

The Occurrence and Context of S-Posture Display by Captive Belugas (*Delphinapterus leucas*)

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The “S-posture” is described in the cetacean literature as a radical flexure of the body which presents an atypically vertical visual signal. It has most commonly been associated with agonistic or sexual high-arousal contexts, and often includes simultaneous acoustic outbursts. Its dynamic qualities – an abrupt retardation of forward motion, sweeping flexure of the flukes, and sustained arch - suggest nits saliency to the cetacean’s motion-sensitive visual system. This study reports on the occurrence of S-postures in four captive beluga whales (*Delphinapterus leucas*) held at SeaWorld San Diego. During approximately 27 hours of video data, a total of 174 S-postures were displayed by three out of four belugas. Interestingly, none of the S-postures recorded co-occurred with an acoustic production, an open mouth or an additional visual display (i.e., bubble clouds, jaw claps). The proportion of S-postures displayed by each subject was analyzed for differences in changing contexts: the state (open/closed) of a rear gate leading to a separate pool, the presence of cohabitant harbor seals (*Phoca vitulina*), and the total number of belugas in the same pool. The beluga displaying the majority of S-postures was most sensitive to these factors. Our results indicate no significant difference in the proportion of S-posture displayed when the rear gate was closed. However, each of the posturing belugas displayed a significant proportion of S-postures when the seals were present, as well as when three or more belugas were present in the same pool. This variation in display proportion across individuals suggests that S-postures are utilized by this beluga population during high-arousal social contexts, but is not associated with other overtly loud or aggressive displays as it is in many other marine mammal species.

The use of visual signals by cetaceans has been suggested to be an important mode of close range communication (Pryor, 1990; Tyack, 2000; Würsig, Kieckhefer, & Jefferson, 1990). They can be used as an alternative to acoustic signaling, which could inadvertently alert predators or prey. Visual signals are advantageous because of their instantaneous rate of transmission, locatability of senders, and short signal fade-out (Alcock, 1989). In cetaceans, visual signals are frequently used at close range and vary according to the social context. For example, Hawaiian spinner dolphins (*Stenella longirostris*) tilt sideways to flash a white belly during affiliative interactions (Johnson & Norris, 1994); orienting away and flinching may indicate submission in *Tursiops* sp. (Samuels & Gifford, 1997; Würsig, Kieckhefer, & Jefferson, 1990); and swimming “belly-up” may initiate courtship interactions in many dolphin species (Tavolga & Essapian, 1957; Würsig & Würsig, 1979).

Cetacean agonistic visual signals contain the prototypical features seen in many terrestrial mammals. Such features include shaking of the head, gaping of the jaws, simulated biting displays, and erect postures (Herman & Tavolga, 1980; Pryor, 1990). The S-posture has been observed in several cetacean species (*Stenella frontalis*, Dudzinski, 1998; *Megaptera novaengliae*, Helweg, Bauer & Herman, 1993; *Tursiops truncatus*, Herman & Tavolga, 1980; *Stenella longirostris*, Johnson & Norris, 1994) and appears similar in form and context to

those described in other mammals. This radical flexure of the body is defined with slight differences across studies, but generally includes an up-or-downward pointing of rostrum, arching of the peduncle, and flexure of the flukes (see Figure 1).

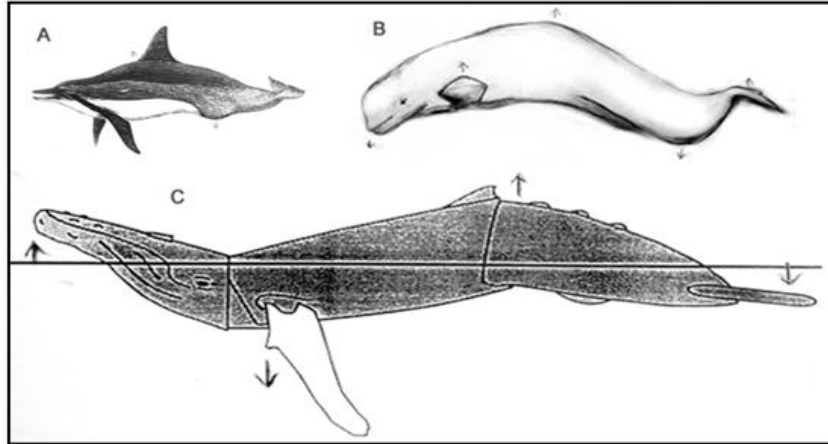


Figure 1. S-posture in (A) Hawaiian spinner dolphin (illustration by Jenny Wardrip, Norris, 1991), (B) beluga (illustration by Whitney Friedman), (C) humpback whale (illustration reproduced from Helweg et al., 1993).

