

# eScholarship

## International Journal of Comparative Psychology

### Title

Seasonal, Diel, and Age Differences in Activity Budgets of a Group of Bottlenose Dolphins (*Tursiops truncatus*) Under Professional Care

### Permalink

<https://escholarship.org/uc/item/3qc0z4dq>

### Journal

International Journal of Comparative Psychology, 30(0)

### ISSN

0889-3675

### Authors

Walker, Rachel T.  
Miller, Lance J.  
Kuczaj, Stan  
[et al.](#)

### Publication Date

2017

### DOI

10.46867/ijcp.2017.30.00.05

### Copyright Information

Copyright 2017 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



## Seasonal, Diel, and Age Differences in Activity Budgets of a Group of Bottlenose Dolphins (*Tursiops truncatus*) Under Professional Care

Rachel T. Walker<sup>1</sup>, Lance J. Miller<sup>2</sup>, Stan A. Kuczaj II<sup>3</sup> and Moby Solangi<sup>4</sup>

<sup>1</sup>*University of the Incarnate Word, U.S.A.*

<sup>2</sup>*Chicago Zoological Society - Brookfield Zoo, U.S.A.*

<sup>3</sup>*The University of Southern Mississippi, U.S.A.*

<sup>4</sup>*The Institute for Marine Mammal Studies, U.S.A.*

Wild bottlenose dolphin (*Tursiops truncatus*) behavior is impacted by a number of factors including season, time of day, and age. However, less is known about how these factors may influence animals under professional care in zoos, aquariums and marine parks. Management practices such as scheduled feeding times, human interactions, lack of predators and show performances may also impact the activity budgets of dolphins. The current study examined the rest, swim and play behavior of seven dolphins (three adults, four calves) at one facility. Data were collected over the entire 24-hour day for a period of one year. Observed behaviors were recorded in mutually exclusive categories including rest, low intensity swim, high intensity swim, low intensity play, high intensity play and social play. Data were analyzed to determine how often dolphins engaged in particular behaviors and if activity budgets varied due to season, time of day and age. These dolphins spent the majority of their time in low intensity swim and low intensity play. The activity budget varied between observational periods. First, seasonal differences were found in low intensity swim, low intensity play, social play and high intensity play behaviors. In the comparison for time of day, differences were found in rest, low intensity swim, low intensity play and social play. Finally, no significant differences were found in age comparisons. Information gained from this study can help to better understand how different factors influence the behavior of bottlenose dolphins under professional care within zoos, aquariums and marine parks.

Animals that live in highly social groups budget their time to a variety of activities such as foraging, travel, socialization, rest and play. These activities can be influenced by a variety of factors (i.e., environmental) and an animal will utilize an efficient strategy based on these factors. Adaptation to environmental and developmental elements can play a role in the activity budgets of an animal (Beltrán & Delibes, 1994) and can provide the ability to interpret animals' reactions to abiotic and biotic factors (Walsberg, 1983; Weathers, Buttemer, Hayworth, & Nagy, 1984). Studying bottlenose dolphin (*Tursiops truncatus*) activity budgets, in a variety of environments, assists in the understanding of the impact of diel, environmental and developmental factors. Specifically, behavior analysis can assist successful management of animals under professional care (Maple & Segura, 2015).

Bottlenose dolphins are naturally found in temperate and tropical waters living in social hierarchies varying from 2 to 10,000 individuals depending on the region (Ridgway & Harrison, 1999). Wild bottlenose dolphins are typically active day and night (Ballance 1992; Irvine, Scott, Wells, & Kaufmann, 1981; Shane, Wells, & Würsig, 1986; Tayler & Saayman, 1972) with factors such as season, time of day and tidal state all influencing behavior (Bearzi, Politi, & di Sciara, 1999; Brager, 1993; Coscarella, Pedraza, & Crespo, 2010; Gregory & Rowden, 2001; Henderson & Würsig, 2007; McHugh, 2010; Shane et al., 1986; Waples, 1995; Wells et al., 2013). However, likely due to the difficulty of studying wild dolphin behavior during the evening,

a majority of what is known about bottlenose dolphins is through diurnal studies (Gregory & Rowden, 2001; Hansen & Defran, 1993; Irvine et al., 1981; Mann & Smuts, 1999; McBride & Hebb, 1948; Norris et al., 1985; Norris & Dohl, 1980; Saayman, Tayler, & Bower, 1973; Scott, Wells, Irvine, & Mate, 1990; Shane, 1990a; Wells, Scott, & Irvine, 1987; Wursig & Wursig, 1980).

The environmental context can play a role in daily activity budgets. For wild dolphins, one comparison regarding the daily activity budgets of dolphins in different regions of the world, show that the most frequently observed behavior is traveling from one location to another (Degrati, Dans, Pedraza, Crespo, & Garaffo, 2008; McHugh, 2010; Waples, 1995; Wells et al., 2013). Degrati et al. (2008) used instantaneous scan sampling to measure the main activity of a group. While traveling was the most observed behavior, milling, foraging, socializing, and resting were also observed. However, in Patos Lagoon Estuary, Southern Brazil dolphin activity budgets are somewhat different, spending the most time feeding as opposed to traveling (Mattos, Dalla Rosa & Fruet, 2007). In this study a group scan sampling technique was used to determine the activity budgets. One thing that is evident and similar across all dolphin populations is that wild dolphins are observed to spend very little time resting during the day (Mattos et al., 2007; Wells et al., 2013). In addition, there is great variability in the time of day that dolphins rest. For example, dolphins in Sarasota Bay are most commonly found resting in the late afternoon compared to the morning hours for dolphins in Argentina and Southern Brazil (Mattos et al., 2007; Waples, 1995; Wursig & Wursig, 1979). Differences in activity budgets could also be influenced by provisioning (i.e., feeding wild dolphins). Foroughirad and Mann (2013) determined that provisioning seemed to impact activity budgets of calves more than the mothers. In this situation it provided information regarding the development and survival of calves in provisioned environments.

