SLEEP BEHAVIOUR

# Sleep in continuously active dolphins

Arising from: O. Lyamin, J. Pryaslova, V. Lance & J. Siegel *Nature* **435,** 1177 (2005).

Sleep has been assumed to be necessary for development and to be a vital function in mammals[1,2] and other animals[3,4]. However, Lyamin *et al.*[5] claim that in bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*), neonates and their mothers show almost no sleep behaviour for the first month after birth; this conclusion is based on their observation that the cetaceans keep swimming, avoid obstacles and rarely close their eyes for 24 hours a day throughout that period. Here we analyse the behaviour and eye closure of three neonate–mother pairs of bottlenose dolphins and find that, although the animals tend to open both eyes when surfacing to breathe, one or both eyes are closed during 'swim rest', an underwater sleeping behaviour that is associated with continuous activity. This observation calls into question the conclusions of Lyamin *et al.*[5], who overlooked this type of sleep by analysing the animals' eye state only when they surfaced to breathe.

Dolphin sleep is characterized by unihemispheric slow-wave patterns in electroencephalograms, indicating that they may be able to continue swimming even when asleep[6]. Unihemispheric slow waves are invariably linked to closure of the contralateral eye[7,8] and captive bottlenose dolphins are assumed to be asleep if at least one eye is closed[9]. These animals rest by staying immobile for long periods either on the bottom of the tank (bottom rest) or at the surface (surface rest); most frequently, they rely on 'swim rest' — during which they execute a slow swimming motion along a fixed trajectory close to the bottom of the tank[9] (Fig. 1a). We note that Lyamin *et al.*[5] consider only the immobile states at the surface or on the bottom as typical sleep behaviour.

Two neonate–mother pairs that we monitored for a week or a month after birth took a considerable amount of swim rest (neonates: 31.3–40.7% and 24.6–33.0%; mothers: 32.5–40.7% and 26.7–33.3% of the observational time, respectively). They took this even during the day, when their activity (as estimated from breathing interval and swim speed) was significantly higher than at night[9]. Although nine dolphins, including the neonate–mother pairs, were housed in the same pool, they never bumped into each other or into the pool wall during swim resting. The occasional emission of click-type sounds recorded during swim rest has indicated that the animals use echolocation to avoid obstacles[9].

The dolphins that we observed, particularly neonates and babies, tended to close their eyes underwater but to open their eyes when they surfaced to breathe, even during swim rest; the percentage of the observational time during which the eyes were closed was considerably smaller at the surface than when underwater (Table 1). When the 1-week-old neonate surfaced to breathe, it often opened the eye that had been closed underwater (94.7% of 19

**Table 1 | Closure of right eye by bottlenose dolphins during swim rest and at the surface**

| | | Postpartum age (weeks) | | | |
|---|---|---|---|---|---|
| | | 1* | 4† | 5‡ | 9‡ |
| Mothers | Surface | 58.8% (68) | — | 42.9% (14) | 63.6% (55) |
| | Underwater | 100% (23) | 64.5% (62) | 72.6% (62) | 88.2% (34) |
| Neonates and babies | Surface | 12.1% (99) | — | 24.2% (33) | 28.5% (63) |
| | Underwater | 91.7% (36) | 52.1% (48) | 63.3% (60) | 88.6% (44) |
| Adults§ | Surface | | | 49.3% (142) | |
| | Underwater | | | 83.3% (96) | |

Percentages indicate the proportion of observational time for which the right eye was closed. Numbers in parentheses give the total number of records. The state of the right eye could be recorded through a viewing window, as in most cases the dolphins swam in an anticlockwise direction round the pool. The percentage of time that the eye was closed at the surface was less than when underwater, especially in neonates; in neonates, it gradually increased with their growth. Observations were supported by Kyeongsoon Kim and Shuhei Hasegawa.
*Female neonate (day 13–14 after birth) at Kamogawa Sea World; born on 9 August 2005.
†Male baby at Minamichita Beachland Aquarium.
‡Male baby at Kamogawa Sea World; born on 20 June 2005.
§Three adult females at Kamogawa Sea World.

