Behaviour patterns of two captive Atlantic white-sided dolphins, *Lagenorhynchus acutus*

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**Abstract**

The behaviour of a little-known species, the Atlantic white-sided dolphin, was investigated by filming two captive individuals. The dolphins exhibited a high degree of social cohesion and engaged in complex forms of social interaction which had not been recorded before. Several other behaviours were also observed which do not seem to have been documented elsewhere. Daily changes in the frequency of some behaviours were noted, as well as tendencies to perform certain behaviours in particular areas of the pool.

Key words: Atlantic white-sided dolphin, *Lagenorhynchus acutus*, cetaceans, marine mammals, behaviour

**Introduction**

Much of what is known about cetacean behaviour has come from work with captive animals, usually bottlenose dolphins (*Tursiops truncatus*). Given the fact that cetaceans have been kept in captivity since the 1860s (Deffran and Pryor, 1980), the number of behavioural observational studies that have been conducted is surprisingly small, especially considering the wealth of information that has been gathered on cetacean sensory systems (cf. Nachtigall and Moore, 1983).

The captive environment provides the opportunity to gather details of cetacean behaviour that would be impossible to observe in the wild. The captive environment may also constrain and modify the normal behaviour and social patterns cetaceans exhibit in the wild. Such effects are not well understood, although Deffran and Pryor (1980) have postulated that while some behaviours may become amplified in captivity, others may drop out entirely. There is evidence, however, that species-typical behaviours are present in the captive environment. Deffran and Pryor (1980) conducted an extensive survey of the behaviour exhibited by 11 species of cetaceans held in human care and found that in many cases they correlated very well with behavioural descriptions of these species in the wild.

Only in recent years has it become feasible to study cetaceans in the wild environment over extended periods of time. To date, most information which has been acquired for wild cetaceans deals with general aspects of their behaviour such as movement patterns, feeding habits, social structure, and the frequencies of broad categories of behaviour such as “sounding” or “resting” (Deffran Santos et al., 1996; Evens, 1987; Leatherwood and Reeves, 1983; Newson et al., 1975; Shane et al., 1986).

We present a detailed behavioural account of two captive Atlantic white-sided dolphins (*Lagenorhynchus acutus*). Behavioural observations were taken during a study of the dolphins’ reactions to novel objects, conducted at the Mystic Marine Life Aquarium in Mystic, Connecticut, from 28 April to 1 June, 1991. This paper deals only with behaviours which were not related to the presence of test objects; information on reactions to objects can be found in Nelson (1992).

There are few published details about the behaviour and biology of the Atlantic white-sided dolphin. It is generally found in offshore, cooler temperate waters of the North Atlantic, entering warmer inshore waters in summer (Leatherwood and Reeves, 1983; St. Aubin and Geraci, 1979). Aggregations of several hundred individuals have been observed, although strandings are usually of smaller groups numbering 9–12 animals (Leatherwood et al., 1976; Leatherwood and Reeves, 1983; St. Aubin and Geraci, 1979).

Males of this species are generally larger than females and attain sexual maturity at approximately five years of age, when they are about 2.40 m in length (Leatherwood and Reeves, 1983; Sergeant et al., 1986; St. Aubin and Geraci, 1979). Females mature at the same age, when they are approximately 2.10 m in length (Leatherwood and Reeves, 1983; Sergeant et al., 1980; St. Aubin and Geraci, 1979). Young females remain with the breeding schools until they are weaned at about two years of age (Sergeant et al., 1980). At this point
they may form their own groups or join other species until mature (Sergeant et al., 1980).

Atlantic white-sided dolphins have been found in association with pilot whales (Globicephala melaena), fin whales (Balaenoptera physalus), and killer whales (Orcinus orca), and are generally wary of boats (Leatherwood et al., 1976; Leatherwood and Reeves, 1983; Sergeant et al., 1980; Sergeant and Fisher, 1977). Prey species include short-finned squid (Illex illecebrosus), herring (Clupea harengus), smelt (Osmerus mordax), silver hake (Merluccius bilinearis), and various species of shrimp (Sergeant and Fisher, 1975; Sergeant et al., 1980; St. Aubin and Gell, 1979).

