minimize the disturbance effect of the boat but to still allow for effective observation of behavior. Sudden and erratic changes in boat speed or directions were avoided to reduce disturbance to the dolphins (Bearzi, 1994; Mann et al., 2000).

Field Effort

A total of 106 d were spent on the water, representing 496.8 daylight hours. Of these, 235.9 h were spent following dolphins, representing 47% of the total time on the water. In total, 113 follows were undertaken, lasting from 9 to a maximum of 417 min (average = 124 min, SD = 89 min) and involving 28 different individuals: nine adult females (113.4 h), nine adult males (79.0 h), two adults of unknown sex (1.9 h), and eight subadults of unknown sex (41.6 h). The total number and length of follows for each focal individual and which individuals were used for the analyses of activity budget across the different time variables are presented in Table 1. All individuals were involved in the analyses of activity durations. The distribution of the data collected is shown on Figure 2.

Data Analysis

Behaviors were categorized into six activities: (1) travelling, (2) foraging, (3) feeding, (4) socializing, (5) resting, and (6) other (a detailed ethogram can be found in Steiner, 2011). *Travelling* was characterized by dolphins moving in one direction and surfacing to breathe together at regular intervals. *Foraging* also involved dolphins moving in one direction, but they surfaced to breathe separately at irregular intervals. Small changes from the general direction of travel were often observed, as well as feeding events (e.g., fish chasing, fish throwing, sudden accelerations). *Feeding* was characterized by repeated dives in various directions in one area

Figure 2. Study area showing positions of the focal dolphins recorded every 3 min during follows (spatial data provided by the Department for Environment and Heritage, Government of South Australia)

or by dolphins chasing fish near the surface, with many surface behaviors such as fish chasing, fish throwing, and sudden acceleration. *Socializing* involved physical contact between the dolphins. *Resting* was characterized by dolphins swimming at a slow speed with intermittent surface resting (i.e., floating motionless at the surface), with or without travel in a general direction. *Other* encompassed all other behaviors which did not meet any of the above descriptions.

Activity budgets were calculated as percentage of time spent in each activity category. As follow durations and individual differences were shown to influence the calculation of activity budgets (Steiner, 2011), the activity budgets were calculated in the following manner: for each follow, activity durations were transformed into percentage (to give the same importance to each follow, regardless of duration); then, a mean value for all follows for each individual was calculated, resulting in the mean value of all individuals for each activity.

Days were divided in five equal periods: Period 1, early morning (until approximately 2.5 h after sunrise); Period 2, morning (approximately 2.5 to 5 h after sunrise); Period 3, mid-day (approximately 5 to 7.5 h after sunrise); Period 4, afternoon (approximately 7.5 to 10 h after sunrise); and Period 5, evening (from approximately 10 h after sunrise until sunset). Each period was defined as length of the daylight divided by five, which means that a period varies from 118 to 174 min depending on the season. Sunrise and sunset times were those given by Geoscience Australia, Australian Government (2012) for Port Adelaide.

Bottlenose dolphins in the study area have a predictable calving period between December and March (Steiner & Bossley, 2008). As the gestation in bottlenose dolphins is 12 mo (Reynolds et al., 2000; Perrin et al., 2002), the calving period also corresponds to the breeding period (December-March; nonbreeding period, April-November).

Differences in activity budgets according to daily period, season, and breeding period were tested among individuals in order to assure the independency of data. When analyzing the daily activity, each follow was divided according to the day period, and percentages of activities were first calculated per day period instead of per follow. Paired tests among the individuals sampled during each variable were performed using the Wilcoxon matched-pairs signed-rank test when two independent variables (breeding period) or a Friedman's two-way analysis of variance when more than two variables (day period and season).

When determining activity durations, activities at the beginning or end of a follow were discarded because their duration was necessarily an

Table 1. Follows' (respectively "follow-day-periods") number and length (into brackets, in min) of focal individuals; M = male, F = female, U = unknown; Sa = subadult, Ad = adult; B = breeding period, NB = nonbreeding period