M. HIRATA

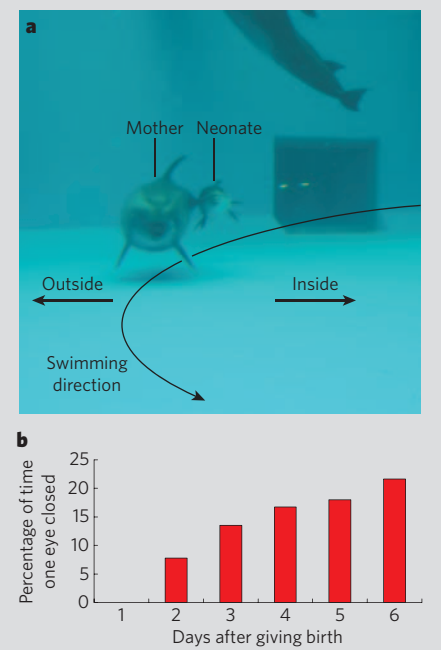


**Figure 1 | Trajectory of a neonate–mother pair during 'swim rest' and associated eye closure by the mother.** **a,** A neonate dolphin and its mother swim-resting at 13 days after birth. **b,** Increase in outer (right-side) eye closure by the mother during the first week after birth (no data were collected on the first day). Observations made with assistance from Satoshi Inoue and Makoto Soichi at Kamogawa Sea World (KSW).

**Methods.** We studied a female neonate of 2–13 days old and a male baby of 5–9 weeks old, with their mothers, in an oval outdoor pool (18 m by 15 m, 3.5 m deep) that included five other dolphins at KSW in Chiba, Japan; we also studied a 4-week-old male and his mother living in a circular outdoor pool (13 m diameter, 3 m deep) with two other dolphins at Minamichita Beachland Aquarium (MBA) in Aichi, Japan. Their behaviour and eye state were monitored through underwater viewing windows and from the poolside during July–August 2005 in KSW and November 1997 in MBA. The total observational time for each pair was 2,820 min, 780 min and 240 min, respectively. Their behaviour was recorded by point sampling at 30-s intervals for 15 min at the start of each consecutive observation period in KSW and by continuous focal animal sampling for 10 min at the beginning of each hour in MBA. Their eye state in water was recorded by random sampling (5–20 records per hour). Slow ($< 2$ m s$^{-1}$) and circular trajectory swimming near the bottom of the pool was recorded as swim-resting behaviour[9]. To record eye state at the surface and during swim rest, three people with transceivers observed the same animals at the same time from an underwater window (one observer) and from the poolside (two observers at opposite sides of the pool to check both eyes) in KSW. The eye state and position exchange of a neonate–mother pair 2–6 days after birth was examined by focal animal continuous sampling for 2,400 min in KSW. Observations were made between 8:00 and 17:00 to avoid effects of artificial light on the dolphins, particularly neonates. We found previously that a considerable amount of resting and sleeping was evident even during the day[9].

records, from simultaneous observation of the right eye at the surface and underwater). The neonate opened both eyes at the surface more frequently (69.0% of 29 records) than did the mother (15.8% of 19 records); this may have been because they were not yet fully proficient at breathing.

The first eye closure (unilateral) of the neonate was recorded 14 hours after birth and that of the mother at 11 hours (unilateral) and 108 hours (bilateral) after birth. Unilateral or bilateral eye closure of the mother during swim rest with the neonate was observed for 35.1% of the observation period (1,440 min, 4–6 days after birth). The mother almost always opened the eye facing the neonate (97.8%), indicating that she might be watching the neonate during swim rest (Fig. 1a). The percentage of eye-closure time (right eye) in the mother during swim rest gradually increased after birth from 7.5% (1 day after birth) to 22% (5 days after birth) (Fig. 1b). Position changes related to unihemispheric sleep[9,10] were also observed during swim rest in this pair.

