

Vigilance in Female Bottlenose Dolphins (*Tursiops* sp.) Before and After Calving

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Previous research has indicated that bottlenose dolphins alternate activity levels between hemispheres while at rest. This rest strategy allows dolphins to maintain continuous vigilance of their external environment. Dolphins in the care of humans exhibit different behaviors while presumably at rest, including floating at the surface, lying at the bottom, and swimming at very slow speeds in stereotyped patterns. Dolphin mothers in the care of humans have been reported to "not rest" and swim continuously for extended periods of time (weeks or even months) when their calves are first born. The current study examined the night-time rest patterns and vigilance of five female bottlenose dolphins before and after parturition. By differentiating between two types of resting behaviors (floating and slow swimming), we found that mothers altered their rest strategy depending on the parturition state. Floating was only observed at high levels pre-parturition. In contrast, mothers primarily exhibited active swims (a vigilant state) the first two weeks, post-parturition. The remaining six weeks were characterized by a steady increase in slow swimming (a resting, vigilance state). This change in swim behavior may be associated with neonatal development and may allow mothers to sustain high levels of vigilance for extended periods of time. The results of a behavioral test of vigilance indicated that the mothers also increased their vigilance level post-parturition. Mothers sustained their increased response rate over the eight-week post-parturition period, demonstrating that dolphin mothers maintain high levels of vigilance for an extended period of time.

Vigilance is defined as an awareness of one's immediate environment for stimuli significant to the survival of the individual and/or its offspring. Significant stimuli can include the appearance of an obstacle (e.g., nets, boats), perceived threats (e.g., predators, other animals), or a needed resource (e.g., food). The level of vigilance displayed by an individual will vary depending on a number of factors, including group size, predator threat, foraging need, available energy resources, the presence of young, current physiological capability, immediate spatial location, type of habitat, and species (Lima, Rattenborg, Lesku, & Amlaner, 2005).

Many group living primates, elephants, meerkats, and migrating birds alternate vigilance duties among individuals (Beauchamp, 1998, 2003; Clutton-

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Brock et al., 1999; Elgar, 1989; Horrocks & Hunte, 1986; Kenward, 1978; Moran, 1984; Munoz-Delgado et al., 2004; Roberts, 1996; Treves, 1998). Some species (e.g., meerkats) have social roles in which specific individuals act as sentinels for the group. Other species (e.g., flocking birds) rely on individuals located at the group's periphery to maintain the greatest levels of vigilance until they are replaced by other animals. The presence of sentinels allows the majority of the social group to rest and forage without having to monitor all other aspects of their environment. The resting or foraging members must simply maintain a level of vigilance that would allow them to respond to an alarm call or behavior of the sentinel. When sentinels are absent or unavailable, individuals must monitor their environment with higher levels of vigilance when they are both awake and resting (Lima et al., 2005).

Cetaceans also monitor their environment for group member activities and location, prey, predators, and environmental barriers such as sand bars and reefs in their natural habitat or pool walls and bottoms when in the care of humans (as reviewed in Connor, et al., 2000). Several lines of evidence suggest that cetaceans in the care of humans use various strategies to monitor their environment. For example, while rest swimming with one eye open and one eye closed (unilateral eye closure), a pair of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) monitored each other's position with their open eye rather than the external environment (Goley, 1999). Moreover, when these dolphins switched positions, the open eye also switched sides. A group of bottlenose dolphins also displayed similar behavior in which the group members tended to monitor each other's activities during unilateral eye closure (*Tursiops* sp.; Gnone, Benoldi, Bonsignori, & Fognani, 2001).

Also like many terrestrial animals, dolphins do not always maintain vigilance. For example, a group of resting dolphins in their natural habitat apparently remained unaware of a juvenile white shark swimming near them and did not disperse until the shark was among them (Connor & Heithaus, 1996). Although it is known that small cetaceans can vary the intensity of their responses to sharks (Wood, Caldwell, & Caldwell, 1970), the above anecdote suggested a lack of environmental awareness or vigilance by the dolphins. Whether dolphins are in a large social group or swimming independently, some level of vigilance must be maintained. Dolphins that are travelling, foraging independently, or have young calves are particularly vulnerable and must maintain heightened levels of vigilance for extended periods.

While the presence of other group members can facilitate environmental monitoring, the need for vigilance is magnified by the presence of a calf. Cetacean mothers are the primary, and usually, sole caregivers to their calves. Allomaternal care has been observed in some cetaceans (e.g., dolphins, sperm whales, and killer whales) in which non-related or related juveniles and adults monitor calves' activities while mothers forage or dive (as reviewed in Whitehead & Mann, 2000). However, the bulk of the care of calves is the mothers' responsibility. Bottlenose dolphin neonates (*Tursiops truncatus*) swim and rise to breathe on their own, although not very proficiently (Cockcroft & Ross, 1990; Mann & Smuts, 1999; McBride & Kritzler, 1951; Miles & Herzing, 2003; Reid, Mann, Weiner, & Hecker, 1995; Tavolga & Essapian, 1957). Dolphin mothers must constantly observe their newborn calves' actions so that they may assist their struggling neonate to the surface for a breath or redirect their erratically swimming offspring away from

potential threats (e.g., dangerous conspecifics, environmental threats such as sharks or pool walls). Constant vigilance on the part of a mother with a neonate is critical whether the mother-calf pair is in their natural habitat or in human care.

As with terrestrial animals, the need for constant vigilance for cetaceans is in direct conflict with their need for sleep or rest as mammals. A period of rest or sleep replenishes depleted energy resources, repairs damage experienced by the body throughout the day, and consolidates memories (Lilly, 1964; Lima et al., 2005; Siegel, 2003). In order to counter the many different constraints species experience as a result of their habitats and survival needs, a number of sleep and vigilance strategies have evolved. One strategy displayed by cetaceans is their capacity for unihemispheric slow-wave sleep (SWS, Lyamin, Mukhametov, & Siegel, 2004; Mukhametov, 1984; Ridgway, 2002; Ridgway et al., 2006). Recordings of brain activity of dolphins during various activity states have indicated that slow-wave sleep (SWS) patterns occur and alternate between each hemisphere (unihemispheric SWS) while the dolphins are at rest, be it a motionless or moving rest behavior (Lyamin et al., 2004; Mukhametov, 1984; Mukhametov, Supin, & Polyakova, 1977; Ridgway, 2002). Occasional bihemispheric SWS for short periods between breaths has also been observed in dolphins (Lyamin et al., 2004; Mukhametov 1984; Mukhametov et al., 1977; Ridgway, 2002, Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008).

The ability to alternate which hemisphere is “sleeping” is a particularly adaptive behavior for animals that must sustain vigilance for extended periods of time. Free-swimming dolphins without calves have been shown to maintain vigilance with few errors for extended periods of time on a variety of behavioral tasks (Hoffman-Kuhnt, 2003; Ridgway et al., 2006). Clearly, this capability would be advantageous to a mother who must be continuously vigilant to ensure her neonate’s survival.

Previous reports have shown that dolphins without calves in the care of humans often float, or remain relatively motionless, for extended periods of time (e.g., surface floats or quiescent hanging behavior, Flanigan, 1974; Gnone et al., 2001; McCormick, 1969; Mukhametov, 1984; Ridgway, 2002). These periods of motionlessness are presumably rest periods during which vigilance may be low or moderate. One eye or both eyes may be shut and floating is often uninterrupted except for periodic breathing (Lyamin et al., 2004; Mukhametov, 1984; Mukhametov et al., 1977; Ridgway, 2002; Ridgway et al., 2006).