Similar outcomes have been found as the result of environmental differences in activity budgets due to the type of enclosed facility. Sekiguchi and Koshima (2003) found that the dolphins spent more time in the rest/sleep behavior during the night, which was a time in which feeding was not offered. Another environmental factor in enclosed facilities could also be related to the shape of the enclosure. For example, the type of swimming behavior, circular or laterally, is also influenced by the type of enclosure as well (Sobel, Supin, & Myslobodsky, 1994; Ugaz, Valdez, Romano, & Galindo, 2013).

Seasonal differences in behavior for wild bottlenose dolphins have also been observed. For example, wild dolphins in the Mississippi Sound spent more time foraging in the fall (Miller, Solangi, & Kuczaj, 2010) whereas foraging was the highest in the winter for dolphins in Southern Brazil (Mattos et al., 2007). Similarly, dolphins in the Mississippi Sound travel more in the winter (Miller et al., 2010) whereas dolphins in Southern Brazil spent a higher percentage of time traveling in the spring (Mattos et al., 2007). However, social behaviors are most prevalent during the spring across both of these areas (Mattos et al., 2007; Möller, 1993; Miller, et al., 2010). There is no evidence of seasonal studies on the activity budgets of bottlenose dolphins in a professional managed care facility. However, seasonal comparisons in other species have been examined in professional care. Kuhar (2008) examined the impact of the crowd size on gorilla (*Gorilla gorilla*) behavior suggesting this may be based on the time of year. It was found that gorillas' at Disney's Animal Kingdom® Theme Park varied in some of their behaviors due to the type of social group and the quantity of the visitors (i.e., small crowd vs large crowd).

In addition to seasonal and diel differences in behavior, dolphin behavior also varies by age. The development of play behaviors have mostly been observed in dolphins in professional care. Specifically, within the first year of life, socialization is at the highest level. This could play a role in the development of social interactions (Gibson & Mann, 2008). Several studies have found that social play is more prevalent during the first year (Mackey, Makecha & Kuczaj, 2014; von Streit, Ganslosser & von Fersen, 2013). In one study during

the first year of life three calves showed a progression of social play behaviors. It is possible that there was a continuous increase in social play in the oldest calf as the result of the birth of the two new calves (Mackey et al., 2014). In addition, calves have a higher display of novel and more complex behaviors than adults (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006). It is important to indicate that in this group of dolphins the adults also engaged in play behavior but less often (Paulos et al., 2010). It has also been recognized that dolphins under professional care engage in more play behavior than their wild counterparts likely due to the lack of environmental pressures (Greene, Melillo-Sweeting, & Dudzinski, 2011).

Information currently available on bottlenose dolphin activity budgets has been limited by the difficulty of nocturnal observations, (Gregory & Rowden, 2001; Hansen & Defran, 1993; Irvine et al., 1981; Mann & Smuts, 1999; McBride & Hebb, 1948; Norris et al., 1985; Norris & Dohl, 1980; Saayman et al., 1973; Scott et al., 1990; Shane, 1990a; Wells et al., 1987; Wursig & Wursig, 1980) consistency of observing the same animal, and reliability between different observational techniques (Karniski et al., 2004). Although the current study does not seek to generalize results to wild populations, the work provides a framework for monitoring possible seasonal, diel and age effects on behavior as well as providing information on factors that impact dolphin behavior under professional care. The goal of the current study was to examine the activity budgets for a group of bottlenose dolphins at one facility. Information gained from this study will add to our general knowledge of bottlenose dolphin behavior. Collecting activity budgets can also help animal care staff at different facilities to routinely monitor animal behaviors to investigate individual, seasonal, diel and age effects on behavior. Finally, by systematically recording and analyzing the behavior of a social group, insight can be used to make informed animal management decisions based on those impacts (Greco et al., 2016; Meehan, Mench, Carlstead, & Hogan, 2016).

## Method

### Study Animals and Location

The subjects of the study included nine Atlantic bottlenose dolphins (*Tursiops truncatus*) at Marine Life Oceanarium Park in Gulfport, Mississippi (Table 1). Dolphins were housed in an outdoor circular pool that measured 20 ft in length and 30 ft in depth. Although there was a roof above the pool to provide shade, the dolphins were in an open air environment with areas of the pool exposed to sunlight and wind. The facility operating hours were between 0900 to 1700 or 1900, depending on the time of year. The dolphins schedule for feeding and education programs varied by season although diet was consistent throughout the year. During the summer, adult dolphins participated in five education programs per day compared to three or four times during the spring and fall and three times during the winter. In between programs or feeding times, dolphins were provided with environmental enrichment such as basketballs or nautical buoys.

### Data Collection

Data collection occurred between June 2000 and May 2001. All observations were conducted via the top level of the circular pool. In addition to surface behaviors the observer also could observe underwater behavior of the dolphins. Data were collected over a full 24-hrs during four different seasons. Within each season eight weeks of behavioral observations was taken for a total of 32 weeks of data. Observations were made during June and July for the Summer; September, October and November for the Fall; January and February for the Winter; March, April and May for the Spring. Observations lasted 30 minutes with scans noting each dolphin's behavior occurring every five mins resulting in seven scans during each observation. The average number of observations and the average air temperature is provided for each season (Table 2). The water temperature was not measured, however our understanding was that the temperature was not held constant which would produce seasonal like effects. Observations were not conducted during the 15 minutes before or following a dolphin performance show. In order to aide observations, two soft artificial lights were positioned and used above the pool during the evening. Dolphins were given four weeks to habituate to the novel light source. Within the first week any orientation towards the lights diminished. Observers used scan sampling (Altmann, 1974) to determine the approximate percentage of time dolphins were engaged in different behaviors. The mutually exclusive operational behaviors included rest, low intensity swim, high intensity swim, low intensity play, high intensity play, social play and not visible (Table 3). Information was also

collected to determine if the dolphin was solitary, paired with another dolphin or in a group of dolphins. All observations were conducted by three trained observers. Reliability testing occurred weekly throughout the study, in which two observers recorded behavior during the same time once a week, to ensure reliable behavioral data. Inter-observer reliability was consistently 95% or higher.