ID	Age	Total	Day 1	Day 2	Day 3	Day 4	Day 5	Spring	Summer	Autumn	Winter	B	NB
F001	Ad	2 (156)											
F005	Ad	5 (845)	1 (4)	2 (203)	4 (184)	2 (241)	2 (212)					5 (293)	6 (552)
F028	Ad	1 (153)											
F033	Ad	3 (294)											
F200	Ad	8 (1,002)						2 (120)	5 (417)	6 (387)	1 (78)	7 (588)	7 (414)
F257	Ad	9 (1,268)	2 (117)	4 (154)	5 (393)	5 (544)	1 (60)					9 (740)	8 (528)
F351	Ad	9 (1,111)	4 (245)	5 (162)	3 (275)	2 (237)	3 (191)	2 (78)	5 (384)	6 (324)	4 (325)	9 (591)	8 (520)
F367	Ad	11 (1,824)	3 (134)	6 (684)	7 (612)	5 (379)	1 (16)	7 (858)	3 (288)	10 (612)	2 (66)	4 (417)	16 (1407)
F400	Ad	1 (153)											
M004	Ad	10 (1,750)	4 (174)	9 (675)	5 (458)	3 (315)	2 (129)	2 (142)	7 (582)	7 (519)	7 (507)	9 (816)	14 (934)
M008	Ad	2 (410)										3 (239)	2 (171)
M013	Ad	3 (576)	1 (99)	2 (143)	2 (157)	2 (173)	1 (4)					3 (204)	5 (372)
M063	Ad	1 (79)											
M080	Ad	3 (66)											
M097	Ad	2 (105)											
M149	Ad	4 (834)						2 (129)	3 (279)	2 (141)	3 (285)	3 (279)	7 (555)
M179	Ad	1 (144)											
M255	Ad	3 (774)	1 (105)	1 (3)	2 (205)	2 (253)	2 (208)	1 (102)	2 (198)	2 (282)	2 (189)		
U100	Ad	1 (27)											
U320	Ad	2 (86)										2 (50)	1 (36)
U329	Sa	5 (571)	1 (54)	2 (163)	2 (165)	1 (107)	1 (82)					2 (198)	5 (373)
U368	Sa	5 (492)	2 (92)	3 (103)	3 (79)	2 (141)	1 (77)					4 (168)	7 (324)
U371	Sa	3 (111)										3 (69)	1 (42)
U377	Sa	1 (222)											
U378	Sa	2 (273)										2 (135)	2 (138)
U385	Sa	3 (396)											
U386	Sa	1 (327)											
US	Sa	1 (102)											

underestimation, as they began before the initiation of follow or finished after the end of follow. In the analyses of differences in activity durations among daily periods, bouts covering more than one day period were removed. To test for differences between breeding periods, data were transformed to achieve normality of their distributions by using the following transformation: $\ln(x+20)$, where x is the activity duration in seconds. Student's *t*-tests were performed, and *P* values were corrected with the sequential Bonferroni technique or Holm's correction (Rice, 1989). There were not enough data per activity per daily period and per season to use a parametric test when testing differences in activity durations. In those cases, a Kruskal-Wallis test was performed. All statistical tests performed were calculated with the software *S-Plus 6.1* (Professional Edition, Insightful Corp., 1988, 2002).

Results

Daily Activity

Nine individuals were followed during each daily period, with 19 follows (17.1 h) during Period 1, 34 follows (38.2 h) during Period 2, 33 follows (42.1 h) during Period 3, 24 follows (39.8 h) during Period 4, and 14 follows (16.3 h) during Period 5. (The daily variation in activity of bottlenose dolphins in the Port River estuary is displayed in Figure 3.)

Resting, foraging, travelling, and feeding varied significantly during the day (Friedman $\chi^2 = 24.45$, 14.58, 14.13, and 11.34, respectively; $df = 4$; $p = 0.0001$, 0.006, 0.007 and 0.023, respectively). There were no significant differences for socializing and other during the day (Friedman $\chi^2 = 4.49$ and 7.88, respectively; $df = 4$; $p = 0.343$ and 0.096, respectively). Because the activity budget varied during the day, results were first pooled by day period instead of by follow to give the same weight to every period. These are referred to as "follow-day-period."

There were 528 bouts of activity measured within day periods. (The daily activity durations are displayed in Figure 4.) There were no significant differences in activity durations during the day (Kruskal-Wallis, H values from 0.835 to 7.763; $df = 4$; p values from 0.101 to 0.934).

Seasonal Variation

Six individuals were sampled during each season, with 16 "follow-day-periods" (23.8 h) during spring, 25 "follow-day-periods" (35.8 h) during summer, 33 "follow-day-periods" (34.4 h) during autumn, and 19 "follow-day-periods" (24.2 h) during winter. (Seasonal variations in bottlenose dolphins' activities in the Port River estuary are displayed in Figure 5.)