The literature provides disparate findings on the function of S-postures. They have been described as both agonistic and sexual, and as occurring only in males and in both females and males. Furthermore, the use and meaning of this visual signal may depend on the species, age, sex and angle of approach of the signaler (Caldwell & Caldwell 1972; Caldwell & Caldwell 1977; Dudzinski, 1998; Helweg et al., 1993; Herman & Tavolga 1972; Norris & Dohl, 1980; Puente & Dewsbury, 1976). Norris and Johnson (1994) identified the “S-shaped threat posture” in Hawaiian spinner dolphins as a possible imitation of the local grey reef shark (*Carcharhinus amblyrhinchos*). They also state that the unique post-anal hump found only on mature males in that species may be a signing structure which visually enhances the threat postures when the tail stock is arched forward (Johnson & Norris, 1994).

Dudzinski (1998) reported that S-postures in sub-adult and adult Atlantic spotted dolphins (*Stenella frontalis*) occurred most often during direct approaches, accompanied by loud intense vocalizations, bubble emissions and aggressive contact behavior. Conversely, juvenile spotted dolphins were observed to display S-postures with an open jaw and an oblique angle of approach during playful contexts (Dudzinski, 1998). Helweg and colleagues (1993) reported on S-posture displays occurring during the courtship competitions of male humpback whales (*Megaptera novaengliae*). Primary and secondary escorts engaged in lengthy bouts of agonistic displays while competing for access to females. These postures were accompanied by head lunges, fluke swishes, and jaw-claps (Helweg et al., 1993, p. 76). The authors note that these events may be indicative of high arousal, rather than aggression in particular. For example, they reported a calf producing an S-posture while two escorts aggressively fought for proximity to its mother (Helweg et al., 1993).

The S-posture is suggested to be an aggressive stance analogous to the erect posture and the fur-raising piloerection seen in many terrestrial mammals during aggressive interactions (Baker & Herman, 1984; Helweg et al., 1993). Such postures may be used to create an illusion that the signaler is larger than their actual size, and possibly to intimidate the intended recipient(s). These ritualized threat displays are also often referred to as “intention movements” (e.g., Alcock, 1993): postures and gestures that are the first step in a recognized sequence of behaviors. In numerous terrestrial animals, intention movements are utilized during agonistic interactions and signal a defensive stance and/or heightened readiness to initiate attack (Alcock, 1993). The threat posture of a herring gull (*Larus argentatus*), its neck stretched upward and head pointed down, is the same posture exhibited when the gull actually pecks its opponent. Therefore, when the gull uses only this intention movement it can be effective as a visual threat signal that may pre-empt a potentially damaging aggressive interaction (Tinbergen, 1960, 1965). In studying S-postures in humpback whales, Helweg et al. (1993) viewed the raised peduncle as a potential preparation for a tail strike, and the raised head as a potential preparation for a head strike.

S-postures are visually salient behaviors, markedly different from general swimming postures. In a class of animals that are almost always in motion, a display that involves halting forward movement is itself informative. They may also increase the apparent size of the cetacean in both horizontal and vertical planes. In this study, we report on the occurrence and contexts of S-posture displays as they were produced by four captive beluga whales (*Delphinapterus leucas*). S-posture display was analyzed for possible co-occurrence with other indications of aggressive and high arousal; such as acoustic production and other visual displays (i.e., bubble clouds, jaw claps). In addition, proportions of S-posture display were analyzed for statistically significant differences in changing social contexts: the state (open/closed) of a rear gate leading to a separate pool, the presence of cohabitant harbor seals, and the total number of belugas present in the same pool.