Table 1  
*Age, Sex, and Age Class for Each Dolphin*

Dolphin	Age at Time of Study	Sex	Age Class
D1	< 1 year	M	Calf
D2	1 year	M	Calf
D3	1 year	M	Calf
D4	2 years	F	Calf
D5	3 years	M	Calf
D6*	17 years	F	Adult
D7*	25 years	F	Adult
D8*	26 years	F	Adult
D9*	27 years	M	Adult

*Note.* \*All ages of the wild caught dolphins are approximate. D1 and D9 were not included in the data set due to incomplete observations. D1 was born and D9 was relocated during that Spring season.

Table 2  
*Mean and Standard Deviation of the Number of Observations and Air Temperature*

Season	Observations		Air Temperature	
	M	SD	M	SD
Summer	1325.3	8.3	83.38	6.66
Winter	1302.7	3.3	71.58	8.46
Spring	1213.3	4.3	68.7	8.1
Fall	1342.1	0.4	82.8	8.12
Total	5174	12.6	69.2	12.65

Table 3  
*Operational Definitions for Behavior States Recorded*

Behavioral Category	Definition
Rest	Floating on the surface, within the water column, or on the bottom. This can occur as a solo, pair or group-resting bout.
Low Intensity Swim	Movement around the tank and throughout the water column. This can occur as a solo, air or group swim.
High Intensity Swim	Short bursts of an increase in swimming speed to above normal levels.
Low Intensity Play	Includes such activities as ball/object tossing, ball/object carries, and bubble biting. Also, interacting with a human through ball tossing or ball play.
High Intensity Play	Includes such things as beaching, solo aerial displays, or jumping on and trying to balance on the larger bumper balls.
Social Play	The individuals under observation interacting with other animals, by chasing, being chased, sexual play, group aeriels or aeriels while in a group.
Not Visible	Dolphin was not visible during the scan.

## Statistical Analysis

All data were corrected for time visible, examined and determined to not be normally distributed. Non-parametric statistics were used for all analysis. A Mann-Whitney U test was used to examine age while a Friedman's test was used to examine seasonal differences and a Wilcoxon signed rank test was used to examine diel differences in behavior. For significant Friedman's test results, all pairwise comparisons were utilized to determine where differences exist. For all statistical tests, alpha level was set at  $p < 0.05$ .

## Results

In general, the dolphins (excluding Dolphin D1 and D9) spent the most time in low intensity swim (63.8%  $\pm$  6.4%) and low intensity play (23.6%  $\pm$  7.6%) behaviors. The behaviors of social play (7.9%  $\pm$  6.0%), rest (4.4  $\pm$  2.9%), high intensity play (0.5%  $\pm$  0.4%), and high intensity swim (0.5%  $\pm$  0.4%) accounted for a smaller percentage of their daily activity budgets. Diel behaviors varied based on the individual (Figure 1).