No significant differences were found among seasons (Friedman χ^2 values from 1.37 to 7.4; $df = 3$; p values from 0.06 to 0.71).

A total of 590 bouts of activity were measured during the study period. (Seasonal activity durations are shown in Figure 6.) Activity durations
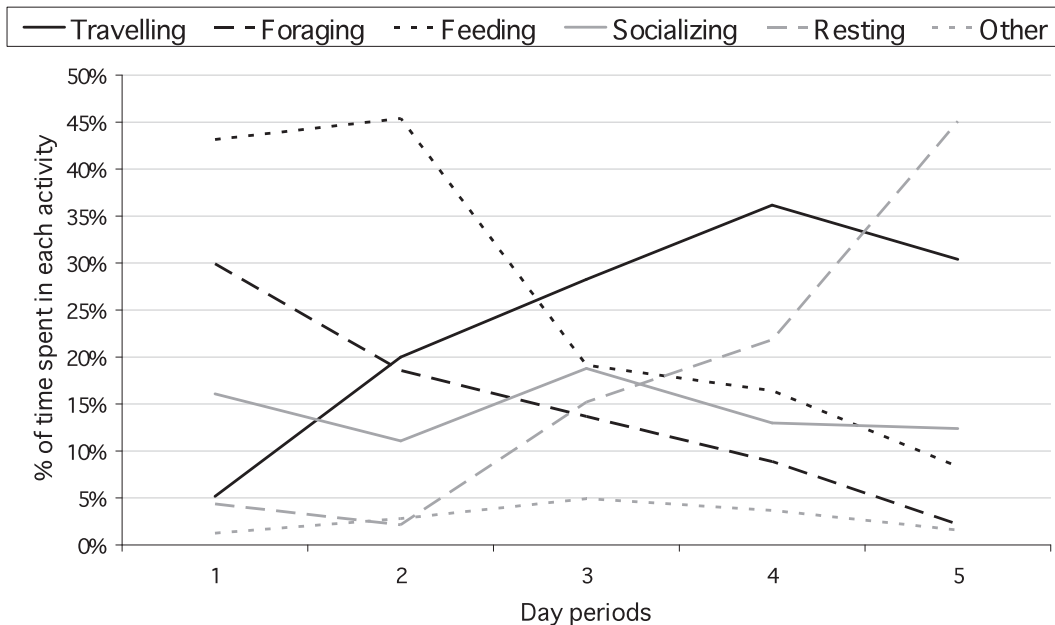