Dolphins also rest as they swim. Dolphins in human care have consistently been observed swimming in slow, stereotyped circular swim patterns periodically throughout the 24-hour day, especially during the nighttime hours when human attendants are absent (Cockcroft & Ross, 1990; Flanigan, 1974; Goley, 1999; Gnone et al., 2001; Gnone, Moriconi, & Gambini, 2006; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; McBride, & Kritzler, 1951; McCormick, 1969; Mukhametov, 1984; Ridgway, 2002; Sekiguchi, Arai, & Kohshima, 2006). Similar slow-moving, group-synchronized resting behaviors have also been observed in many species of dolphins in their natural habitat (Connor & Heithaus, 1996; Norris & Dohl, 1980; Wursig & Wursig, 1980). Wild dolphins swim into shallow, well-protected bays where they may also float or engage in synchronized slow-

paced swims (Scott, Wells, & Irvine, 1990; Shane, 1990). Surface floating is considered a reduced vigilance state (Connor & Heithaus, 1996; Lyamin, Pryaslova, Lance, & Siegel, 2005; Norris & Dahl, 1981;) while slow swimming and active swimming are described as states with increasing levels of vigilance (Goley, 1999; Gnone et al., 2001).

Although data on wild dolphins mothers is lacking, research with dolphins in human care has suggested that mothers do not stop to rest or float for extended periods of time after their calves are born (Lyamin et al., 2005). Rather, they appear to swim continuously until their neonates become more proficient swimmers at around two months of age (Fellner, Stamper, Losch, Dahood, & Bauer, 2005; Lyamin et al., 2005). These observations have two implications: (1) mothers of neonates may experience few periods of SWS (i.e., sleep) as indicated by the lack of corresponding eye closures, which have been found to be associated reliably with SWS by some studies (Lyamin et al., 2004; but see Supin et al., 1978), and (2) mothers of neonates should have heightened levels of vigilance during this critical survival period.

The current study investigated the rest and swim patterns of bottlenose dolphin mothers in the care of humans the month before and two months after parturition. Based upon previous research with animals in the care of humans, the following hypotheses were tested:

1. As anticipated from previous research examining mother-calf swim patterns, shortly after birth, female dolphins should alter their night-time resting patterns pre-parturition to post-parturition. Specifically, females will surface float more, pre-parturition, and engage in more active swim patterns, post-parturition (Flanigan, 1974; Goley, 1999; Gnone et al., 2001; Gnone et al., 2006; Lyamin et al., 2005; McCormick, 1969; Mukhametov, 1984; Ridgway, 2002; Sekiguchi et al., 2006).
2. More specifically, mothers will not exhibit substantial surface floating, post-parturition, but rather should increase the frequency of slow circular swims, post-parturition (Cockcroft & Ross, 1990; Gubbins et al., 1999; Gnone et al., 2001; Gnone et al., 2006; McBride & Kritzler, 1951; Sekiguchi et al., 2006).
3. Parity (whether this was the mother's first calf or the mother had experienced births in the past) was expected to be related to post-parturition resting activities.

We also investigated the level of vigilance displayed by our female dolphins pre- and post-parturition, at night. The following hypotheses were tested:

4. Female dolphins should respond more often to the vigilance stimulus when engaged in an active swim or a slow swim than when surface floating (Connor & Heithaus, 1996; Goley, 1999; Gnone et al., 2001; Lyamin et al., 2005; Norris & Dahl, 1981).
5. Female dolphins should respond more frequently (i.e., be more

vigilant) post-parturition as compared to pre-parturition, when given a behavioral test of vigilance. This hypothesis was derived from observations of unilateral eye closures of mothers swimming with their calves and their reported responses to changes in their environment, including avoidance of other swimming mother-calf pairs or dolphins (Cockcroft & Ross, 1990; Gnone et al., 2001; Gubbins et al., 1999).

6. If swimming occurred continuously for two weeks or more, mothers were expected to decrease their levels of vigilance due to physical fatigue (in part from Lyamin et al., 2005).
7. Parity was hypothesized to be related to level of vigilance, although it was unclear how they might be related due to the lack of available information.
8. Mothers were hypothesized to demonstrate laterality in their responses to a behavioral vigilance task due to their capacity for unihemispheric SWS and previous studies demonstrating behavioral laterality (Lyamin et al., 2004; Mukhametov, 1984; Ridgway, 2002; Ridgway et al., 2006).

Method

Subjects

Six pregnant bottlenose dolphins (*Tursiops* sp.) located at the Navy Marine Mammal Program (MMP) in San Diego, California were observed during the summer of 2002. Within a period of two and a half weeks, five of the six dolphins gave birth to healthy calves. The remaining dolphin did not give birth until December 2002. However, she (dolphin C) remained in the study and served as a pregnant control. A listing of the dolphins, their parity, and the birth dates of their calves may be found in Table 1.

Table 1
Summary of Descriptive Information for Each Dolphin

Mother	Age of Mother	Parity	Calf	Birth Date	Total Pre-Parturition Samples	Total Post-Parturition Samples
O	27	M	M ^a	5/31/2002	127	434
S	22	M	H ^b	6/6/2002	167	421
B	37	P	I ^b	6/10/2002	208	400
K	16	P	T ^b	6/16/2002	261	370
A	16	M	D ^a	6/18/2002	266	371
C	15	--	----- --	-----	608	-----

Note. M = Multiparous; P = Primiparous.

^a Male. ^b Female.

All female dolphins were housed in the same 18m x 18m enclosures prior to parturition. The MMP facility is located in San Diego Bay and is constructed as a series of floating enclosures that rise and fall with the tidal range. All the enclosures are connected by gates which allow for a number of different social groupings (schematic shown in Figure 1).

During the four-month study, all six subjects were initially housed together during the night-time hours. As the birth date approached, determined by ultrasound examination and behavior, the pregnant dolphin and one other companion female, the next dolphin due, were placed into an adjacent birthing enclosure each night until parturition occurred. The other pregnant females were housed overnight with one another. After parturition, the mother and neonate were in the birthing enclosure until the veterinarian and training staff had determined that the pair had bonded well and nursing was regular. Most mothers and their calves were re-located to a nursery enclosure and grouped with a pregnant female or mother-calf pair within four days of the calf's birth. As all calves were born within a two and half week period, the social groupings were fairly consistent with the exception of an animal being removed every couple of days due to the next calf delivery. After the last calf was born, all five mother-calf pairs and the pregnant female were housed together at night by the end of the study. Mother-calf pairs had access to all enclosures identified as nursery enclosures in Figure 1.