Methods

Facility

Behavioral observations were filmed at the Wild Arctic exhibit, at SeaWorld San Diego, California. The beluga enclosure is comprised of a front viewing pool (96 feet in width, 61 feet in length, and 18 feet in depth) that is connected by a large gate-modulated window to a rear handling pool. A secondary handling pool housing five harbor seals is adjacent, but not connected to, the main rear handling pool. On varying days, up to five of these seals shared the front pool with the belugas. The SeaWorld staff managed the state (open or closed) of the rear gate leading to the handling pool, and thus managed the presence of each individual beluga and seal in the front viewing pool.

Subjects

A total of four captive belugas, three female (BF-1, age 23; BF-3, age 42; BF-4, age 29), and one male (BM-2, age 37) comprised the subjects for this study. BF-3 and -4 have been housed at SeaWorld San Diego since 2000. BM-2 was transferred to Sea World San Diego in the summer of 2004, and BF-1 was transferred in August 2005.

Video Data Collection

Data were collected from July 12 - August 24, 2006, for a total of 25 days. Observations were filmed for roughly an hour between 4 - 7pm, as this gave the best lighting for video quality. Footage was shot by two synchronized mini-DV digital camcorders, JVC (GR-DF450u) and Canon (ZR85), positioned to cover approximately 85% of the front viewing pool. These data were later digitized into iMovie (iMovie HD 6.0.3 (267.2)) by a Sony deck (Video Walkman GV-1000). The

iMovie files were then exported into QuickTime (QuickTime™ Version 7.2.0, Player Version 7.2 (7.2)). The QuickTime video files from each camera's viewpoint were then placed next to each other for a double screen image.

Video Coding

Roughly one hour observed from each day was analyzed (N = 1604 minutes). Behavioral data was collected using an all-occurrence sampling method (Altmann, 1974). Video data was scanned and coded by two observers (Cohen's Kappa $\kappa = 0.88$) using a specifically constructed Excel® database. On a timeline scale, each video segment was scanned for S-postures, as well as the occurrence of bubble clouds, jaw claps, open mouth and acoustic production in order to compare the results with the literature (see Table 1).

Each video segment was also scanned for changing contextual factors that could influence S-posture display rate. These rates were calculated by dividing the total number of S-postures occurring during each context by the total number of minutes each context was recorded. These contexts include the state of the rear gate leading to a separate handling pool and the presence of cohabitant seals. We recorded whether the gate was open or closed for each segment in view of the fact that the closed gate would prevent exiting or entering the front pool. The presence of harbor seals was recorded as either yes or no for the entire segment due to the lack of reliability in identifying each seal's position in the tank. The presence of each beluga was recorded in order to weigh the amount of time each individual was available for observation, as well as to monitor the number of belugas in the same pool. All binomial tests were calculated using the Statistical Package for the Social Sciences (SPSS)®, version 14.0.

Table 1.

Behavioral events and contextual factors recorded for each video segment.

| Behavioral Event | Operational Definition |
|--------------------------|---|
| Bubble Cloud | Bubble cloud released from blowhole. |
| Jaw Clap | Loud popping sound coupled with a fast closing motion of the jaws. |
| Open Mouth | A sustained (at least 2 seconds) gaping of the jaws, usually oriented to a recipient. |
| S-posture | 1. Downward flexure of the neck 2. Upward extension of the pectoral fins 3. Forward arching of the peduncle 4. Outward flexure of the fluke |
| Contextual Factor | Operational Definition |
| Gate | Marked as either <i>open</i> or <i>closed</i> throughout a single segment. |
| Seals | Marked as either <i>present</i> or <i>not present</i> throughout a single segment. |
| Number of Belugas | The number of belugas present in the front pool was recorded throughout a single segment. |

Acoustic Data

A single Deep Sea Power and Light hydrophone was positioned in the front viewing pool. This hydrophone had a 32 kHz bandwidth, providing a Nyquist frequency at 16kHz. The hydrophone fed directly into the JVC camcorder, providing simultaneous recordings of videographic and acoustic data. Under these conditions, we were generally not able to identify which beluga was producing each acoustic production. To verify the presence of jaw claps or phonations, acoustic data was extrapolated from movie data files, and analyzed in Raven© Cornell Lab of Ornithology. These analyses were conducted to verify the presence of jaw claps that may have occurred when the belugas mouth were not visible to the camera, as well to determine any regularity in the phonations produced during the observed S-postures.