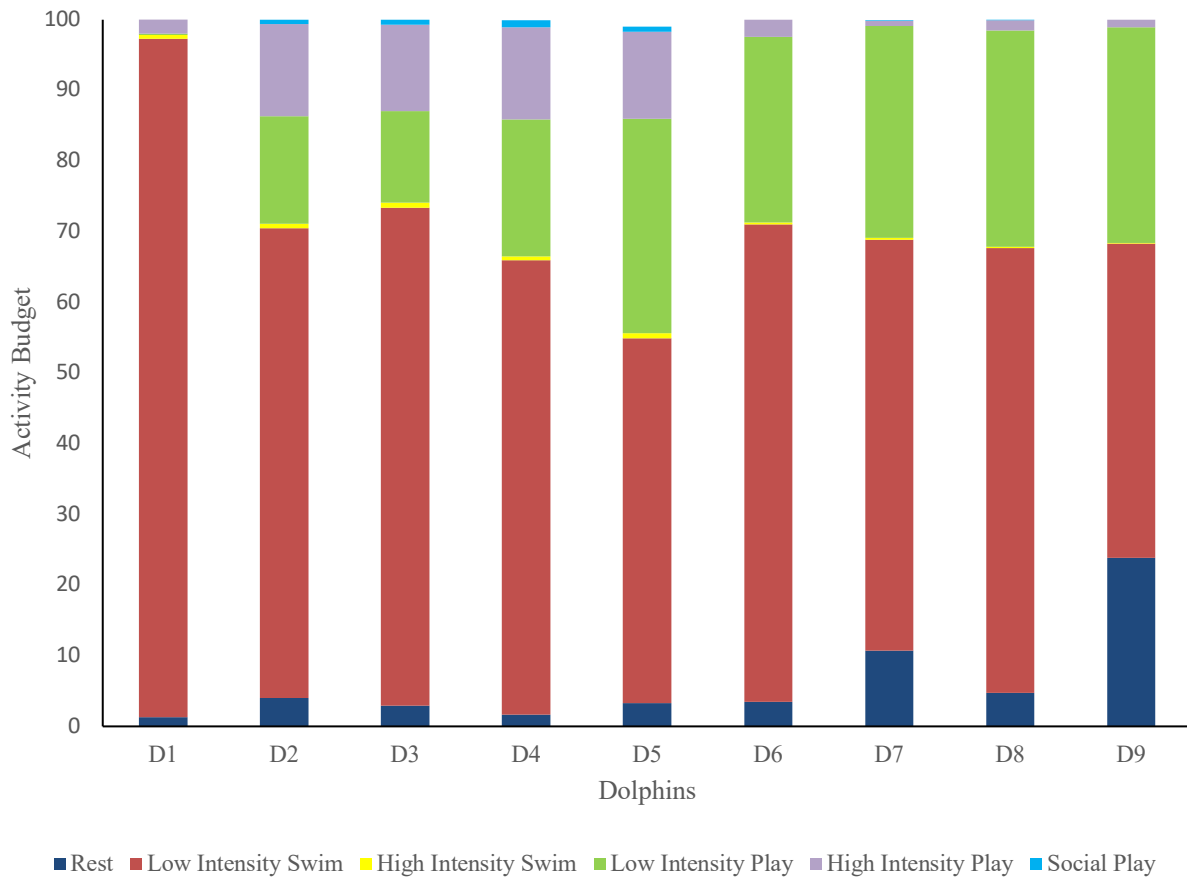


Figure 1. Activity budgets of each dolphin over the diel observational period.

Diel observations were divided into diurnal (0600 – 1759) and nocturnal (1800 – 0559) conditions for comparisons. Rest ( $Z = -2.4, n = 7, p < 0.05$ ), low intensity swim ( $Z = -2.4, n = 7, p < 0.05$ ), low intensity play ( $Z = -2.4, n = 7, p < 0.05$ ) and social play ( $Z = -2.4, n = 7, p < 0.05$ ), were all different based on time of day. However, there were no diel differences in high intensity swim ( $Z = -0.4, p = \text{n.s.}$ ) or high intensity play ( $Z = 1.2, p = \text{n.s.}$ ). Rest was significantly higher during nocturnal hours ( $Mdn = 6.3 \pm 5.5$ ) than diurnal ( $Mdn = 0.5 \pm 0.6$ ). Low intensity swim was higher during nocturnal hours ( $Mdn = 83.0 \pm 4.2$ ) than diurnal ( $Mdn = 44.4 \pm 9.4$ ). Low intensity play was observed more during diurnal hours ( $Mdn = 44.6 \pm 13.0$ ) than in the nocturnal period ( $Mdn = 4.2 \pm 1.6$ ). Finally, social play was observed more in the diurnal period ( $Mdn = 15.9 \pm 8.6$ ) than in the nocturnal period ( $Mdn = 6.3 \pm 3.5$ ) (Figure 2).

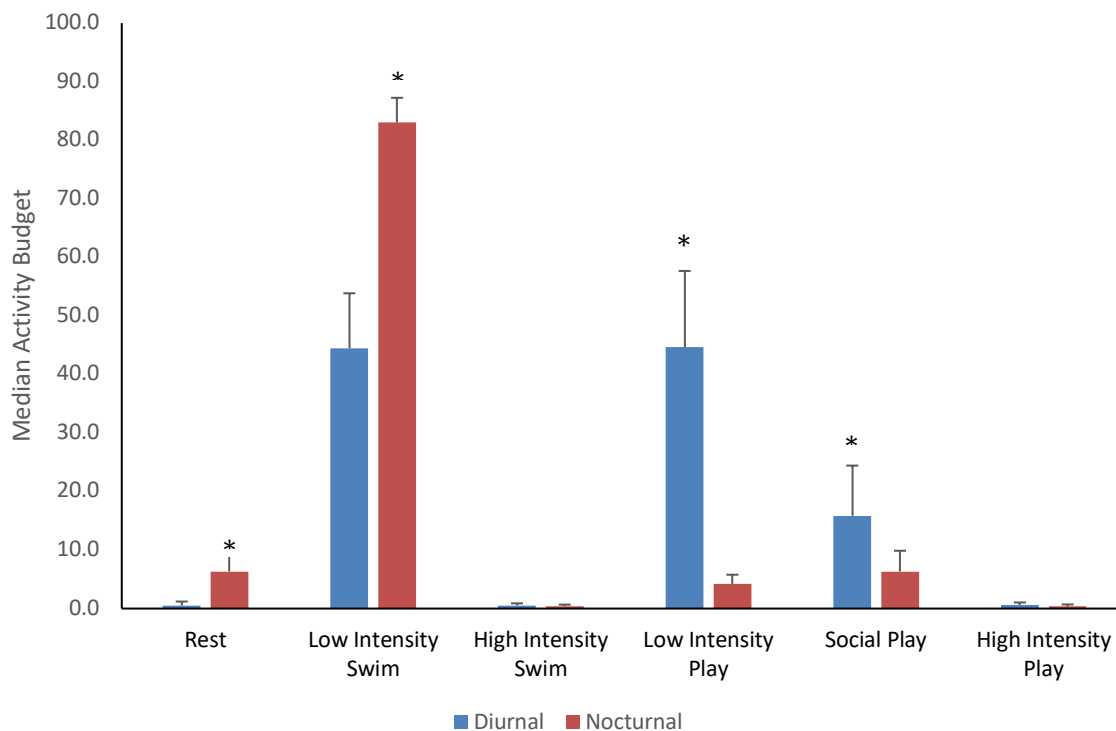


Figure 2. Diel differences in mutually exclusive behaviors.