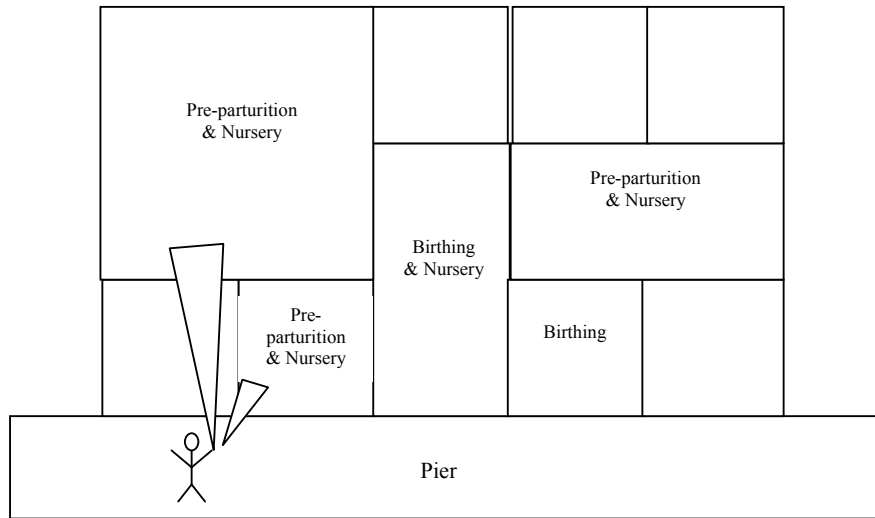


Figure 1. Spatial layout of housing enclosures and vigilance testing procedure for study dolphins. Schematic is not drawn to scale. A trained observer stood on a pier, approximately three to six meters, above the free-floating enclosures. Baseline behaviors were determined for both behavioral and vigilance aspects of the study for each female using a scan sampling procedure. To administer the vigilance test, the target female was identified, her baseline behavior was recorded, and the flashlight beam was directed near the eye that was facing the observer. The light was shined near each eye (within a third of a meter above the eye) and never directly into any animal's eye. If any other animal was in close proximity (including the calf), the observer did not administer the test until the target animal or the confounding animal had cleared the area. In the case of the calf, the observer administered the test with the greatest precision possible to avoid stimulating the calf. Animals were presumed vigilant if they responded to the light.

Behavioral Data

Procedure. This study was conducted between May 2002 and August 2002. Instantaneous behavioral samples were collected with an observation data sheet using a scan sampling procedure (Altmann, 1974/1996; Mann, et al., 2000; Martin & Bateson, 1993). That is, once a female was identified and her initial behavior recorded, the next visible female was sampled, and so on until all females had been sampled or five minutes had passed. Sample points were taken every hour during the night between 2100 and 0600 by a single observer, before the training staff came to work and began the day's activities. As the facility was a working one, observations were made outside of the normal training day to avoid the influence of human activities on the dolphins' behaviors. The females were identified by large zinc oxide markings placed in pre-determined locations by trainers during the last feeding session of the day. These marks were long-lasting and were re-applied when necessary throughout the study.

Prior to the onset of the study, a pilot study was performed to test the efficacy of the above procedure with several adult males and females in a night-time housing set-up similar to the pregnant females. Zinc oxide marks were easy to see with the ambient lighting from the pier, and the observer's appearance on the pier never disturbed the animals' night-time behavior. These potential confounds did not appear during the pilot study nor during data collection for the final study. Furthermore, all adult and juvenile animals at this facility were habituated to the appearance of individuals on the pier as night security guards patrolled the area at regular intervals.

Five of the six pregnant females were observed for a month prior to the birth of the first calf. The control dolphin was also observed during this time. Table 1 presents the number of sample points available for each mother observed. The sample points increased across mothers due to their longer pre-parturition observation periods, ranging between one month to one and half months. The control female produced three months of data as her calf was not born during the course of the study.

The same data collection procedure was used once the calves were born. Observations of the night-time behaviors of the mothers and calves were made every night for the first two months of calf life. The total number of post-parturition sample points (summed across two months of data) for each mother are presented in Table 1¹.

Dolphin behaviors were coded into one of four categories for the current study: floating, slow swimming, active swimming, and other. Floating was defined as maintaining a stationary position at the surface for at least five seconds; this behavior was considered a resting behavior. Slow swimming involved a slow (less than 1 m/s), stereotyped, circular swim, which is also a resting behavior. Active swimming was defined as any swim greater than 1 m/s in which dolphins were clearly alert and continuously altering their swim patterns. Finally, other behaviors were defined by any other non-swim behaviors observed, including but not limited to bows, dives, spy hops, or breaches. Definitions were adapted from Goley (1999), Gnone et al. (2001), and Mann and Smuts (1999).

Tests of Vigilance

In addition to the data collection of the dolphins' night-time behaviors, behavioral tests of vigilance were also conducted during those times.

Apparatus for Vigilance Testing. A Mag-lite 2 D cell flashlight with a well defined beam was used to administer the vigilance tests. During pilot testing with adult male and female dolphins, the flashlight was initially set at low intensity. The pilot subjects responded to this low level light immediately whether they were resting or awake. Thus, the intensity of the light beam was ultimately filtered by placing two plastic, semi-opaque filters inside the lens cover in front of the beam. The final light intensity was sufficient to travel 10m (approximately the farthest distance to be tested) and still be detected by an animal that was awake. Thus, the light was not detectable by floating dolphins, who were presumed to be sleeping. It did, however, elicit an observable reaction in an alert animal.

Behaviors of Interest. As in the behavioral part of the study, floating, slow swimming, active swimming, and other behaviors were of interest for the behavioral tests of vigilance. However, this portion of the study focused on the responses of each animal to the vigilance stimulations. A response to the vigilance stimulation was defined as a change in behavior from the initial behavior recorded. Thus, if the animal performed a behavior (e.g., active swim) different from the baseline behavior (e.g., surface float) then the animal was considered to be vigilant. If a change in behavior did not occur, the animal was considered not vigilant (e.g., baseline behavior: surface float, post-stimulation behavior: surface float).

Procedure

Pre-parturition. Figure 1 presents a diagram and an explanation of the procedure used to administer the behavioral tests of vigilance. Prior to the birth of the first calf, all females received three vigilance tests per night, 4 to 5 times a week for the month of May. The frequency of the tests was chosen for two reasons: (1) to determine if the animals would become habituated or sensitized to the stimulations, and (2) to have a number of stimulations that would be

¹ As with the pre-parturition data, the total number of sample points fluctuated some depending on the arrival date of the calves. Other sources of differences included animals not being visible during the allotted sampling time frame (5 minutes) or missed observation times by the observer.

comparable to those completed once the calves were born and observed for eight weeks. The females did not appear to habituate or become sensitized to the multiple stimulations either across the night or across the pre-parturition period².

Three time frames were chosen to randomly administer the stimulations across the night: (1) 2100-2359, (2) 2400-0259, and (3) 0300-0600. Thus, stimulations were given during one of the three time frames at previously determined hours. For example during the pre-parturition period, each of the six females was individually tested within the 2300 hour, the 0100 hour, and then the 0500 hour. These time frames were chosen to spread the stimulations across the night so that animals never experienced more than one “back-to-back” stimulation (i.e., a stimulation at 2300 and another one at 2400) in the course of the night. Most importantly, all animals had a minimum of an hour to return back to their normal activity level before the next observation was made.