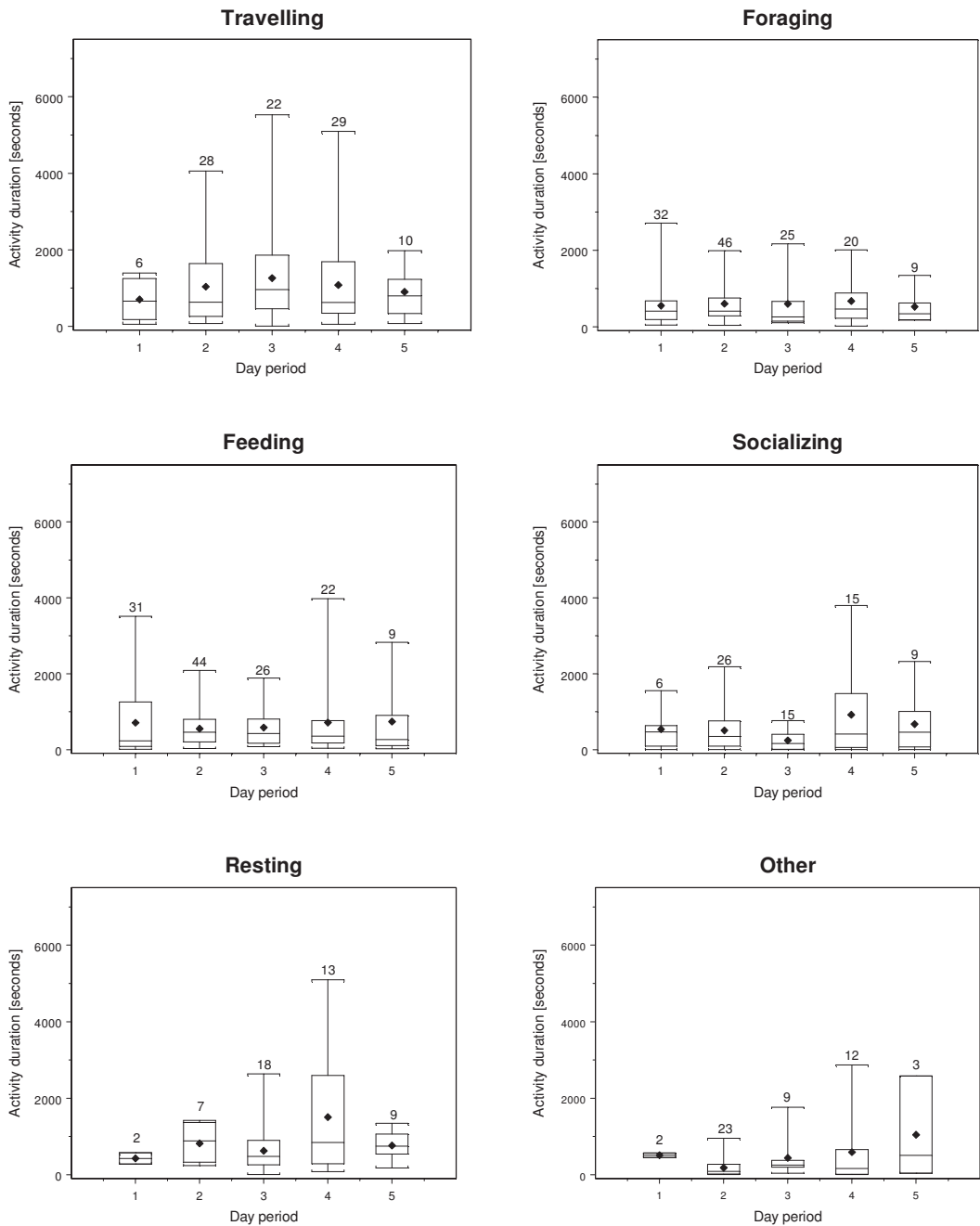**Figure 3.** Daily activity budget of bottlenose dolphins in the Port River estuary

Figure 4. Durations of activities per day period; numbers above each box represent the number of activity bouts in each category; ♦ = mean activity duration, box limits = 25th and 75th percentiles, whiskers = min and max.

did not vary significantly across seasons (Kruskal-Wallis; H values from 1.259 to 6.407; *df* = 3; *p* values from 0.093 to 0.739).

Fourteen individuals were followed during breeding and nonbreeding periods. When combining data into breeding (December to March, 65 "follow-day-periods," 79.8 h) and nonbreeding (April to November, 89 "follow-day-periods," 106.1 h) periods (Figure 7), only foraging varied significantly (paired Wilcoxon test; *n* = 14; *p* = 0.013). All
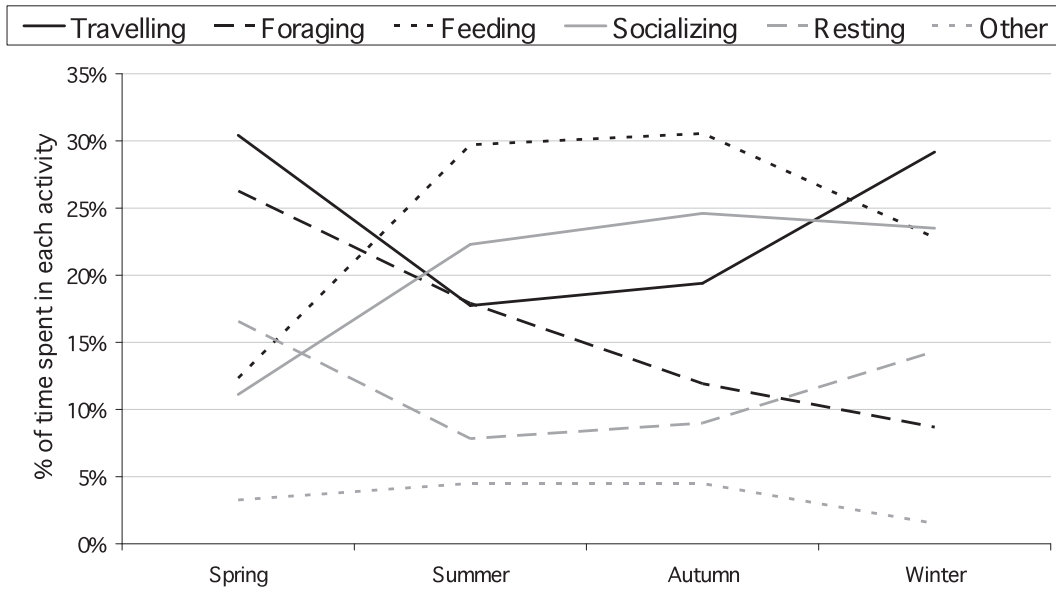
Figure 5. Seasonal activity budget of bottlenose dolphins in the Port River estuary