Seasonal differences were observed for the behaviors low intensity swim ( $\chi^2(3) = 11.2, p < 0.05$ ), low intensity play ( $\chi^2(3) = 17.6, p < 0.01$ ), social play ( $\chi^2(3) = 12.1, p < 0.01$ ) and high intensity play ( $\chi^2(3) = 11.4, p < 0.05$ ). However, there were no seasonal differences observed for rest ( $Z = 3.7, p > 0.05$ ) or high intensity swim ( $Z = 7.9, p > 0.05$ ). Pairwise comparisons showed that low intensity swim was significantly higher during the winter ( $Mdn = 68.2 \pm 6.4$ ) when compared to the summer ( $Mdn = 59.4 \pm 9.7; Z = -1.9, p < 0.01$ ). Low intensity play was significantly higher in the summer ( $Mdn = 33.3 \pm 10.0$ ) when compared to the winter ( $Mdn = 21.9 \pm 5.9; Z = 1.9, p < 0.05$ ) or spring ( $Mdn = 18.8 \pm 7.9; Z = 2.7, p < 0.01$ ). Low intensity play was also significantly higher in the Fall ( $Mdn = 26.5 \pm 7.9$ ) when compared to the spring ( $Z = -1.9, p < 0.01$ ). Social play was significantly higher in the spring ( $Mdn = 18.5 \pm 9.3$ ) when compared to the winter ( $Mdn = 7.6 \pm 4.3; Z = -2.1, p < 0.01$ ), and summer ( $Mdn = 9.6 \pm 5.0; Z = -2.0, p < 0.05$ ). High intensity play was significantly higher in the spring ( $Mdn = 0.9 \pm 0.5$ ) when compared to the summer ( $Mdn = 0.2 \pm 0.3; Z = -2.1, p < 0.05$ ) (Figure 3).

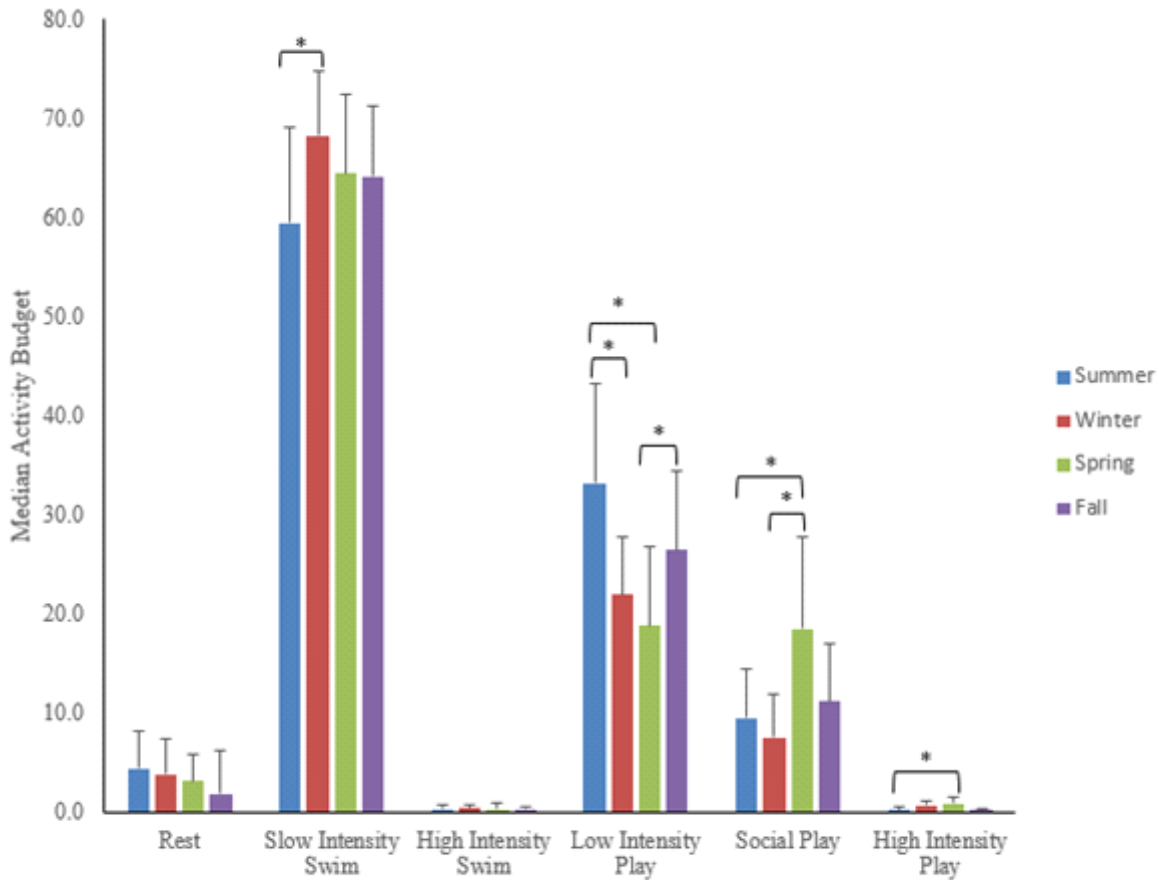


Figure 3. Seasonal differences in activity budgets.

No differences in behavior were found based on the age of the subjects: rest ( $U = 1.0, p > 0.05$ ), low intensity swim ( $U = 5.0, p > 0.05$ ), high intensity swim ( $U = 0.0, p > 0.05$ ), low intensity play ( $U = 2.0, p > 0.05$ ), social play ( $U = 0.0, p > 0.05$ ) and high intensity play ( $U = 0.0, p > 0.05$ ).

## Discussion

Overall, there were many differences in behavior observed based on seasonal, and diel related factors. This demonstrates that dolphins in an outdoor managed care environment are impacted by several factors. In the current study, low intensity swim was the most predominant behavior. Previous research has shown that wild bottlenose dolphins spend between 18% - 69% of their time traveling (Barham, Sweeney, Leatherwood, Beggs, & Barham, 1980; Bearzi, 2005; Goodwin 1985; Hanson & Defran, 1993; Lear & Bryden, 1980; Möller & Harcourt, 1998; Shane, 1990b; Shane et al., 1986) which was the most predominant behavior for the majority of those populations. This is important due to the concerns surrounding having cetaceans, such as dolphins, in



an exhibit different from their natural habitat. Even with this difference, dolphins spent a majority of their time swimming similar to their wild counterparts. A possible limitation is that the operational definition of low intensity swim could have also included some instances of rest behaviors. At the time of the study it was determined to specifically define rest as non-movement. In more recent studies rest was defined as a stationary behavior with little to no movement (Degrati et al., 2008; Mattos et al., 2007; Miller et al., 2010) or as swim rest (Sekiguchi & Koshima, 2003). While it is possible that some of the low intensity swim behavior observed could have actually been resting, Lyamin, Pryaslova, Lance, and Siegel (2006) suggest that dolphins typically sleep in the hanging behavior.