Although it was possible that the females could have influenced the behavior of each other during the pre-parturition period in which multiple stimulations occurred during a given time frame, we followed a rigorous protocol to minimize these concerns. First, a habituation period occurred prior to all stimulations. This procedure was to ensure that the animals were not responding to the presence of the observer³. Second, the behaviors of all females were recorded before administering the stimulations (i.e., were they surface floating, slow swimming, active swimming, or engaged in another behavior?). Third, after a stimulation was conducted, the observer re-assessed the remaining females to be tested. An animal that had not changed her behavior from the previously recorded behavior was selected for the next stimulation test. This re-assessment was used only during the pre-parturition study to ensure that the previous stimulation had not alerted the other animals, as multiple females were tested during the same hour. This process was continued until all six females had been tested. If the testing protocol lasted most of the hour, a minimum of an hour was observed before a new round of tests was performed.⁴

Post-parturition. Using the same protocol as described above, each mother was initially tested two to three days after her calf was born and bonding had occurred. After the first night of vigilance testing, each mother was tested on her calf’s weekly birthday for the first two weeks and then again during weeks five through eight. The number of vigilance tests conducted during weeks three and four was increased for each mother. This change in the testing protocol reflected our concern that stimulation sessions conducted once a week would not give us sufficient data to address our fatigue hypothesis sufficiently.

As described above, the mothers and their calves were initially housed independently. As additional calves were born, mother-calf pairs were housed in a common nursery. Thus, the social groupings remained fairly consistent over the course of several nights as calves were born. Once all the calves were born, all mother-calf pairs were given access to the nursery. The nursery was a combination of multiple enclosures, which encompassed a very large area. Mothers were able to control their proximity to one another (Figure 1). Moreover, in an effort to minimize the potential influence of other animals during vigilance testing, only one mother was targeted during each testing interval. All testing involved three stimulations a night, each during one of the three previously described time intervals. Again, a minimum of an hour had to pass before the next test was administered to control for the potential carryover effect of the vigilance tests.

As in the pre-parturition period, no evidence was found that baseline behaviors were related to the administration of the vigilance tests in the post-parturition period. Furthermore, no evidence was found that the frequent appearance of the observer on the pier during this part of the study reliably disturbed or altered the behavior of the study animals or of non-study animals

² Chi square tests of independence indicated that responses to the light stimulus were independent of the order in which they were given, both across the night and the pre-parturition period. Thus, the dolphins did not respond any more or any less to the stimulations over the course of the night or before the calves were born.

³ By all behavioral indications, the presence of the observer never affected the animals’ behavior. No changes in behavior occurred between the time the observer appeared on the pier and the baseline behavior was recorded.

⁴ A visual inspection of the data indicated that the females did not appear to influence each other’s behaviors during the pre-parturition period in which stimulations were given. That is, baseline behaviors remained the same for the remaining animals before and after stimulations were given to each target animal. Sessions in which multiple light stimulations were administered generally lasted less than 15 minutes.

in adjacent enclosures. Although we were unable to control any influence the calf's behavior may have had in alerting the mother to a change in her environment, we attempted to minimize this confound as well. If the mother or calf had responded to the actions of the observer, then the test was not conducted at that time.

Finally, we were also interested in whether or not laterality of vigilance could be ascertained. In order to assess vigilance laterality, when possible, a second stimulation was given to the other non-stimulated eye after determining a baseline behavior. We felt that it was particularly important to assess the vigilance of the contralateral side without additional delay. If stimulations to both eyes were possible, the observer administered both stimulations at approximately equal distances, to control for changes in light intensity due to distance from the animal. The ambient lighting at the facility was not sufficient to consistently determine if a subject's eye was open or closed, and these data were not collected.

Results

Behavioral Data

All behavioral data were examined using Wilcoxon Matched-Pairs Signed-Ranks Tests for pre- and post-parturition analyses and Friedman Analysis of Variance by Ranks Tests for changes in maternal behaviors over time. Additionally, a Mann-Whitney U test was conducted to assess the influence of parity on the mothers' behaviors. Behaviors are reported as mean percentages and mean ranks when appropriate for group comparisons. These procedures were chosen due to the repeated measures design and ordinal dependent measure (Gibbons, 1993; Haslom & McGarty, 2003).

Activity Patterns Pre- and Post-Parturition. Results of a series of Wilcoxon matched-pairs signed-ranks test supported the hypothesis that mothers would engage in different night-time activities between pre- and post-parturition. Specifically, the five mothers were significantly more likely to rest by floating ($M = 56.9\%$, $SD = 26.5\%$) before parturition than after parturition ($M = 3.9\%$, $SD = 3.1\%$), $z = -28.8$, $N = 2,043$, $p < .001$, two-tailed, Point biserial $r = -.50$. Comparably, mothers were significantly more likely to slow swim ($M = 57.9\%$, $SD = 4.8\%$) and active swim ($M = 38.0\%$, $SD = 4.7\%$) after parturition than before parturition (slow swim: $M = 23.7\%$, $SD = 18.6\%$, $z = -23.3$, $N = 2,043$, $p < .001$, two-tailed, Point biserial $r = .39$; active swim: $M = 20.6\%$, $SD = 10.4\%$, $z = -15.4$, $N = 2,043$, $p < .001$, two-tailed, Point biserial $r = .25$). There was no difference for the other behavior category before and after parturition. Table 2 presents the positive and negative ranks for each behavior category.

Results of a series of Friedman tests supported the hypothesis regarding the time course and frequency of surface floating and slow circular swims, post-parturition. Figure 2 presents a graphical representation of the numerical data presented in Table 3. The data represent the average percentage of each behavioral category, calculated using the relative percentage of the four categories for each mother. These data are presented by week to demonstrate the chronological trends of the two resting behaviors. As a group, mothers did not return to their baseline floating levels by the end of the eight week study, supporting our hypothesis. They engaged in significantly more floating pre-parturition than they did across the eight week, post-parturition period, χ^2 ($df = 8$, $N = 5$) = 19.80, $p < .049$, $W = .50$. The mothers also significantly increased their slow swimming rest behavior over the course of the study, again supporting our hypothesis, χ^2 ($df = 8$, $N = 5$) = 31.21, $p < .001$, $W = .80$.

Specifically, mothers engaged in the least slow swimming prior to and the first week following parturition. The percentage of slow swims steadily increased with each week with three quarters of the night-time activities being slow swims the last few weeks of the study.

Table 2
Results from Wilcoxon Matched Pairs Signed Ranks Test for Pre- and Post-Parturition Behaviors

		<i>N</i>	Rank Sums
Float	Negative Ranks	937	457256.00
	Positive Ranks	38	18544.00
	Ties	1068	
Slow swim	Negative Ranks	162	88938.00
	Positive Ranks	935	513315.00
	Ties	946	
Active swim	Negative Ranks	191	78787.50
	Positive Ranks	633	261112.50
	Ties	1219	
Other	Negative Ranks	27	634.50
	Positive Ranks	19	446.50
	Ties	1997	

Note. All calculations were performed by subtracting the pre-parturition behaviors from the post-parturition behaviors.

Although not specifically hypothesized, our mothers also significantly altered the frequency with which they actively swam over the eight week post-parturition period, χ^2 ($df = 8$, $N = 5$) = 31.89, $p < .001$, $W = .78$. As demonstrated in Figure 2 and Table 3, mothers almost quadrupled the frequency with which they actively swam during the first week post-parturition as compared to their active swims pre-parturition. Mothers engaged in their greatest levels of active swims the first two weeks post-parturition. Then as the calves matured, mothers gradually decreased their active swims while steadily increasing their slow swims. The category including other behaviors did not significantly change over the study's duration.