other activities did not show significant differences (paired Wilcoxon test; $n = 14$; p values from 0.067 to 0.952).

There were 590 bouts of activity measured during breeding and nonbreeding periods. (Activity durations according to the reproduction cycle of the bottlenose dolphins in the study area are displayed in Figure 8.) Activity durations did not vary significantly (Student t-tests; data transformation = ln(x+20); t values from -1.153 to 0.535; df from 52 to 144; p values from 0.253 to 0.924).

Discussion

Bottlenose dolphins in the Port River estuary displayed a clear daily activity pattern, with the relative amount of travelling, feeding, foraging, and resting varying during the day. Dolphins fed more during the first two periods of the day and far less from the mid-day period onward. Foraging also decreased during the day. Travelling increased during the day, with a peak at Period 4. Dolphins showed a small amount of resting during the two first periods, followed by a continuous increase in resting behavior for subsequent periods.

In most of the bottlenose dolphin populations studied around the world, the feeding activity tended to be at its maximum during both the morning and evening (Tayler & Saayman, 1972; Saayman et al., 1973; Shane, 1990a, 1990b; Bräger, 1993; Hanson & Defran, 1993; Bristow & Rees, 2001). However, Würsig & Würsig (1979) found a greater amount of feeding in the afternoon; Hart (1997) at midday;

Harzen (1995) at midday and in the evening; and Lynn (1995) and Liret (2001) during mornings only, or throughout the day during winter (Liret, 2001) or fall (Bräger, 1993). Allen et al. (2001) found a morning peak in feeding during summer, but they did not sample long enough to observe an eventual second peak in the evening. Most authors hypothesized a relationship between the daily pattern of feeding and availability of prey, but no study has presented quantitative data on this. Benoit-Bird & Au (2003) studied the abundance of spinner dolphins (*Stenella longirostris*) and their prey acoustically and found that dolphins followed the diel and vertical migration of their prey.

The other activity regularly reported by researchers to vary within the day is socializing, with peaks during afternoon (Würsig & Würsig, 1979; Bräger, 1993), afternoon and evening (Hart, 1997; Bristow & Rees, 2001), or evening (Shane, 1990b). Saayman et al. (1973) found socializing activity to occur in between two feeding peaks (i.e., from 0800 to 1700 h), with a first peak around 0900 h and a second one around noon; and Tayler & Saayman (1972) found a socializing peak during midday in captive dolphins. Daily activity of bottlenose dolphins varies widely among populations around the world. This probably reflects the wide behavioral flexibility of this species, with adaptations to local ecological conditions.