A jaw clap was identified as a short, very intense, broadband sound (McBride & Hebb, 1948). To classify other phonations, we used the following broad acoustic categories: low bandwidth, high bandwidth, mixed, and click trains. A low bandwidth call was identified visually as a harmonic structure that represented integral multiples of the fundamental frequency, or as a single continuous frequency modulated whistles. High bandwidth calls were identified as broadband pulses of sound energy, with a variable harmonic structure (Sjare & Smith, 1986). Mixed calls were identified as continuous acoustic productions that contained distinct high and low bandwidth components. Click trains, which were identified as a sequence of short, broadband pulses.

Results

Out of the total 1604 mins and 37 s of video data coded, BF-1 was visible 80% of the time ($n = 1280.85$ mins), BM-2 was visible 50% of the time ($n = 788.42$ mins), BF-3 was visible 92% of the time ($n = 1472.5$ mins), and BF-4 was visible 80% of the time ($n = 1282.9$ mins). There were considerable individual differences in the likelihood of S-posture display, with a total of 174 S-postures observed (BF-1 = 81 S-postures, BM-2 = 46 S-postures, and BF-4 = 47 S-postures). Interestingly, BF-3 was observed 92% of the time, and yet did not display a single S-posture. There were no clear recipients for any of these 174 S-postures.

None of the observed S-postures co-occurred with another visual display (i.e., jaw claps, bubble clouds, or open mouth) by the posturing whales. Of the 157 S-postures for which acoustic data were available, only 13 (8%) co-occurred with an acoustic production by any of the whales present. Of these, we found 5 S-postures that co-occurred with a low bandwidth phonation, 5 S-postures that co-occurred with a high bandwidth phonation, 2 S-postures that co-occurred with a mixed call production and 1 S-posture that co-occurred with a click train.

Gate

The rear gate dividing the front pool from the handling pool was closed 20.5% ($n = 383.9$ mins) of the total time recorded. If the null hypothesis was true, and the state of this rear gate did not affect the subjects' behavioral state, each of the posturing belugas should then have displayed 20.5% of their total S-postures while the gate was closed. Only BF-1 displayed significantly more S-postures than expected ($p < 0.001$, one sample binomial test), displaying 27% ($n = 22$ S-postures) when the gate was closed. BM-2 and BF-4 did not display a statistically significant difference in S-posture display when the gate was open or closed (see Fig. 2).

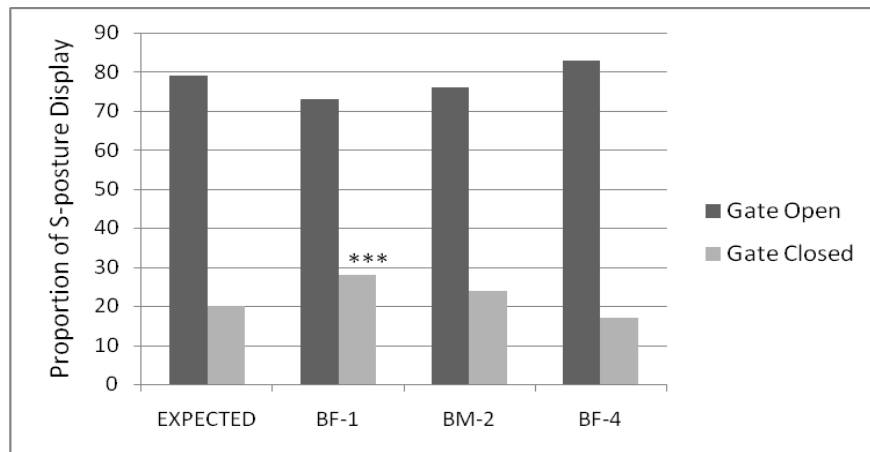


Figure 2. The expected proportion of S-posture display given the amount of time the rear gate was open or closed, and the observed proportion of each of the posturing belugas (** $p < 0.001$, one sample binomial test).

Cohabitant Harbor Seals

The harbor seals were present in the front pool with the belugas 66.4% of the total recorded time ($n = 1239$ mins). Assuming that the cohabitant seals do not influence the belugas' behavioral state, we should then expect 66.4% of the S-postures observed to occur when the seals were present. Interestingly, this was not the case. All three posturing belugas displayed significantly *more* S-postures than expected when the seals were present (BF-1, $p < 0.001$; BM-2 and BF-4, $p < 0.05$; one sample binomial tests) (see Fig. 3).