Pregnant control. This study also provided an opportunity to observe the night-time activities of a pregnant female (Dolphin C) who was housed with the mother-calf pairs across the duration of the study. Although not specified as a particular hypothesis, we expected that the activities of the pregnant control would be similar to the mothers' pre-parturition behaviors. Results of a Chi Square Goodness of Fit test indicated that she engaged in a pattern similar to the mothers' averaged pre-parturition behaviors. The pregnant control was significantly more likely to float (58.9%, $N = 359$) than active swim (21.7%, $N = 132$) and slow swim (17.6%, $N = 107$) and least likely to engage in other behaviors (1.8%, $N = 11$) χ^2 ($df = 3$) = 427.95, $p < .001$. Interestingly, she displayed significant variation in her activities across the four months, Pearson Chi Square Test of Independence: χ^2 ($df = 9$) = 41.44, $p < .001$, $V = .15$. As seen in Table 4, surface floating accounted for close to three quarters of all her activities during May (before calves) and August (after all the calves were two months of age), significantly more than during June and

July. During the month of June when the calves were the youngest, C continued to primarily float at night but was significantly more likely to engage in slow swims. Surface floating continued to be her primary behavior in July, however she was significantly more likely to swim actively. She returned to her baseline levels by August.

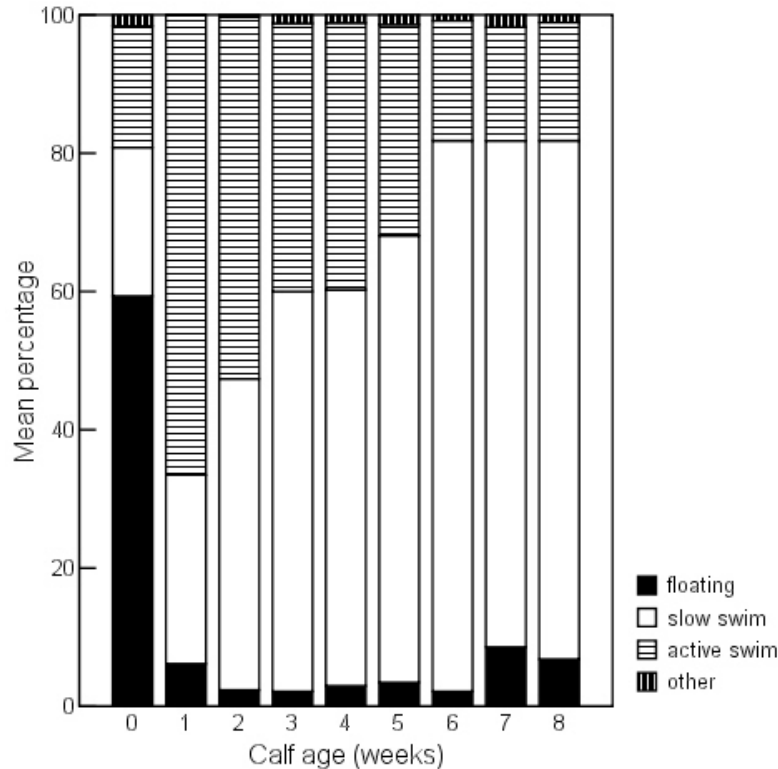


Figure 2. Average percentage of night-time behaviors by mothers pre- and post-parturition. *Note.* The calf age, zero weeks, indicates pre-parturition.

Parity. A Mann-Whitney U test was conducted to investigate the relationship between parity and post-parturition behaviors. The test indicated that primiparous mothers were generally similar to multiparous mothers in their overall activity level across the two months, post-parturition. Thus, there were no differences in the type of rest behavior exhibited by mothers with different degrees of calf rearing experience, which failed to support our hypothesis

Tests of Vigilance

Analyses of the vigilance data were primarily conducted using Chi Square Tests of Independence. Although data were collected from the same subjects multiple times, we assumed that the sample points were independent of one another as they were obtained at distinct intervals and independently of each other (Gibbons, 1993; Haslom & McGarty, 2003). Laterality was also assessed using Chi Square Tests of Independence.

In general, a Binomial test indicated that as a group, the five mothers were significantly more likely to respond (0.71, $N = 330$) than not respond

(0.29, $N = 132$) during initial vigilance tests, $p < .001$. The pregnant control also exhibited this trend by always responding to her vigilance tests (1.0, $N = 41$, $p < .001$).

Table 3
Mean Percentage of Night-Time Behaviors Pre- and Post-Parturition ($n=5$).

	Calf Age (weeks)								
	0	1	2	3	4	5	6	7	8
Float*									
<i>M</i>	59.4	6.2	2.4	2.2	3.0	3.5	2.2	8.6	6.8
(<i>SD</i>)	(26.6)	(8.6)	(2.2)	(2.1)	(3.3)	(3.0)	(1.2)	(7.3)	(7.5)
<i>n</i>	615	15	7	7	9	9	5	17	7
Mean rank	9.0	5.5	2.7	3.4	3.7	4.2	4.3	6.2	6.0
Slow swim**									
<i>M</i>	22.3	27.3	45.0	57.8	57.3	64.6	79.6	73.2	75.0
(<i>SD</i>)	(18.5)	(6.0)	(8.3)	(13.1)	(13.8)	(8.3)	(9.8)	(10.6)	(14.9)
<i>n</i>	232	71	133	180	171	181	166	149	100
Mean rank	1.4	1.8	3.8	4.8	4.2	6.0	8.0	7.4	7.6
Active swim**									
<i>M</i>	16.7	66.6	52.3	38.8	38.6	30.5	17.3	16.5	17.1
(<i>SD</i>)	(9.2)	(13.0)	(7.1)	(15.6)	(16.9)	(8.0)	(8.1)	(7.7)	(17.4)
<i>n</i>	164	172	1556	114	118	87	40	34	30
Mean rank	2.6	8.8	7.4	6.4	6.8	4.8	3.0	2.5	2.7
Other									
<i>M</i>	1.6	0.0	1.6	1.3	1.2	1.4	.9	1.8	1.1
(<i>SD</i>)	(0.7)	(0.0)	(0.0)	(2.9)	(2.6)	(1.3)	(1.3)	(1.9)	(2.5)
<i>N</i>	16	--	1	4	3	3	2	4	2

Note. The calf age, zero weeks, indicates pre-parturition.

* $p < .01$, Friedman test. ** $p < .001$, Friedman test.