In the Port River estuary, bottlenose dolphins fed and foraged during the morning, then gradually moved to travelling and resting, with socializing remaining steady throughout the day. If feeding was related to the availability and distribution of
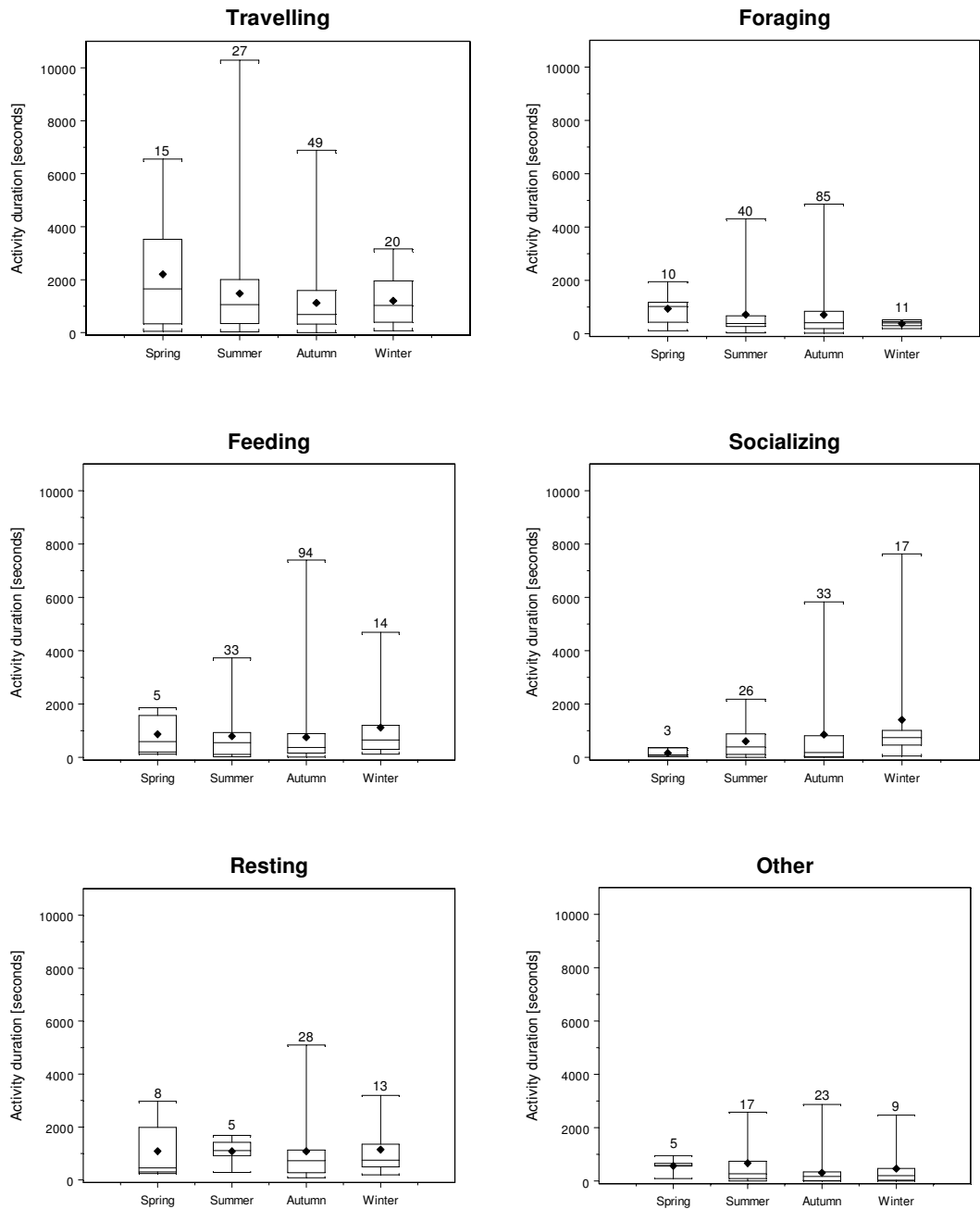
Figure 6. Durations of activities per season; numbers above each box represent the number of activity bouts in each category; ♦ = mean activity duration, box limits = 25th and 75th percentiles, whiskers = min and max.