Atlantic white-sided dolphins have rarely been maintained in captivity. Dr. Fred and Pryor (1980) list New England, probably referring to the New England Aquarium in Massachusetts and the Mystic Seaport Aquarium in Connecticut, as the only locale to have held this species.

Subadult animals

The two subjects for this study, one male and one female Atlantic white-sided dolphin, were found stranded off Wellfleet, Massachusetts on 15 February, 1991. At this time the male weighed 173.2 kg and was 241 cm in length, while the female weighed 186.8 kg and was 207 cm in length. The dolphins were thought to be mature. The aquarium considered their health to be critical and unstable (T. Binder, pers. comm.). Both dolphins lost weight continuously, by 28 May the male weighed 157.2 kg and the female 113.7 kg. Repeated physical examinations failed to find any pathologic problems, although each had fungal infections on various portions of their bodies. It was not known if the infections represented a significant health problem. The female died on 9 June, eight days after the present study concluded. A necropsy revealed a deep abscess in her right lung which she may have harboured since stranding. The male dolphin was released on 25 October, 1991, at which time he showed no evidence of behavioural problems, physical disorders, or clinical signs of disease (N. Goodyear, pers. comm.).

From their arrival until 4 March, the dolphins were housed in SPA, one of two outdoor pools 12 m diameter and 3 m deep. They were maintained with a female harbour porpoise (Phocoena phocoena) calf from 21–26 February, and originally had access to various toys such as hoops and balls, but showed no interest in them (T. Binder, pers. comm.). On 4 March the dolphins were moved to the second pool; SP3. The dolphins were housed in SP3 until 9 May, at which time they were moved back to SPA. Most of the study was carried out with the dolphins in SP4, which was quieter and provided more shade than SP3.

Observational methods

All observations were conducted from the roof of the adjacent aquarium which was approximately 15 m high. A Sony 8 mm video recorder was set on a tripod and fitted with a wide-angle lens so that most of the pool could be recorded on film. Because SP4 was very close to the side of the aquarium, it was possible to film almost straight down into it. SP3 was more distant and was viewed at a considerable angle. This difference in filming angle meant that part of the analysis had to be conducted separately for each pool.

Filming sessions originally began each day at 8:00 AM. The 8:00 session lasted 30 minutes, while other sessions took place daily on the hour from 10:00 AM to 5:00 PM, and lasted for 15 minutes each. Because the dolphins were fed daily from 7:00 to 10:00, no filming was conducted during this time period. After 12 May, the 8:00 session was dropped, and the 10:00 session was increased to 30 minutes in length.

For analysis of the tapes, each filming session was broken into three minute segments. For each segment, the frequency and duration (where applicable) of every behaviour were recorded, as well as the location of the dolphin in the pool when exhibiting the behaviour. These data were collapsed into 15 minute intervals for subsequent analysis because most behaviours were too infrequent to analyze at the three-minute level. All footage was viewed twice by the first author, and 10% was viewed a third time to check for reliability of the observations.

During the first viewing, information on repetition rates and interaction bouts were recorded in a notebook along with descriptions of all other behaviours. All behaviours are described in Table 1; the more visually complex behaviours are illustrated in Figure 1.

During the second viewing, each instance of a particular behaviour was recorded on a diagram of the pool, to indicate the location of the dolphin when that behaviour took place. This was done by placing a gridded sheet of clear plastic over the television screen, passing the film when a behaviour took place, and transferring the location of the dolphin's head at that moment to a similarly gridded diagram of the pool. The grid was used for locating particular dolphins, and did not correspond to any physical measurement of the pools.