Table 4
Percentage of Night-time Behaviors for Pregnant Control by Month

	May	June	July	August
Float				
%	73.8	49.4	57.7	74.5
<i>n</i>	79	115	123	41
Slow swim				
%	15.0	26.6	11.7	7.3
<i>n</i>	16	62	25	4
Active swim				
%	10.3	21.9	28.2	18.2
<i>n</i>	11	51	60	10
Other				
%	0.9	2.1	2.3	0
<i>n</i>	1	5	5	--

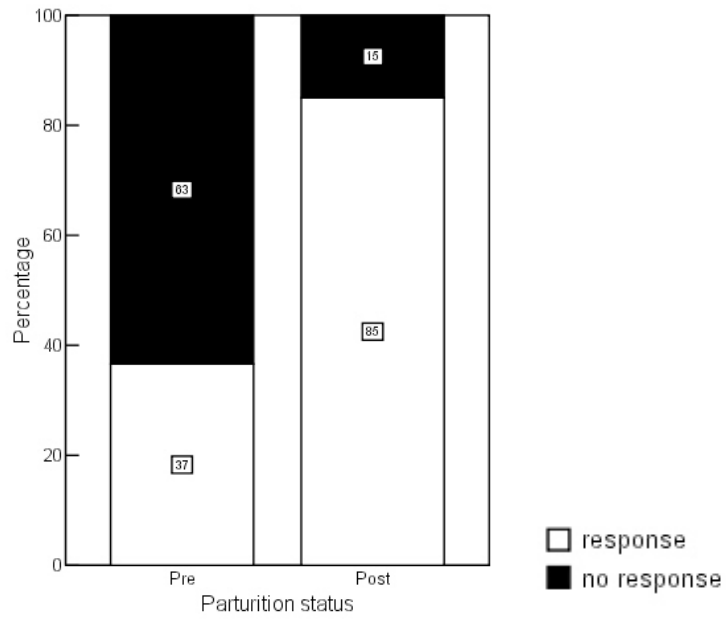
Current Behavioral Activity and Vigilance Test Outcome. A Chi Square Test of Independence was conducted to test our hypothesis that more active behaviors were linked with more vigilant states and less active behaviors were linked to less vigilant states. The results partially supported our hypothesis as the outcome of the vigilance tests were significantly related to the behavior recorded immediately before administration of all vigilance tests, $\chi^2 (df = 3) = 26.56, p < .001, V = .25$. Mothers were more likely to fail to respond while floating, $N = 62$ (47.7%) and were more likely to respond while slow swimming, $N = 130$ (45.0%).

Pre-Parturition versus Post-Parturition Vigilance. The results of a Chi Square Test of Independence supported the hypothesis that mothers should exhibit greater vigilance post-parturition as compared to pre-parturition, $\chi^2 (df = 1) = 35.63, p < .001, V = .29$. Specifically, mothers were significantly less likely to respond to initial vigilance tests, pre-parturition, $N = 106$ (42.6%), and significantly more likely to respond to initial vigilance tests, post-parturition, $N = 146$ (84.9%). Figure 3a displays these relationships.

The distribution of vigilance responses of the contralateral eye in follow-up vigilance tests was also examined for its relationship to parturition status. A Spearman's rank correlation indicated that a significant moderate, positive correlation ($r_s = .44, N = 421, p < .001$) existed between the responses of an initial vigilance test and an immediate follow-up vigilance test of the contralateral eye. That is, if mothers responded to the first test they would also respond to the second test, $N = 31$ (31.0%), and if mothers failed to respond to the first test, they also failed to respond to the second test, $N = 41$ (40.6%). Interestingly, unlike the results of the initial vigilance tests, mothers were just as likely to respond (0.42, $N = 42$) as they were not to respond (0.58, $N = 58$) to the follow-up vigilance tests of the contralateral eye (Binomial test: $p = .13$). Also similar to the results of the initial vigilance tests, the distribution of responses to the follow-up vigilance tests was significantly related to the parturition status, $\chi^2 (df = 1) = 19.92, p < .001, V = .44$. That is, mothers were significantly less likely to respond to the follow-up vigilance tests, pre-parturition, $N = 42$ (71.2%), and significantly more likely to respond to the follow-up vigilance tests, post-parturition, $N = 31$ (73.8%). Figure 3b displays these relationships.

Influence of Possible Fatigue on Vigilance Testing. In order to assess our hypothesis that mothers might become fatigued by weeks three and four due to their constant swimming activities since the birth of their calves, we collapsed the outcomes of initial vigilance tests for individual weeks into two week intervals so that we could minimize the number of cells with expected counts of less than 5. The results of the Chi Square Test of Independence failed to support our hypothesis that mothers would become less vigilant over the course of the eight weeks. We would like to point out though that the mothers failed to respond the most often between three and four weeks, post-parturition, $N = 16$, (9.5%), compared to the next highest frequency of no responses during weeks five and six, $N = 4$, (2.4%).

a. Initial Vigilance Tests



b. Follow-up Vigilance Tests

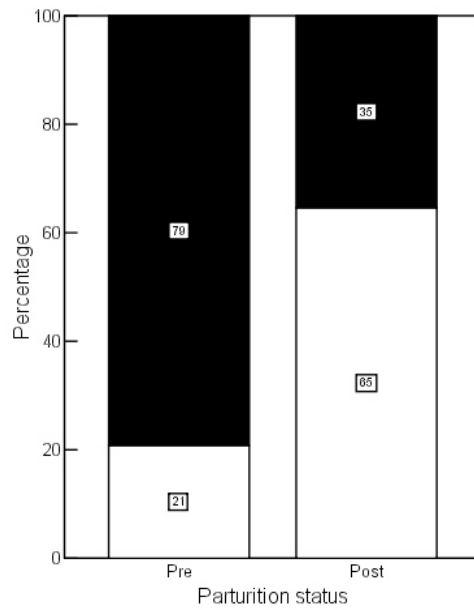


Figure 3. Results from vigilance tests conducted pre- and post-parturition.

Parity. Chi Square Tests of Independence were conducted to examine the relationship between parity and vigilance. Parity was found to be independent of vigilance for both the initial and the follow-up vigilance tests.

Laterality. Mothers received a total of 101 vigilance tests pre- to post-parturition in which both sides were tested sequentially— an initial test and a follow-up test. Of these tests, $N = 28$ (28.0%) indicated laterality or unihemispheric sleep.

Pre-parturition. There were a total of 54 instances in which mothers sequentially received two tests of vigilance. A Chi Square Test of Independence failed to fully support our hypothesis that dolphins would show laterality of vigilance as the test approached significance, $\chi^2 (df = 1) = 3.38, p = .066, V = .25$. Five (9.3%) test combinations resulted in responses for both eyes, 35 (64.8%) test combinations resulted in no response for either eye, and 14 (26.0%) test combinations resulted in a response for one of the two eyes. Additionally, a Chi Square Test of Independence indicated that the side to which the stimulus was presented was not related to the test's outcome.

Post-parturition. There were a total of 47 instances in which mothers received an initial test of vigilance and a follow-up test. A Chi Square Test of Independence partially supported our hypothesis of laterality in vigilance, $\chi^2 (df = 1) = 4.48, p = .034, V = .31$. Specifically, mothers were more likely to respond to a follow-up test if a response had occurred during the first test, $N = 27$ (57.4%) and were more likely to fail to respond to a follow-up test if they had done so during the first test, $N = 6$ (12.8%). However, they were also likely to respond with one side and not the other (i.e., laterality) although significantly less often than expected, $N = 14$ (29.8%). Finally, a Chi Square Test of Independence indicated that the side to which the stimulus was presented was not related to the test's outcome.

Discussion

The night-time activities and levels of vigilance for pregnant female dolphins in the care of humans were examined one month prior to parturition and two months after parturition. A number of hypotheses were tested. The first series of hypotheses involved night-time activities with an emphasis on changes in types of resting behaviors over the course of the study. The second series of hypotheses tested various aspects of vigilance in female dolphins, including differences between parturition states and laterality.