prey, this marked difference in daily activity budget suggests dolphin prey in the estuary was available mostly during the morning. Researchers studying diel variations in fish abundance have frequently found diurnal-nocturnal differences, with fish changing behavior and locations between day and night (Rountree & Able, 1993; Gray et al., 1998; Methven et al., 2001; Jaafar et al., 2004). Hanson & Defran (1993) hypothesized that the crepuscular peaks in feeding by bottlenose dolphins of the
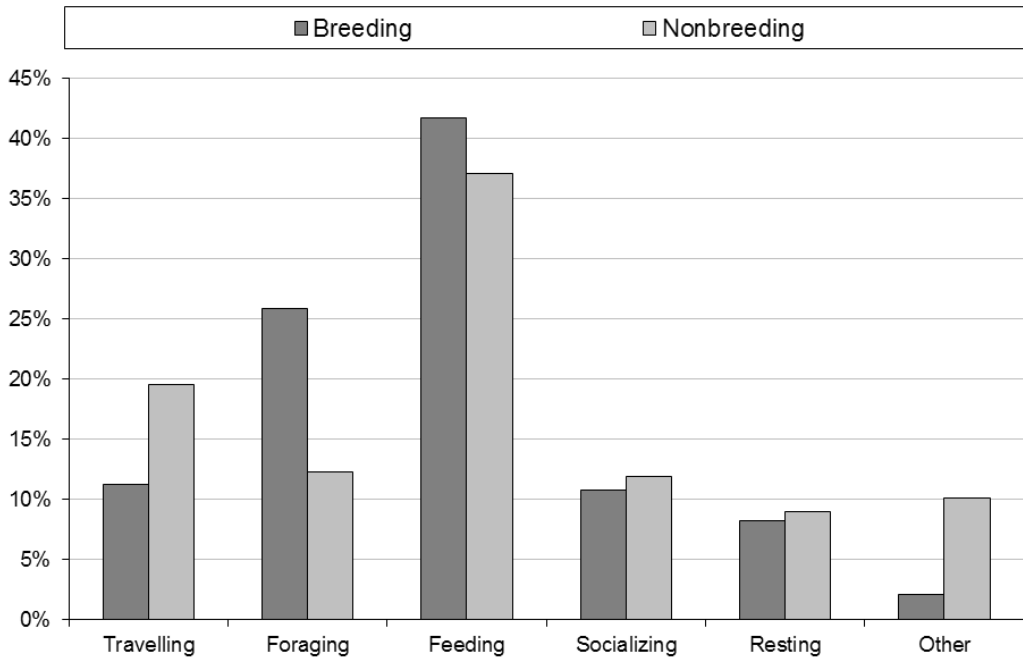
Figure 7. Activity budget of bottlenose dolphins in the Port River estuary according to breeding/nonbreeding periods
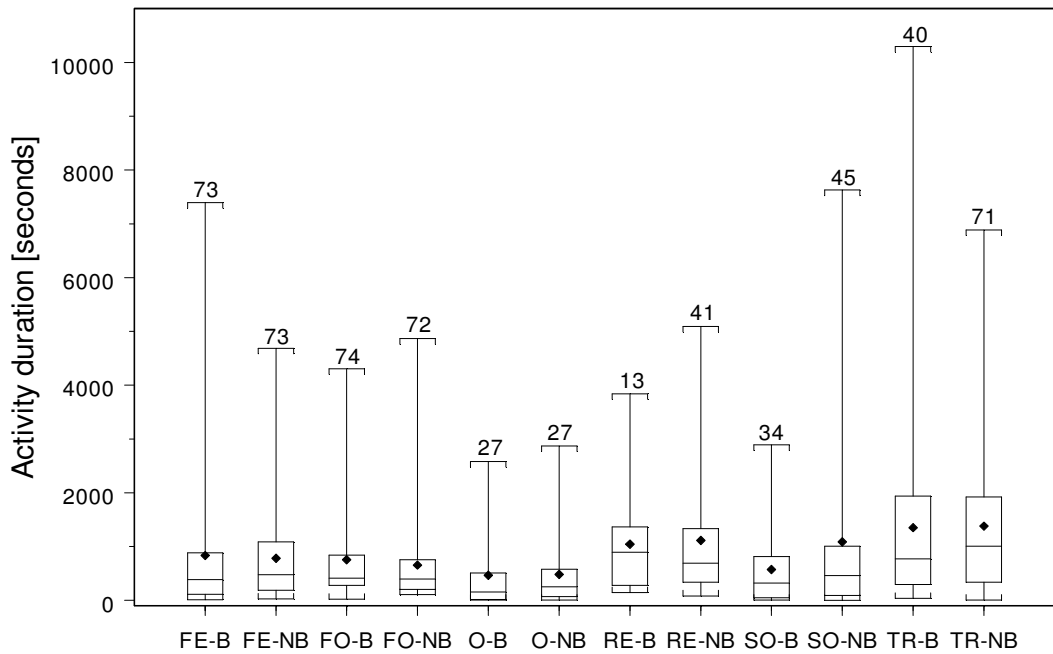

Figure 8. Durations of activities according to breeding/nonbreeding periods; FE = feeding, FO = foraging, O = other, RE = resting, SO = socializing, and TR = travelling; B = breeding, NB = nonbreeding; numbers above each box represent the number of socializing bouts in each season; ♦ = mean duration, box limits = 25th and 75th percentiles, whiskers = min and max.