Instances of behaviours that were unclear were viewed several times until a decision could be
reached as to their identity. Locations were not recorded for breaths, which were too frequent to make this procedure feasible or for interaction bouts. Because interaction bouts could last from a few seconds to several minutes, during which time the dolphins might circle the pool once or more, the occurrence of a bout could not be summarized by a single position.

**Figure 1.** Various behaviours. (A) twist; (B) roll, down; (C) tail up; (D) throwback; (E) arch; (F) & (G) interaction type 10 (see Table 1).
Table 1. Behaviours observed during the study. Category names were developed for use in this study only; they may not correspond to behaviour names used by other authors.

| Breath: | The dolphins rose to the surface and took a breath. When breaths of the two dolphins came within two seconds of each other, they were considered synchronous. For analysis, the percentage of breaths taken by each dolphin that were synchronous with breaths taken by the other was determined. |
| Twist: | The dolphins turned their heads and rolled alternately from one side to the other. This movement was sometimes exaggerated to such a degree that the dolphins would roll onto its side when turning (see Figure 1A). |
| Tail-Down: | The dolphin lowered its tail stock while holding its flukes relatively horizontal, keeping this position for a second or longer. This may or may not have been accompanied by lowering or raising of the head (see Figure 1B). |
| Tail-Up: | The dolphin raised its tail stock and held this position for a second or longer. This may or may not have been accompanied by lowering of the head (see Figure 1C). |
| Throwback: | The dolphin rapidly lifted both head and tail to an exaggerated degree, possibly turning its side at the same time (see Figure 1D). |
| Tail-Wag: | The dolphin rapidly moved its flukes from side to side. |
| Side-Swim: | The dolphin swam on its side. |
| Jerk: | This behaviour consisted of any slight, rapid jerking of the body. |
| Arch: | The dolphin lifted its head while arcing its tail stock and tossing it to one side (see Figure 1E). |
| Startle: | The dolphin suddenly jolted forward with a quick burst of speed. Except for one case when the female startled on her own, this behaviour always occurred simultaneously between the two animals. Usually, there was no apparent cause for the behaviour, although once it appeared to be caused by the shadow of a bird that passed directly overhead, and another time by a careless inadvertently hitting the edge of the pool. |
| Roll: | This was observed rarely, and only by the female. She would quickly and forcefully roll her body onto its side. |
| Penis Display: | The male's penis became erect. The male was not observed to position himself near the female while displaying. No reaction was ever noted by the female to such a display. |
| Interaction: | This consisted of any behaviours which involved physical contact between the two animals. A "bouts" of interaction began when one dolphin touched the other, and continued until they moved greater than one body length apart. If one dolphin clearly approached the other to begin interacting, that dolphin was labelled the initiator of the bout. If the initiator was not clear, the bout was considered to have been initiated by both dolphins. For analysis, the percentage of bouts initiated by each dolphin was determined. |

There were several kinds of interaction. The most commonly seen form of each is described here, although there were variations, such as which side each individual played in the encounter. No distinction was made between the different types of interaction during analysis. Often, a single bout of interaction would consist of several of the following. No sexual intercourse was observed during the study.

1. Male swam up and down the female's body while touching her with a pectoral flipper.
2. Male swam in back of the female and touched her tail with a pectoral flipper.
3. Male swam in back, and to the side, of the female, and stroked the side of her tail stock with a pectoral flipper.
4. Male swam in back, and to the side, of the female, while she moved her flukes sideways to rub them against one of his pectoral flippers.
5. Female swam underneath male, rubbing her head against one of his pectoral flippers.
6. Male swam alongside female side-by-side with a pectoral flipper of each touching.
7. Female swam up alongside male with his pectoral flippers touching his.
8. Male swam alongside female on his side, "holding" her back of her dorsal fin with his pectoral flippers.
9. Male swam behind female with a pectoral flipper touching her flukes, while both ceased swimming and gazed along, turning onto their sides.
10. Female touched her flukes to the male's dorsal fin, while both ceased swimming and gazed along. See Figure 4F & G for two different examples of this behaviour.
11. Male and female stopped swimming, and gazed along side-by-side with only their flukes touching.