Our results show that eye state at the water surface, as monitored by Lyamin *et al.*[5], is not adequate as an indicator of continuous activity without eye closure: it is likely that the bottlenose dolphins and killer whales described by Lyamin *et al.* also experienced periods of swim-resting sleep. This type of cetacean sleep profoundly differs from sleep behaviour in terrestrial mammals.

**Yuske Sekiguchi*, Kazutoshi Arai†, Shiro Kohshima‡**

*Research Center of Physical Fitness, Sports and Health, Toyohashi University of Technology, 1-1 Tempaku Toyohashi-city, Aichi 441-8580, Japan
e-mail: ysekiguc@coeprt.issrc.tut.ac.jp
†Kamogawa Sea World, 1464 Higashicho Kamogawa-city, Chiba 296-0041, Japan
‡Department of Biological Sciences, Graduate School of Bioscience and Biotechnology, Tokyo Institute of Technology, 2-12-1-W3-43 Ookayama Meguro-Ku, Tokyo 152-8551, Japan

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**doi:**10.1038/nature04898

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# Activity and sleep in dolphins

**Arising from: O. Lyamin, J. Pryaslova, V. Lance & J. Siegel *Nature* 435, 1177 (2005).**

According to Lyamin and co-authors, neonate bottlenose dolphins (*Tursiops truncatus*) almost never sleep, unlike all other mammals that have been studied[1]. Although we agree that young dolphins never stop and float at the surface, we find that they spend a considerable amount of time asleep while swimming. Our findings therefore call into question the conclusions of Lyamin *et al.*[1].

It is known that bottlenose dolphins use only unilateral sleep and that this state is compatible with swimming and with surfacing to breathe[2–5]; it is also known that young bottlenose dolphins never stop at the surface to rest[6], as adults sometimes do. However, this should not be interpreted as an indication of sleep absence, particularly as 'swim rest' is the most frequent resting behaviour in adult bottlenose dolphins[7,8].

We observed a healthy bottlenose dolphin male calf and its mother during the first year of its life and compared its rest behaviour with that of a sub-adult male (4 years old) who formed a pair with his 8-year-old brother, and also with that of an adult female (about 20 years old) who formed a pair with her daughter (4 years old). We monitored and measured the incidence of the two main rest behaviours identified in dolphins: slow stereotypic circular swimming and quiescent hanging behaviour[6–9].

During slow stereotypic circular swimming, the dolphin moves slowly, following a regular trajectory, and surfaces only to breathe; the animal shows no interest in its environment and produces no sound. Most of the time, one eye is closed while the other performs a sentinel function. Such swim-resting can be displayed by a single individual but it is more usual for two dolphins to pair off and rest together, swimming side by side in close synchrony. Each dolphin keeps one eye open; the open eye is constantly the eye that is directed towards the partner. This pairing behaviour is typical of the mother–calf relationship, but adults also seem to do it in order to save energy and to maintain a state of vigilance while resting.

During quiescent hanging behaviour, the dolphin hangs at the water surface, keeping its blowhole above it. No active swimming is evident, but the animal still has to balance to maintain its position. The animal again shows no interest in its environment and makes no sound. The state of the eyes during this behaviour is hard to monitor and is often uncertain[6].

We monitored the calf's behaviour using 24-hour underwater video–acoustic recording over 20 separate days during its first year. The sub-adult male was observed for 96 hours during the day and night, and the adult female was observed for 48 hours during the day and night. The state of the calf's eyes was monitored during diurnal hours (8:00–20:00), and those of the sub-adult male and of the adult female were directly observed during diurnal and nocturnal hours (for 96 and 48 hours, respectively).