Pacific coast were due to greater accessibility of prey transiting between nocturnal and diurnal habitats. Hart (1997) expected the same tendency but found feeding peaks during morning, midday, and afternoon, and linked those to the fact that prey were located in shallow seagrass beds during the day and easier to catch there than in deeper waters. Methven et al. (2001) found that fish species in a Newfoundland estuary moved to shallow areas at night from adjacent deeper waters. Those differences were noticeable at 4 m deep. In the Port River estuary, the deepest area is the dredged channel reaches 12 m, a depth easily achieved by diving bottlenose dolphins (Hastie et al., 2006). In the western part of the estuary, depths are even shallower, reaching a maximum of approximately 3 to 4 m in the channels. Dolphins in the Port River estuary were often observed "diving" (a behavior linked to feeding; Steiner, 2011) in the deepest part of the estuary (i.e., the dredged channel). Thus, it is possible that prey in the estuary were available throughout the day. This suggests another hypothesis: that dolphins first feed to meet their energy requirements for the day before performing other activities in the remaining time available. Differentiating between the two hypotheses—that is, whether the morning feeding peak was due to a difference in prey availability or to energetic requirements—would require information on diel variation in fish abundance and distribution in the estuary. Knowledge of the night behavior of bottlenose dolphins would also help to elucidate these diel patterns.

The durations of activity did not show significant variations during the day, unlike the activity budget. This indicates that the differences in percentages of activity found for feeding, foraging, resting, and travelling were not the result of longer or shorter activity bout durations but, rather, of a different number of those bouts during different daily periods. However, caution should be made in interpreting these results as there were some categories with only a small amount of data.

Bottlenose dolphins in the Port River estuary did not show seasonal differences in activity, and only foraging was significantly higher during the breeding than the nonbreeding period. The durations of activities did not vary across season or according to the reproductive cycle of the dolphins. Water temperature in the estuary showed a variation of 14° C (Wade, 2002; median monthly temperatures from 12° C in July to 25.5° C in February, 1995 to 2000). Other bottlenose dolphin populations living in environments with a wide range of temperatures showed seasonal variations with increasing feeding rates during autumn, which was hypothesized to be linked with the build up of fat stores for winter (Shane, 1990a; Hart, 1997). However, Bearzi et al. (1997) found no consistent patterns in seasonal

variations of feeding in the Kvarneric, an environment with wide differences in water temperature between summer and winter, suggesting feeding variation is more likely related to prey availability than changes in energetic requirements due to water temperatures. This hypothesis was also suggested by Hanson & Defran (1993), who found no trends in feeding variations with season and suggested that this was related to the year-round presence of prey. Chilvers et al. (2003) found a higher summer feeding peak in the non-trawler (i.e., dolphins which have never been observed foraging around trawlers) bottlenose dolphins of Moreton Bay, also suggesting that feeding variations were linked to prey availability rather than changes in water temperature. In the Port River estuary, abundance of the dominant fish species found in the area showed little monthly variation, and they were among the species showing the least inter-annual variability (Jackson & Jones, 1999), suggesting a relatively constant prey availability for bottlenose dolphins. This could explain the lack of seasonal variation in feeding rates in the estuary, and it also suggests that bottlenose dolphin behavior is directly influenced by prey availability but not by energetic requirements due to changes in water temperature. However, prey availability can be influenced by water temperature in other regions, resulting in an indirect influence on bottlenose dolphin behavior.

Although births mainly occur in the December to March period, this is not matched by a corresponding increase in socializing in this period. No differences in socializing rates were found between the breeding and the nonbreeding periods. It was impossible to differentiate copulative behavior from other contact behaviors in the field. Bottlenose dolphins seem to use sexual and contact behaviors in other contexts than reproduction such as to reinforce social bonds, to test dominance patterns, or to play (Brown & Norris, 1956; Herman & Tavolga, 1980; Östmann, 1991; Connor & Peterson, 1994; Reynolds et al., 2000). In the estuary, bottlenose dolphins socialized all year round, suggesting that social contacts are important not only for reproduction during the breeding period. It is possible, however, that a change in the proportion of copulative behaviors versus other social behaviors occurred during the breeding period, but this was not detected by the sampling method.

This quantitative behavior budget data provides an important baseline against which to measure the effect of the numerous potential impacts on dolphins in the Port River estuary. For example, a decrease in prey availability would be expected to lead to an increase in feeding/foraging time for dolphins; a decrease in the amount of resting behavior may be indicative of too much attention from dolphin watching vessels; and an

increase in travelling may indicate environmental degradation. In the long term, changes to seasonal behavior budgets may be expected to relate to climate change impacts. Differences between behavior budgets displayed by Port River estuary dolphins and those of dolphins in other habitats may also provide indications of human impacts.

Acknowledgments

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