Analytical methods
To determine whether there were differences in the rates of behaviour occurrences between the two dolphins, a One-Factor ANOVA with the two dolphins as the predictor and the occurrence rate of a behaviour per 15 minutes as the dependent variable was performed separately for every behaviour. Behaviours were also tested for periodicity; that is, whether frequency changes occurred regularly each day. For example, Sasyma et al. (1973) found that social interactions among both captive and
wild bottlenose dolphins were generally more frequent in the middle of the day than at other times. In this study, each 15 minute filming session was compared across the days to determine if there were any such periodicity. A One-Factor ANOVA with "session" as the predictor and the occurrence rate of a behaviour per 15 minutes as the dependent variable was carried out separately for each behaviour.

Finally, the spatial pattern of behaviour was examined. Pool diagrams showing behaviour positions were divided into quarters called upper left, upper right, lower left, and lower right. These labels reflect the view of the pool as seen by the camera. Because the filming angle varied between SP3 and SP4, the use of the two pools in this study were not the same. Therefore, analyses were carried out separately for each pool. Each behaviour was also analyzed separately. A Chi-square analysis was used to determine whether the occurrences of the behaviours were equal in all four quarters.

Results

The dolphins were filmed for a total of 42 hours. To check for reliability of the observations one 15 minute filming session per day was randomly selected, 12 minutes of which were reviewed: this resulted in a third viewing of 4 hours and 48 minutes. All behaviours except for breaths and interaction bouts were re-scored for each dolphin. A paired t-test between the scores for the second and third viewings indicated that there were no significant differences between them (t(8) = 0.623, p>0.5402). Thus, the observations were reliable.

The main effect of the original study was to determine the dolphins' reactions to novel objects. However, the report is concerned only with behaviours not related to the presence of objects. Thus, analyses reported here were only conducted on data collected when no objects were being tested in the pool, to remove the effect that these objects may have had on the behaviours. There were eight such days interspersed throughout the study, making a total of 14 hours, 35 minutes of observation time.

The results are reported here by behaviour type. These results are given in Figures 2-5. In Figures 3-5, only significant results are reported.

Breaths: There were no significant differences in the respiration rate between the two dolphins. Each took an average of 48 breaths per 15 minutes, and 82% of these were synchronous (Figure 2). Both dolphins showed an increase in breathing rate during the middle of the day (Figure 3).

Twists: There was a significant difference in rates of twisting between the two dolphins. The male twisted, on average, 2 times per 15 minutes, while the female twisted once per 15 minutes (Figure 2). There were non-random distributions of this behaviour in SP3 for each dolphin (Figure 4). Male twists were most common on the right side of the pool, while female twists were most common in the lower part of the pool.

Tail-Downs: There was no significant difference in the rate of tail-down displays between the two dolphins. Each displayed, on average, 2 times every 15 minutes (Figure 2). There was periodicity in the rate of tail-downs for the male. This behaviour was higher during the 10:00 session than during other sessions (Figure 3). The male showed a non-random distribution of tail-down displays in both SP3 and SP4 (Figures 4 & 5). In SP3, displays were most common in the upper portion of the pool, while in SP4 they were most prevalent in the upper right portion of the pool.

Tail-Ups: There was a significant difference in the rate of tail-up displays between the two dolphins. The female displayed about once per 15 minutes, while the male only displayed about once every 45 minutes (Figure 2). The female showed a non-random distribution of tail-up displays in both pools. In SP3 they were concentrated in the lower left corner, while in SP4 they were most common in the lower portion of the pool (Figures 4 & 5).

Throwbacks: There were significant individual differences in the number of throwbacks. The male averaged one throwback per 15 minute interval, while the female only exhibited this display a total of two times (Figure 2).

Tail-Wage: There were no individual differences for this behaviour. The rate averaged less than one tail-wag per 15 minutes (Figure 2). There was a non-random distribution for the female in SP3, with the behaviour being concentrated in the lower left corner of the pool (Figure 4).