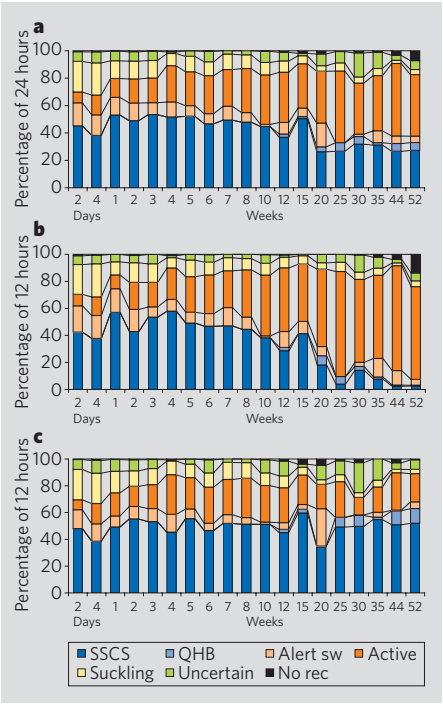


**Figure 1 | Trends in the rest behaviour over different periods of a dolphin calf during its first year. a–c,** Rest trends were monitored **a**, over 24 hours; **b**, during the day-time (8:00–20:00); and **c**, during the night (20:00–8:00). SSCS, slow stereotypic circular swimming; QHB, quiescent hanging behaviour; 'alert sw', alert swimming (when the calf is swimming while awake but is not involved in any specific activity); active, playful and exploratory activity; suckling, nursing activity; no rec, behaviour not recorded. **Methods.** Observations were made at the Genoa Aquarium from August 2002 to August 2003. Dolphins were housed in a pool with a large transparent acrylic wall (23.5 m by 8–10 m; 5 m deep; volume, 1,104 $m^3$). The pool was illuminated during the night with three 150 W lamps (9.3 lux at the water surface). Data were collected on 20 days by underwater video–acoustic recording continuously over 24 hours. A single researcher analysed all the video–acoustic sequences. The behavioural categories were measured by using a 1–0 sampling technique during 1-min periods. Further details are available from the authors.

The newborn carried out slow stereotypic circular swimming during the day and night for about 12 hours a day. After one year, the dolphin rested (both hanging and swim resting) for about 8 hours a day, mainly during the night time (Fig. 1). The sub-adult male rested for about 7 hours in 24 and the adult female for about 9 hours in 24; both took their rest mainly during the night. In these three animals, slow stereotypic circular swimming was the most frequent type of rest behaviour observed (constituting at least 85% of the total rest time) and was nearly always associated with unilateral eye closure (90–100%), in agreement with previous observations.

It is generally agreed that dolphins are able to rest and sleep under different and adverse conditions by using different rest strategies. In this respect, the total rest that an individual takes may change, depending on age, health and the physical and social environmental conditions[6,8]. Nevertheless, the rest behaviour in the dolphin calf that we observed was clear, showing a negative diurnal trend that was only party compensated for by a nocturnal positive trend. This behaviour resembles that of (diurnal) terrestrial mammals, including humans.

**Guido Gnone, Tiziana Moriconi, Giorgia Gambini**
Acquario di Genova, Area Porto Antico Ponte Spinola, 16128 Genova, Italy
e-mail: ggnone@acquariodigenova.it

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**doi:**10.1038/nature04899

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# *Lyamin* et al. *reply*

**Replying to: Y. Sekiguchi, K. Arai & S. Kohshima *Nature* 441, doi:10.1038/nature04898 (2006); G. Gnone, T. Moriconi & G. Gambini *Nature* 441, doi:10.1038/nature04899 (2006).**

All terrestrial mammals studied so far do maximal amounts of sleeping at birth, with sleep time gradually decreasing to adult levels. This has led to the concept that sleep, with its characteristic immobility and unresponsiveness, is necessary for brain and body development. We reported[1] that dolphins and killer whales have a very unusual developmental pattern: neonates are maximally and continuously active at birth, and this activity diminishes over a period of months to the adult level; in the postpartum period, mothers also abruptly cease the characteristic 'hanging' that constitutes the typical sleep behaviour in bottlenose dolphins and killer whales[2–5]. We did not claim that all sleep was abolished in the postpartum period. Rather, we reported that immobility was absent and that typical sleep posture increases with age, a pattern opposite to that seen in all land mammals studied so far. Sekiguchi *et al.*[6] and Gnone *et al.*[7] challenge our conclusions.