The second most abundant behavior following low intensity swim was low intensity play. In one study, play has been referred to as a luxury behavior (e.g., Cronin, West, & Ross, 2016) likely due to the fact that play is initiated when an animal has no competing systems such as feeding, mating or predator avoidance (Burghardt, 2005). For many species in the wild, play behavior is often lower than 10% of an animal's activity budget (Burghardt, 1984, Burghardt, 1988). Indeed, some studies of wild dolphins have found lower levels of play behavior than the current study (Hansen & Defran 1993). However, within this group of professionally managed dolphins they engaged in this behavior approximately 25% of their time. This could suggest that the animals' basic biological needs have been met and more time can be spent engaged in other behaviors such as play. Previous studies on dolphins in professional care have demonstrated that play behaviors are influenced by enrichment and social groups. However, the description and understanding of how play behaviors can identify wellness should still be further examined (Held & Spinka, 2011). Clearly additional information is needed to better understand this complex behavior in dolphins as well as other species.

In the current study, there were no differences observed based on the age of the individuals. Previous research has shown that elephants walk less as they age (Holdgate et al., 2016) and horses become more inactive with age (McKeever & Malinowski, 1997). These relationships may be due to changes in aerobic capacity and amount of aerobic work animals are able to perform (McKeever & Malinowski, 1997). However, these age related differences were not observed in the current study and more information would be necessary to better understand why these changes were not observed.

Seasonal differences have been found in a variety of settings for dolphins. Previous research on wild bottlenose dolphins has demonstrated that they are seasonal breeders (Harrison & Ridgway, 1971; Mead & Potter, 1990; Ross, 1977; Scott et al., 1990). There are physiological changes associated with mating such as hormone surges in females (Schroeder, 1990; Yoshioka, Mohri, Tobayama, Aida, & Hanyu, 1986) and seasonal peaks in testosterone in males (Harrison & Ridgway, 1971; Schroeder & Keller, 1989). Previous research has also demonstrated that there is an increase in social behavior for wild dolphins during the spring associated with breeding (e.g., Miller et al., 2010). It is possible that during the current study the increased social play, high intensity play and low intensity swimming behavior is associated with changes in hormone levels. Future research combining behavior with physiology could help to understand the seasonal differences observed. Although air temperature changed across the seasons during the current study there was also a change in the social group during the spring. At this time, a new calf was born and the adult male dolphin was relocated to a new facility. This change could have also influenced the difference observed during that time. Finally, the number of education program presentations could have also had an impact on their behavior. However, additional information would be necessary to tease apart exactly what is contributing to the seasonal changes in behavior that were observed.

In addition to seasonal differences, bottlenose dolphin behavior was significantly different depending on the time of day. During the day there was an increase in low intensity play and social play with a decrease

in rest, and low intensity swim. This is not surprising as those times correlate with facility hours and when animals would be engaged with animal care staff. Notably, animals in the current study spent approximately 90% of the nocturnal hours resting or in low intensity swim. If low intensity swim includes some resting behavior as previously discussed, this would suggest that the dolphins have adapted to the schedule of feeding during the daytime education programs and sessions. However, if the greater than 80% of the time spent engaged in low intensity swim represents an active time for the animals, then animal care should explore alternative techniques or strategies to ensure the animals have environmental enrichment to meet the behavioral needs of the animals over a full 24 hour day.

In general, behavioral differences were associated with time of day and season. Systematic observations and behavioral analysis from the current study can help to better understand bottlenose dolphin behavior under professional care. The goal is not to generalize information from the current study to wild populations, but to use information from both zoos/aquariums as well as wild dolphins to better understand their complex behavior (Wells, 2009). As can be seen from the current study, there are many similarities between professionally managed and wild bottlenose dolphin behavior. The important aspect is also trying to understand any differences that may exist for institutions to provide the best welfare possible for animals under their care. While zoological environments vary in their design and composition, they also vary in management techniques and schedules. These variations may have a positive or negative impact on dolphins and further research can help us better understand those differences. Information gained from the study suggests that there are environmental factors that impact bottlenose dolphin behavior. A basic understanding of the effects of a professional care environment may also be used to determine the factors that lead to optimal welfare for bottlenose dolphins. Additionally, this could lead to future research on the impact of cognitive enrichment on dolphin welfare (Clark, 2013). For example, longitudinal studies can utilize repeated observations that examine possible individual and group development and changes over the years (Wells, 1991). Finally, differences found in activity budgets and occurrence of particular behaviors may be a factor of developmental requirements and evolutionary significance.

## Acknowledgments

We would like to express thanks to Marine Life Oceanarium and in Gulfport, MS. Additionally, we are grateful to Jeffrey Siegel and Kymbr Wright for their assistance in data collection. Correspondence concerning this article should be sent to Dr. Rachel Walker, Department of Psychology, University of Incarnate Word, San Antonio, TX, [rtwalker@uiwtx.edu](mailto:rtwalker@uiwtx.edu).

## References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227–267.
- Ballance, L. T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science*, *8*, 262–274.
- Barham, E. G., Sweeney, J. C., Leatherwood, S., Beggs, R. K., & Barham, C. L. (1980). Aerial census of the bottlenose dolphin, *Tursiops truncatus*, in a region of the Texas coast. *Fisheries Bulletin*, *77*, 585–595.
- Bearzi, G. (2005). Aspects of the ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. *Journal of Cetacean Research Management*, *7*, 75–83.
- Bearzi, G., Politi, E., & di Sciara, G. N. (1999). Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). *Marine Mammal Science*, *15*, 1065–1097.