Side-Swims: The female exhibited more of this behaviour than the male. She averaged one side-swap per 15 minutes, while the male's rate was much lower than this (Figure 2). In SP3, side-swims were concentrated in the upper left area of SP4 (Figure 5).

Jerks: There were no significant differences with time, location, or gender for this infrequent behaviour, which was observed less than once every 15 minutes (Figure 2).

Arches: The male exhibited much more arching behaviour than the female, averaging nearly one arch every 15 minutes (Figure 2). The female was only observed once.

Starrles: There were no significant differences with time, location, or gender for starrles, which occurred very infrequently (Figure 5).

R allele: Rolls were observed only three times by the female, and not at all by the male (Figure 2).
Figure 2. Individual differences in rates of behaviour combined for all days (mean per 15 minutes + 1 S.D.). Behaviours which are boxed indicate significant results. The results are for One-Factor ANOVA's performed separately for each behaviour, with the two dolphins as the predictor and the occurrence rate of a behaviour per 15 minutes as the dependent variable.

SB = percentage of breaths taken by each dolphin that were synchronized with breaths taken by the other; (F_{1,110}=2.023, p=0.158)

B = breaths: (F_{1,110}=0.378, p=0.4487)

T = tail: (F_{1,110}=3.742, p=0.0572)

TD = tail-dorsal: (F_{1,110}=0.111, p=0.7395)

TU = tail-up: (F_{1,110}=20.011, p=0.0001)

TW = tail-wedge: (F_{1,110}=21.679, p=0.0001)

SS = side-swim: (F_{1,110}=12.032, p=0.0006)

I = jibe: (F_{1,110}=1.436, p=0.2016)

A = arch: (F_{1,110}=10.783, p=0.0043)

There were no significant differences with time, location, or gender.

Genital Displays: This behaviour was observed only four times in total (Figure 2). There were no significant differences for time or location.

Interaction: The female initiated more interaction bouts than the male. On average, the female initiated 40% of all the bouts during each 15 minute interval, while the male initiated only 7% (Figure 2). Each bout lasted an average of 28 sec. The dolphins interacted for approximately one and a half minutes out of every 15 minute interval. Interaction bout lengths were longer at the beginning and end of each day (Figure 3).

Discussion

The dolphins in this study showed a high level of synchronicity. They were usually observed to swim in close proximity to each other. During the days analyzed here, they breathed in unison 82% of the time, and were in actual physical contact about 10% of the time, with interactions consisting of a complex and varied set of behaviours involving rubbing, stroking, and various body positions. Sexual intercourse was never observed, however, and penile displays were rare.

Few studies provide similarly detailed accounts of social interactions with which to compare these results. Belly-to-belly swimming has been seen in other pairs of this species (T. Binkley, pers. comm.). Swimming with pectoral fins touching is a social behaviour known to occur in several species, and may represent a form of bonding (Defran & Pryor, 1980). Several sources also indicate that using flippers or flukes to stroke another individual is commonly seen in various species (Defran & Pryor, 1980; McBride & Hebb, 1948; Puente & Dewsbury,
Tavolga and Esuapian (1957) detail the social interactions of a group of captive bottlenose dolphins which parallel some of the findings in this study. In particular, their description of "rubbing" closely matches interaction types 1, 4, 5, and 7 identified here (Table 1). They considered rubbing to be the least vigorous and energetic type of social activity. In addition, Sazymian et al. (1973) describe "rubbing" in bottlenose dolphins similar to interaction types 1 and 4.

Another courtship behavior documented in bottlenose dolphins is "displaying". The female exposure her underrides to another by rolling onto her side (Pantie & Dewbury, 1976; Sazymian et al., 1973). It may also represent a form of greeting or a sign of submission (Pryor, 1996; Würsig et al., 1990). This kind of behavior might correspond to "rolls" or "side-swims" described here. Rolls were only exhibited by the female, and she engaged in side-swims more often than the male (about once per 15 minutes). The function of these two behaviors was not obvious, however. No reaction to either behavior was ever noted, while in some instances it did not even appear as if the second animal would be able to view the display. In fact, side-swims often involved turning toward the side of the pool and away from the other dolphin.