Behavior

Pre-Parturition and Post-Parturition Night-Time Activities. As expected from previous research with non-pregnant dolphins in the care of humans, pregnant female dolphins, located at a working and research facility, in natural ocean water with a regular tidal exchange, were generally not very active at night (Flanigan, 1974; Goley, 1999; Gnone et al., 2001; Gnone et al., 2006; Lyamin et al., 2005; McCormick, 1969; Mukhametov, 1984; Ridgway, 2002; Sekiguchi et al., 2006). Our females displayed two types of resting patterns during night-time activities: surface floats and very slow, stereotyped circular swims. On average, 60% of their nightly activities involved surface floating and 20% involved slow swims. The remaining 20% of their activities included active, alert swims and other kinds of activities such as bows, breaches, and interactions.

As anticipated, the arrival of the calves altered the females' night-time activity levels. Surface floating immediately dropped to minimal levels (< 10% of the activities) and was replaced by active swims with the calves, during the first two weeks of life. Despite the variability in social groupings, mothers followed similar trends whether they were alone with their calves or if multiple mother-calf pairs were present. These observations complement previous observations that bottlenose dolphin and killer whale mothers rarely float post-parturition (Lyamin et al., 2005) and observations of a captive dolphin calf who displayed no surface floating until 15 weeks (Gnone et al., 2006). Our results also correspond with the high level of calf dependence on maternal vigilance during the first few weeks of life when the calves have the greatest need for continuous monitoring in terms of swimming proficiency and susceptibility to danger (Cockcroft & Ross, 1990; Fellner et al., 2005; Mann & Smuts, 1999; McBride & Kritzler, 1951; Miles & Herzing, 2003; Reid et al., 1995; Tavolga & Essapian, 1957). However, the increase in active swimming may also be related to the hydrodynamic benefits received by calves when swimming in close proximity to their mothers, such as slipstreaming while in an echelon or infant position (Fellner, Bauer, & Harley, 2006; Gubbins et al., 1999; Noren & Edwards, 2007; Weihs, 2004). These benefits include decreased energy expenditure, navigation and respiration assistance, and thermoregulation opportunities for the calf.

By the third and fourth weeks, the mothers had significantly reduced their active swimming and were more likely to swim slowly in a stereotyped circular pattern (almost 60% of their night-time activities). This change in behavior may have occurred for several reasons: (1) mothers may have begun to tire and therefore engaged in less active swimming and more slow swimming, (2) the mothers may have altered their behaviors as their calves no longer needed to be monitored as constantly because they now had greater control over their swim and respiration patterns, (3) calves were growing, becoming more efficient at nursing and consuming more milk or (4) a combination of these reasons. Whatever the reason, these data suggest that the presence of calves dramatically changed the mothers' night-time activities.

It is unclear how much rest dolphin mothers are able to obtain while caring for a neonate. Lyamin et al. (2005) suggested that dolphin mothers could not have engaged in extended periods of sleep until sometime after the first month. They drew this conclusion for two reasons: (1) their mothers did not display a significant amount of surface floating during the first month, and (2) the mothers' monitoring activities would have constantly interrupted any sustained sleep. Our mothers also did not return to their baseline floating levels by the end of two months. However, they did engage in a significant proportion of slow swimming beginning at two weeks, a rest behavior not specifically measured by Lyamin et al. (2005). We suggest that these periods of slow swimming could have been periods in which the mothers slept for substantive periods of time, via unihemispheric sleep (Flanigan, 1974; Mukhametov, 1984; Ridgway, 2002).

As noted earlier, slow swimming (i.e., additional resting opportunities) steadily increased over the course of the second month while active swimming decreased. By the second month, calves are much better at maintaining their echelon swim position and slipstream advantage (Fellner et al., 2006; Gubbins et al., 1999; Noren & Edwards, 2007; Weihs, 2004). The increase in slow

swimming may also provide the mothers opportunities to restore her own energy levels. Slow swimming is a slower paced, less active behavior that involves relatively long periods of gliding. Hypothetically, this swim pattern may allow the mothers to expend less energy, and thus restore their energy reserves from the exertions required during the first month of their calf's life and provide for the neonate's increasing demands for nursing. Slow swimming, rather than surface floating, may also be beneficial to the calves as they may still require additional assistance in thermoregulation, respiration maintenance, and navigation of their environment during this second month of life (Cockcroft & Ross, 1990; Fellner et al., 2005; Lyamin et al., 2005; Mann & Smuts, 1999; McBride & Kritzler, 1951; Miles & Herzing, 2003; Reid et al. 1995; Tavalga & Essapian, 1957).

Pregnant control. When the activities of Dolphin C were examined, we found that they differed dramatically from the mothers' activities. Unlike the mothers, C continued to engage in surface floats for at least half of her night-time activities once the calves were present. This trend persisted across a variety of social groupings. However, she was not immune to the presence of the calves and their subsequent effect on night-time activities.

During the month of June when the calves were young, the pregnant control engaged in a greater number of slow swims while resting (27%) as compared to the previous month when no calves were present (15%). This change in behavior may have reflected a disruption in the night-time activity routine with the increased swimming levels of the mother-calf pairs. For example, surface floating may have been more difficult to maintain with the increased number of mother-calf pairs present. Another explanation may simply have involved a social facilitation effect, in which the control dolphin swam more because more animals were swimming.

Surprisingly, July brought a greater increase in activity. Although C was still likely to rest while floating, she did increase her active swims. It is unclear why C became more active at a time when most of the mothers and calves were beginning to engage in slow swims. However, by the end of the study, she had returned to her pre-calf activities, which included resting by surface floats.

Vigilance. We also examined the vigilant state of each female before and after parturition. Overall, our female dolphins maintained high levels of vigilance with and without calves present, supporting previous research on sustained vigilance in dolphins (Hoffman-Kuhnt 2003; Ridgway et al. 2006). Moreover, the outcome of the vigilance tests was correlated with the type of behavior exhibited just prior to the administration of an initial vigilance test. Previously, floating had been associated with low levels of vigilance (Connor & Heithaus, 1996; Lyamin et al., 2005; Norris & Dahl, 1981) while slow swimming and active swimming were associated with increasingly higher levels of vigilance (Goley, 1999; Gnone et al., 2001). The results corroborated these previous observations as our females were more likely not to respond while surface floating and more likely to respond while slow swimming.

Vigilance Pre-Parturition and Post-Parturition. As expected, mothers were more vigilant post-parturition than pre-parturition. They were more likely to respond to vigilance tests when their calf was present, and they were more likely to not respond when their calf was absent. When immediate follow-up tests of vigilance were conducted for the contralateral eye, mothers tended to

respond if they had responded on the first test. In fact, mothers and the pregnant control were generally vigilant for both tests.

There were occasions though in which the females were not vigilant for either test suggesting that both hemispheres were “sleeping.” These behavioral data support previous empirical evidence for occasional bihemispheric sleep in dolphins (McCormick, 1969; Ridgway, 2002; Ridgway et al., 2006). The majority (85%, $N = 35$) of these proposed bihemispheric periods occurred pre-parturition. However, six instances did occur post-parturition. Clearly, mothers altered their vigilance efforts when calves were present, corroborating the behavioral changes observed in their night-time activities. Overall, they were much more vigilant across the eight week period compared to the month before parturition.