- Beltrán, J. F., & Delibes, M. (1994). Environmental determinants of circadian activity of free-ranging Iberian lynxes. *Journal of Mammalogy*, *75*, 382–393.
- Brager, S. (1993). Diurnal and seasonal patterns of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *9*, 434–438.
- Burghardt, G. M. (1984). On the origins of play. In: P. K. Smith (Ed.), *Play in animals and humans* (pp. 5–41). Oxford, UK: Basil Blackwell.
- Burghardt, G. M. (1988). Precocity, play, and the ectotherm-endotherm transition. In: E. M. Blass (Ed.), *Handbook of behavioral neurobiology. Vol. 9. Developmental psychobiology and behavioral ecology* (pp. 107–148). New York, NY: Plenum.
- Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge, MA: MIT Press.
- Coscarella, M. A., Pedraza, S. N. & Crespo, E. A. (2010). Behavior and seasonal variation in the relative abundance of Commerson's dolphin (*Cephalorhynchus commersonii*) in northern Patagonia, Argentina. *Journal of Ethology*, *28*, 463–470.
- Clark, F. E. (2013). Marine mammal cognition and captive care: A proposal for cognitive enrichment in zoos and aquariums. *Journal of Zoo and Aquarium Research*, *1*, 1–6.
- Cronin, K. A., West, V., & Ross, S. R. (2016). Investigating the relationship between welfare and rearing young in captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, *181*, 166–172. <http://dx.doi.org/10.1016/j.applanim.2016.05.014>
- Degrati M., Dans S. L., Pedraza S. N., Crespo E. A., & Garaffo G. (2008). Diurnal behavior of dusky dolphins, *Lagenorhynchus obscurus*, in Golfo Nuevo, Argentina. *Journal of Mammalogy*, *89*, 1241–1247.
- Foroughirad, V., & Mann, J. (2013). Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biological Conservation*, *160*, 242–249.
- Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, *76*, 375–387.
- Greco, B. J., Meehan, C. L., Miller, L. J., Shepherdson, D. J., Morfeld, K. A., Andrews, J., ... & Mench, J. A. (2016). Elephant management in North American zoos: Environmental enrichment, feeding, exercise, and training. *PLOS ONE* *11*, e0152490. doi: 10.1371/journal.pone.0152490
- Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology*, *24*, 292–306.
- Gregory, P. R., & Rowden, A. A. (2001). Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals*, *27*, 105–113.
- Goodwin, D. E. (1985). *Diurnal behavior patterns of Tursiops truncatus off Mobile Point, Alabama*. (Unpublished master's thesis, San Francisco State University). Retrieved from [http://digital.mlml.calstate.edu/islandora/object/islandora%3A607/datastream/OBJ/download/Diurnal\\_behavior\\_patterns\\_of\\_Tursiops\\_truncatus\\_off\\_Mobile\\_Point\\_Alabama.pdf](http://digital.mlml.calstate.edu/islandora/object/islandora%3A607/datastream/OBJ/download/Diurnal_behavior_patterns_of_Tursiops_truncatus_off_Mobile_Point_Alabama.pdf)
- Hansen, L. J., & Defran, R. F. (1993). The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquatic Mammals*, *19*, 127–142.
- Harrison, R. J., & Ridgway, S. H. (1971). Gonadal activity of some bottlenose dolphins (*Tursiops truncatus*). *Journal of Zoology*, *165*, 355–366.
- Held, S., & Spinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, *81*, 891–899. doi: 10.1016/j.anbehav.2011.01.007
- Henderson, E. E., & B. Würsig. (2007). Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. *Gulf of Mexico Science*, *2*, 153–161.
- Holdgate, M. R., Meehan, C. L., Hogan, J. N., Miller, L. J., Soltis, J., Andrews, J., & Shepardson, D. J. (2016). Walking behavior of zoo elephants: Associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. *PLoS ONE* *11*, e0150331. doi:10.1371/journal.pone.0150331
- Irvine, A. B., Scott, M. D., Wells, R. S., & Kaufmann, J. H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*, 671–688.
- Karniski, C., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., Stanton, M. A., & Mann, J. (2015). A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. *Marine Mammal Science*, *31*, 839–852.

- Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology, 19*, 223–240.
- Kuhar, C. W. (2008). Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science, 110*, 377–385.
- Lear, R. J., & Bryden, M. M. (1980). A study of the bottlenose dolphin, *Tursiops truncatus*, in eastern Australian waters. *Occasional Papers Australian National Parks and Wildlife Service, 4*, 1–25.
- Lyamin, O. I., Pryaslova, J., Lance, V., & Siegel, J. M. (2006). Sleep behaviour: Sleep in continuously active dolphins; Activity and sleep in dolphins (Reply). *Nature, 441*, E11–E11.
- Maple, T. L., & Segura, V. D. (2015). Advancing behavior analysis in zoos and aquariums. *The Behavior Analyst, 38*, 77–91.
- Mackey, A. D., Makecha, R. N., & Kuczaj, S. A. II. (2014). The development of social play in bottlenose dolphins (*Tursiops truncatus*). *Animal Behavior and Cognition, 1*, 19–35.
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns. *Behaviour, 136*, 529–566.
- Mattos, P. H., Dalla Rosa, L., & Fruet, P. F. (2007). Activity budgets and distribution of bottlenose dolphins (*Tursiops truncatus*) in the Patos Lagoon estuary, southern Brazil. *Latin American Journal of Aquatic Mammals, 6*, 161–169.
- McKeever, K. H., & Malinowski, K. (1997). Exercise capacity in young and old mares. *American Journal of Veterinary Research, 58*, 1468–1472.
- Mead, J. G., & Potter, C. W. (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin* (pp. 165–195). San Diego, CA: Academic Press.
- Meehan, C. L., Mench, J. A., Carlstead, K., & Hogan, J. N. (2016) Determining connections between the daily lives of zoo elephants and their welfare: An epidemiological approach. *PLOS ONE 11*, e0158124. doi: 10.1371/journal.pone.0158124
- McBride, A. F., & Hebb, D. O. (1948). Behavior of the captive bottlenose dolphin, *Tursiops truncatus*. *Journal of Comparative Physiology, 41*, 111–123.
- McHugh, K. A. (2010). *Behavioral development of free-ranging juvenile bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida*. (Doctoral dissertation). Available from ProQuest Dissertations and Theses database. (UMI No. 4327396)
- Miller, L. J., Solangi, M., & Kuczaj, II., S., A. (2010). Seasonal and diurnal patterns of behavior exhibited by Atlantic bottlenose dolphins (*Tursiops truncatus*) in the Mississippi Sound. *Ethology, 116*, 1127–1137.
- Möller, L. M. (1993). Observations on the behavior and ecology of Boto, *Tursiops truncatus*, in the Patos Lagoon Estuary, RS, Brazil. (Unpublished graduation monograph). Federal University of Rio Grande Foundation, Brazil.
- Möller, L. M., & Harcourt, R. G. (1998). Social dynamics and activity patterns of bottlenose dolphins, *Tursiops truncatus*. *Jervis Bay, southeastern Australia. Proceedings of the Linnean Society NSW, 120*, 181–189.
- Norris, K. S. & Dohl, T. P. (1980). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bulletin, 77*, 821–849.
- Norris, K. S., Wursig, B., Wells, R. S., Wursig, M. Brownlee, S. M., Johnson C., & Solow, J. (1985). The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. (Administrative report LJ-85-06C) National Marine Fisheries Service, Southwest Fisheries Center, San Diego, CA.
- Ridgway, S. H., & Harrison, R. J. (Eds.). (1999). *Handbook of marine mammals: The second book of dolphins and the porpoises*. San Deigo, CA: Academic Press.
- Ross, G. J. B. (1977). The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. *Ann. Cape Prov. Mus. (Nat. Hist.), 11*, 135–19.
- Saayman, G. S., Tayler, C. K. & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian ocean-bottlenose dolphins (*Tursiops aduncus* Ehrenburg). *Behaviour, 44*, 212–233.
- Schroeder, P. J. (1990). Breeding bottlenose dolphins in captivity. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin* (pp. 435–446). San Diego, CA: Academic Press.
- Schroeder, P. J. & Keller, K.V. (1989). Seasonality of serum testosterone levels and sperm density in *Tursiops truncatus*. *Journal of Experimental Psychology, 249*, 316–321.

- Scott, M. D., Wells, R. S., Irvine, A. B., & Mate, B. R. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235–244). San Diego, CA: Academic Press.
- Shane, S. H., Wells, R. S., & Wursig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, 2, 34–63.
- Shane, S. H. (1990a). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245–265). San Diego, CA: Academic Press.
- Shane, S. H. (1990b). Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin*. (pp. 541–558). San Diego, CA: Academic Press.
- Sobel, N., Supin, A. Y., & Myslobodsky, M. S. (1994). Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). *Behavioural Brain Research*, 65, 41–45.
- Tayler, C. K. & Saayman, C. S. (1972). The social organization and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): Some comparisons and assessments. *Annals of the Cape Provincial Museums Natural History*, 9, 1–49.
- Ugaz, C., Valdez, R. A., Romano, M. C., & Galindo, F. (2013). Behavior and salivary cortisol of captive dolphins (*Tursiops truncatus*) kept in open and closed facilities. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8, 285–290.
- von Streit, C., Ganslosser, U., & von Fersen, L. (2013). Behavioral development of two captive mother-calf dyads of bottlenose dolphins (*Tursiops truncatus*) in the calves' first year. *International Journal of Comparative Psychology*, 26, 176–196.
- Walsberg, G. E. (1983). Avian ecological energetics. *Avian Biology*, 7, 161–220.
- Waples, D. M. (1995). *Activity budgets of free-ranging bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida*. Unpublished master's thesis, University of California, Santa Cruz.
- Weathers, W. W., Buttemer, W. A., Hayworth, A. M., & Nagy, K. A. (1984). An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk*, 101, 459–474.
- Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199–225). Berkeley, CA: University of California Press.
- Wells, R. S. (2009). Learning from nature: bottlenose dolphin care and husbandry. *Zoo Biology*, 28, 635–651.
- Wells, R. S., McHugh, K. A., Douglas, D. C., Shippee, S., McCabe, E. B., Barros, N. B., & Phillips, G. T. (2013). Evaluation of potential protective factors against metabolic syndrome in bottlenose dolphins: Feeding and activity patterns of dolphins in Sarasota Bay, Florida. *Frontiers in Endocrinology*, 4, 2–16.
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. Genoways (Ed.), *Current mammology* (pp. 247–305). New York, NY: Plenum Press.
- Wursig, B., & Wursig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bulletin*, 77, 399–412.
- Wursig, B., & Wursig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bulletin*, 77, 871–890.
- Yoshioka, M. A., Mohri, E., Tobayama, T., Aida, K. K., & Hanyu, I. (1986). Annual changes in serum reproductive hormone levels in captive bottlenose dolphins. *Bulletin of Japanese Society of Scientific Fisheries*, 52, 1939–1946.

**Financial conflict of interest:** No stated conflicts.

**Conflict of interest:** No stated conflicts.

*Submitted: August 9<sup>th</sup>, 2016*

*Resubmitted: April 8<sup>th</sup>, 2017*

*Accepted: April 10<sup>th</sup> 2017*