The "arch" display observed in this study appears, through comparison of drawings, to be the same behavior as "poutting" described by Tavolga and Esuapian (1957) for captive bottlenose dolphins. They found that pouting was performed by the male in view of the female and indicated "that anticipatory activities were about to become more intense". However, Pantie and Dewbury (1976) rarely observed this behavior in their bottlenose dolphins. When it was seen, it was usually performed by the female "just before the male gained intercommunication". This difference between these two studies remains to be explained. Observations reported here appear to relate more closely to those of Tavolga and Esuapian (1957), since the arches occurred commonly (about once every 15 minutes) and more often than the female. As with rolls and side-swims, however, arches did not appear related to any other behaviors or actions.

Several types of social behavior which have been described elsewhere were not seen in this study. These include "mounting" of a pair, "rubbing" of the closed mouth against another individual, head butting, leaping, display swimming (swimming inverted at high speeds just below the surface), and chasing (Pantie & Dewbury, 1976; Sazymian et al., 1973; Tavolga & Esuapian, 1957).

In summary, both Tavolga and Esuapian (1957) and McBeath and Hebb (1988) indicate that captive male bottlenose dolphins generally initiate most...
sexual activity. These findings differ from this study, which found that the male initiated only 7% of interaction bouts.

Finally, the two dolphins exhibited a variety of behaviours which do not appear to have been observed in other studies. We were unable to find any mention of behaviours analogous to the twists, tail-downs, tail-ups, throwbacks, or tail-wags. Dolphins are known to use many types of non-auditory communication, including body postures (Pryer, 1990; Würsig et al., 1990). It is likely that some of these displays had communicative value. For example, tail-wags may be an indication of stress or annoyance, as the female exhibited this behaviour 55 times during one 15 minute interval when a very loud delivery truck was parked beside the pools (Nelson, 1992). At other times, tail-downs took place less than once every 15 minutes. Tail-down displays may bear some relationship to feeding, as the frequency of this behaviour was generally greater for the male in the filming session directly after feeding ended. The preceding points are merely speculation, and do not explain why the changes in behaviour frequencies for both tail-wags and tail-downs were only found in one of the two dolphins.

It is also unclear why some behaviours showed non-random distributions within the pool. Female
side-swims usually occurred near the filtration system in SP4, which was located in the upper left corner of the pool. However, other behaviours that were non-randomly distributed showed considerable variation in their location. It is possible that there were reference points used by the dolphins which were not apparent to the observer, such as differences in sound intensity or texture variations in the walls or bottom of the tank. It is also possible that some behaviours were simply more obvious when performed in a particular area of the pool, and were therefore rated as only occurring in that area.

It should be emphasized that the animals had stranded and the health of the two dolphins in this study had not stabilized when the experiment was conducted, and that the female subsequently died. Some activities may have been the result of illness rather than reflecting species-typical behaviours. For example, it seems likely that “jorks” indicated a reaction to some discomfort. Unfortunately, because so little is known about the behavioural repertoire of Atlantic white-sided dolphins, it is impossible to differentiate between species-typical and atypical behaviour.

Other than the health state of the animals, uncontrollable variables such as weather, water temperature, and the amount of human activity near the pools may have affected the dolphins’ responses. For example, aquarium employees noted that during the first three months of care, the dolphins would not eat when construction was taking place around the tanks or when the pool filters were operating. Finally, the pool temperature may have played a role in regulating the dolphins’ behaviours, as it was several degrees higher than normally seen in the wild environment.

This study offered a short, but detailed, glimpse of the behaviour of a little-known dolphin species that is rarely seen in captivity. It is a starting point from which to gain a better understanding of the behaviour of the Atlantic white-sided dolphin.

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References