Like their terrestrial counterparts, a state of sustained sleep comes at a cost for dolphins, particularly those with very young offspring (Lima et al., 2005; Lyamin et al., 2005). Failures to respond to stimuli, in this case, a light stimulus, may be the result of occasional bihemispheric sleep patterns, fatigue, divided attention from monitoring their calves’ activities and the activities of other animals, or simply a failure to perceive the stimuli. Clearly, having alternative vigilance strategies, such as resting as part of a group with periphery members having vigilance duties, having sentinels present, or sleeping in a protected place is advantageous to the survival of a species (as reviewed in Lima et al., 2005). In group settings, such as in the current study, mothers could possibly decrease their levels of awareness for brief periods, and “sleep” because the care of their calves is taken over by some member of the group. However, this vigilance strategy did not seem to be supported by the night-time behavioral data and responses to the vigilance tasks. Mothers did not rely on other mothers to care for their calves during the night-time hours as calves were observed only swimming with their mothers during the observations. Similarly, the mothers were highly responsive to the behavioral tests of vigilance. Alternatively, the mothers may have relied more heavily upon a different vigilance strategy, induction of unihemispheric SWS (Lilly, 1964; Mukhametov, 1984; Mukhametov et al., 1977; Ridgway, 2002; Lyman et al., 2008), as indicated by their slow swimming behavior. This strategy would enable the mothers to maintain vigilance over their calves and rest simultaneously. Additional research should examine rest patterns of mothers and their calves during the day as well to determine if mothers use different vigilance strategies depending on the context and social groupings.

Influence of Fatigue on Vigilance. Despite these increases in rest opportunities over the two month period, the first two weeks were characterized by active swimming. Two weeks of continuous swimming and nursing neonates were expected to tire the mothers and result in a decrease of vigilance. Our results did not support this hypothesis as mothers did not significantly change their level of vigilance (i.e., more response failures) over time. Lyamin et al. (2005) had previously ruled out the possibility that the ability to swim continuously was not facilitated by parturition status or hormonal state as there were no differences in stress hormones pre- to post-parturition. It is possible that the mothers became sensitized to the vigilance tests as the frequency of the tests during weeks three and four did increase. However, this explanation does not appear to be adequate as they consistently performed on the vigilance task over the eight weeks and they did fail to

respond more often during the third and fourth weeks than they did at any other point in the study, post-parturition. Perhaps the best explanation is that with the increase in slow swims after the second week of parturition, mothers were able to rest enough to sustain high levels of vigilance. This transition to slow swims may have also been facilitated by the establishment of regular nursing and slipstreaming.

Laterality. Although we were unable to directly measure the mothers' brain activity to determine the presence of unihemispheric SWS, the vigilance tests provided some indirect evidence. Our females showed laterality in their responses to approximately 30% of the dual vigilance tests given pre- or post-parturition. Laterality was indicated when females responded with one side or the other, but not both, to two successive light stimuli. Lyamin et al. (2004) showed that eye closure corresponded to unihemispheric SWS in the brain hemisphere opposite the closed eye in about 75 % of their observations. Opposite eye closure is to be expected because the dolphin optic nerves cross completely at the optic chiasm and directly supply only the opposite brain hemisphere (Tarpley, Gelderd, Bauserman, & Ridgway, 1994). These data support previous research indicating that dolphins are capable of unihemispheric sleep and constant vigilance (Lyamin et al., 2004; Mukhametov, 1984; Mukhametov et al., 1977; Ridgway, 2002; Ridgway et al., 2006, Lyamin et al., 2008).

Parity. In the current study, parity was not related to the mothers' resting activities or to their performances on the vigilance tests. These outcomes were not surprising considering the biological importance of maintaining high levels of vigilance around very young offspring. Calf survival is the ultimate goal for both experienced and inexperienced mothers. Thus, parity should not influence level of vigilance. However, it is possible that differences in activity and/or vigilance may exist between individual mothers. Recent research has suggested that dolphins have unique and stable characteristics (Highfill & Kuczaj, 2007) and exhibit different degrees of maternal control (Hill, Greer, Solangi, & Kuczaj, 2007). Thus, mothers may differ in their activity level and selected rest strategies. Future research should continue to examine the role of maternal experience in combination with individual differences when examining vigilance and calf outcomes.

Conclusion

In summary, the current study specifically examined the night-time activities of females before and after parturition, unlike previous studies in which the swim activities and positions of mothers and their calves were only generally described (Cockcroft & Ross, 1990; Gnone et al., 2001; Gubbins et al., 1999; Mann & Smuts, 1999; Miles & Herzing, 2003; Reid et al., 1995). By differentiating between two types of resting activities, floating and slow swimming, we documented an important change in the mothers' nightly rest strategies that may be associated with neonatal development and enable mothers to sustain high levels of vigilance for extended periods of time. Lyamin et al. (2005) observed that dolphin mothers swam almost continuously, which led them to propose that dolphins may engage in little sleep for extended

periods of time. In contrast, we suggest that the slow circular swimming we observed is likely a form of unihemispheric sleep, which may enable the mothers to sleep as they maintain vigilance over their calves. As demonstrated in continuously swimming porpoises two and half decades ago, unihemispheric slow wave activity alternated between the hemispheres (Mukhametov & Poliakova, 1981). Therefore, stopping to rest or becoming immobile is not an absolute requirement for sleep.

We suggest that future research must also examine alternative rest strategies (i.e., slow swimming). Similar to the different vigilance strategies adapted by various group living terrestrial animals, cetaceans may have evolved a vigilance strategy appropriate to their aquatic environment and their specific biological capabilities. Namely, mothers may incorporate one of their sleep strategies (slow swimming) to a greater degree when they are no longer able to float for long periods of time immediately after birth due to their calves' limitations. Through neonatal slipstreaming during slow swims, mothers are able to sleep or conserve energy for extended periods of time while continuing to monitor their environment and provide the neonate with nursing opportunities, thermoregulation, and navigational assistance. This alternative swim and vigilance strategy may not deprive mothers of sleep as long as Lyamin et al. (2005) suggested. As we did not continuously record behaviors, we cannot provide an estimate of the average time mothers engaged in floating, slow swimming, or active swimming. Future studies in which these behaviors are measured continuously throughout the day would elucidate the importance of slow swimming to maternal sleep and vigilance. This knowledge would be especially important for dolphin mothers in their natural habitat, since floating is not a frequently observed resting strategy.

The current study also provided the first empirical evidence for high levels of vigilance in bottlenose dolphin mothers over an extended period of time. These findings augment those of Ridgway et al. (2006) in which two bottlenose dolphins independently demonstrated continuous auditory vigilance for five days. Finally, our findings suggested that mothers showed laterality in their vigilance both before and after their calves were born. These results imply that mothers may engage in a unihemispheric sleep strategy at times to remain continuously vigilant while resting even though they continue to swim slowly or glide with the calf at their side. Future studies should follow mothers' resting activities beyond the first two months of their calf's life as well as include observations during the daylight hours. These studies would enable researchers and managers of dolphins in human care to ascertain when mothers return to pre-parturition activities. Knowledge of the developmental course of the night-time rest and vigilance activities could facilitate better care of mothers and their calves, including the timing of mother-calf separations and weaning and management of group composition and habitat. Studies should also continue to examine the calves' activities. Lyamin et al. (2005) indicated that their killer whale calves engaged in less floating than their mothers. This behavioral trend was replicated by a captive study examining the resting activities of a bottlenose dolphin calf over the course of the first year of life (Gnone et al., 2006). Although much of the calves' behaviors are regulated by the mothers, it is also important to examine the rest patterns of calves as they develop to begin to assess the influence calves have on their mothers' activities.

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