Figure 1 of Sekiguchi *et al.*[6] shows that maternal eye closure at the surface increases with age, which is consistent with our findings. Like us, they find that swimming is well coordinated, that neither neonate nor mother collide with the other animals, that animals vocalize during swimming, and that there is no hanging behaviour in the immediate postnatal period. We have serious reservations about their behavioural and eye-closure data because of the very small number of observations, the making of observations only when the animals approached a single underwater observation window, and the observations of eyelids only during the day rather than during the normal nocturnal sleep period (which also applies to the observations made by Gnone *et al.*[7]). By contrast, we monitored the animals' behaviour continuously and recorded the state of both eyes during both day and night.

Gnone *et al.*[7] conclude from their findings that the observed behavioural pattern "resembles [the sleep attitude] of (diurnal) terrestrial mammals, including humans". However, this claim is contradicted not only by our results[1] and by those of Sekiguchi *et al.*[6], but is also inconsistent with their own data: they report an absence of hanging behaviour in the neonate and mother, with this behaviour not appearing in the neonate until 12 weeks of age and then increasing until one year of age; they also claim that alert swimming is maximal at birth and decreases with age. Both of these observations[7] agree with our earlier findings[1].

This claim of Gnone *et al.*[7] also ignores research documenting dolphins' unihemispheric slow waves, avoidance of obstacles while in motion for 24 hours a day, and likely absence of sleep characterized by rapid eye movement (REM)[8]. However, we completely agree with the conclusion of Sekiguchi *et al.*[6] that cetacean sleep differs profoundly from that of terrestrial mammals.

One might try to draw an analogy between the neonates' continuous activity and sleep walking. However, sleep walking is a pathological, episodic state, in which coordination is grossly impaired and injuries frequently occur; it has not been established that sleep walking effectively substitutes for normal sleep, and it is interspersed with normal sleep episodes. In contrast, the postpartum swimming of dolphins and killer whales is characterized by precise course adjustments and vocalizations as the animals circumnavigate the irregular dimensions of the pools[1]. Neonates surface to breathe at 10–40-second intervals, keeping both eyes open, as also described by Sekiguchi *et al.*[6]; such open eyes are an indicator of electroencephalogram-defined wakefulness[5]. After each breath, the neonate locates, pursues and catches up with the mother, who breathes less frequently. It seems reasonable to us to state that typical sleep behaviour as seen in adult cetaceans and land mammals[4,5] is greatly reduced in dolphins and killer whales in the postpartum period[8], and that sustained periods of sleep lasting 10–40 seconds do not occur. Such interrupted sleep does not fulfil sleep's function in land mammals[1,8].

Whatever terminology is used, it is clear that the sensorimotor coordination seen in postnatal dolphins and killer whales not only involves extensive muscular activation, but also necessitates widespread activation of the brainstem[9–11] and most likely of forebrain neurons — in contrast with the neuronal activity pattern seen in the sleep of terrestrial mammals[12]. This difference in postpartum behaviour and neural function between cetaceans and terrestrial mammals has important implications for theories of sleep function and particularly for theories of the role of sleep in development[8].

**O. I. Lyamin*†, J. Pryaslova†, V. Lance‡, J. M. Siegel***
*University of California, Los Angeles & Veterans Administration Greater Los Angeles Healthcare System, Sepulveda, California 91343, USA
e-mail:jsiegel@ucla.edu
†Utrish Dolphinarium, Moscow 119071, Russia
‡San Diego State University, San Diego, California 92182, USA

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**doi:**10.1038/nature04900