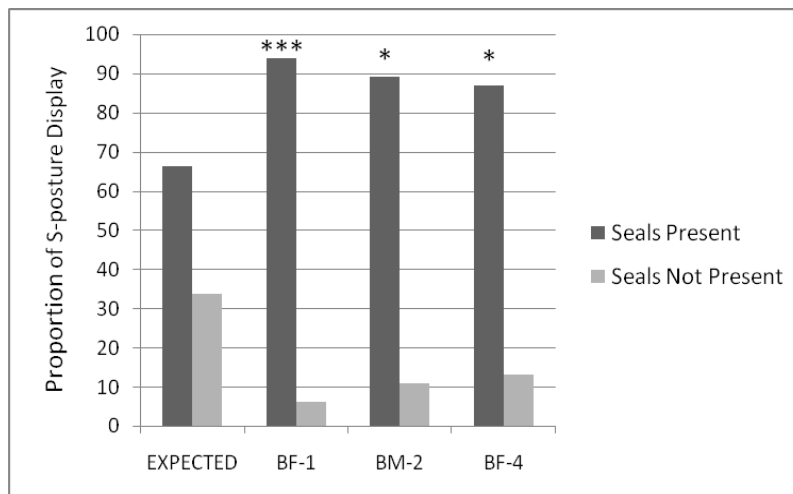


Figure 3. The expected proportion of S-posture display given the amount of time the harbor seals were present with the belugas, and the observed proportion of each of the posturing belugas (** $p < 0.001$, * $p < 0.05$; one sample binomial test).

Number of Belugas

In order to analyze a difference in S-posture proportion given the number of belugas present in the same pool, the data was split into two categories: the least amount of belugas (1 or 2), versus the most amount of belugas present (3 or 4). In

addition, in order to control for an increase in the number of potential performers, the data was analyzed on an individual level.

BF-1 was recorded to be in the front pool alone or with one other beluga roughly 14.4% of the time ($n = 184.8$ mins). Therefore, we should expect to see 14.4% of her S-postures to be displayed during these minutes. However, only 6.2% ($n = 5$ S-postures) of BF-1 S-postures were displayed while 1 or 2 belugas were present. On the other hand, BF-1 was recorded to be with 3 or 4 belugas present roughly 85.6% of the time ($n = 1095.2$ mins), and she displayed a significantly larger proportion of S-postures, 94% ($n = 76$ S-postures), when the majority of belugas were present in the front pool ($p < 0.05$, one sample binomial test) (see Fig. 4).

BM-2 was recorded to be with the least amount of belugas 5.8% of the time ($n = 46.4$ mins), and with the majority of the belugas 94.2% of the time. The results indicate that BM-2 did not display a significantly different proportion ($p = 0.24$, one sample binomial test) of S-postures during either of these contexts; with 4.3% occurring with 2 or less belugas present ($n = 2$ S-postures) and 95.6% ($n = 44$ S-postures) occurring when 3 or more belugas were present (see Fig. 5).

Finally, BF-4 was recorded to be in the front pool alone or with one other beluga 23.7% of the time ($n = 305$ mins), and with the majority of the belugas 76.3% of the time ($n = 976.9$ mins). Interestingly, BF-4 displayed a very significant difference ($p < 0.001$, one sample binomial test) in proportion of S-postures, with 4.2% ($n = 2$ S-postures) occurring with 1 or 2 belugas present, and 95.8% ($n = 45$ S-postures) occurring when 3 or 4 belugas were present (see Fig. 6).

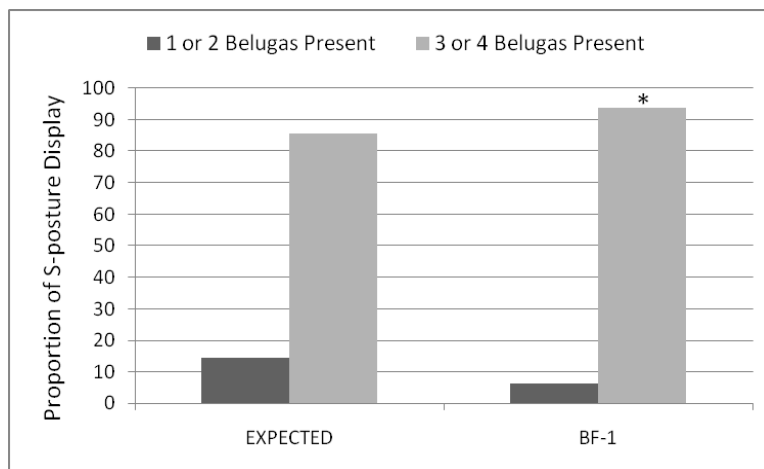


Figure 4. The expected and observed proportion of S-posture display for BF-1 based on the amount of time she was observed to be with the fewest versus the majority of belugas present ($*p < 0.05$; one sample binomial test).

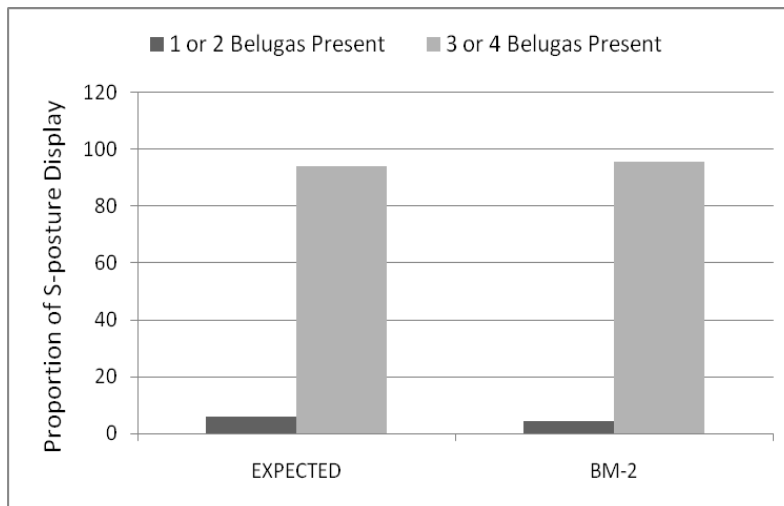


Figure 5. The expected and observed proportion of S-posture display for BM-2 based on the amount of time he was observed to be with the fewest versus the majority of belugas present.

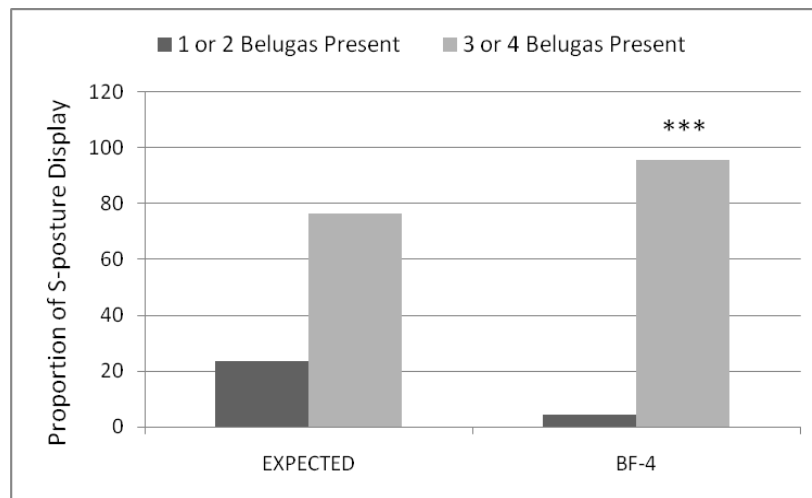


Figure 6. The expected and observed proportion of S-posture display for BF-4 based on the amount of time she was observed to be with the fewest versus the majority of belugas present (***) $p < 0.001$; one sample binomial test).

Discussion

The objectives of this study were to 1) document the occurrence of S-postures in belugas, and 2) analyze the contexts in which this visual display was observed. During the approximately 27 hours of video data analyzed for this study, a total of 174 S-postures were displayed by three of the four subjects. Surprisingly, none of the S-postures observed co-occurred with an acoustic production or another visual display (i.e., bubble clouds, open mouth, jaw clap). This is a stark contrast to the “S-shaped threat postures” described in the literature; where they are often accompanied by boisterous acoustic outbursts and energetic visual displays (Dudzinski, 1998; Helweg et al., 1993; Herman & Tavolga, 1980; Johnson & Norris, 1994).

The results indicate that the state (open/closed) of a rear gate leading to a separate pool did not influence the amount of S-postures displayed by the subjects.

On the other hand, when cohabitant harbor seals were present in the same pool all three posturing belugas displayed significantly more S-postures than the expected proportion. The final context analyzed in this study, the number of whales present in the same pool, had mixed results. Both BF-1 and BF-4 displayed a significant proportion of S-postures when the majority of belugas were present, while BM-2 did not.

There has been much debate on relating behavioral changes, particularly aggression, in captive delphinids to the relative size of the pool enclosure (i.e., Bassos & Wells, 1996; Gygax, 1997). Indeed, the addition of more bodies to an enclosed area will inevitably decrease the personal space and maneuverability of each inhabitant. This decrease in personal space requires a negotiation of the social space. Caldwell and Caldwell (1972) related behavioral changes in captive bottlenose dolphins to the restriction of social space. They suggested that captive bottlenose dolphins may form microterritories when confined to a single enclosure defending their preferred spot with aggressive visual displays (e.g., jaw claps, open-mouthed gesture, or directed stares) (Caldwell & Caldwell 1972). It is unclear whether the increase in S-posture display in the present study is a defense of microterritories, or a simple reaction to a highly arousing context, as none of the S-postures observed were directed at a clear recipient. Nevertheless, the rate of S-posture display for each of the posturing belugas increased when all four belugas were present in the same front pool (see Figure 2). Conversely, each of the posturing belugas displayed significantly fewer S-postures when only one other beluga shared the front pool. Taking these findings into account, it can be projected that S-postures are utilized by these belugas during contexts in which the shared social space is reduced.

The addition of seals to the front pool also reduced the personal space of each beluga. Each of the posturing belugas displayed significantly more S-postures when the seals were present in the front pool. Not only do the cohabitant seals constantly move at a speed greater than the belugas, but they sometimes physically collide with belugas. There were five occurrences, visible to the camera, of a beluga open mouth chasing a seal. Forty jaw claps were observed to be directly oriented to a cohabitant harbor seal. Castellote and Fossa (2006) documented the effects of the introduction of cohabitant harbor seals on captive belugas. They monitored the acoustic responses of two captive belugas after a transfer to a different pool, and later to the addition of four harbor seals into the pool. They report that the belugas' vocalization rate was immediately reduced following the introduction of the harbor seals and remained low for two weeks (Castellote & Fossa, 2006). The results in this study also indicate that cohabitant harbor seals have the potential to affect the behavioral state of the belugas. The belugas may respond to high arousal situations with a swift decrease in acoustic production. Visual signals, such as the S-posture, may provide an alternative to acoustic communication in such contexts.

In addition to being visually salient, the S-postures observed in the present study were generally silent. Only 13 S-postures observed co-occurred with a production of sound, while none were observed to co-occur with another visual display (such as jaw claps, bubble clouds) by the posturing whale. Our results do not indicate a dominant call type. In contrast, bottlenose dolphins (Caldwell & Caldwell, 1972), spotted dolphins (Dudzinski, 1998) and humpbacks (Helweg et

al., 1993) have all been reported to simultaneously produce either loud vocalization and/or visual displays while displaying an S-posture. In a species as vocal as belugas are (Bel'kovitch, & Sh'ekotov, 1993; O'Corry-Crowe, 2002) the paucity of vocalizations during S-posture may be an informative aspect of the display. Numerous studies have reported on the possibility for captive and free-ranging belugas to regulate to stress or fear by ceasing vocalizations (Morgan, 1979; Lésage et al., 1999; Karlsen et al., 2002; Van Parijs et al., 2003; Castellote & Fossa, 2006; Azorín, Castellote & Esteban, 2007). This reduction in acoustic production during such threatening contexts can be interpreted as a survival strategy to avoid detection by predators.

The use of visual signals greatly depends on the reception ability of the signaler and receiver, as well as the environment in which the modality is used. Research has found that cetacean visual anatomy consists of numerous rods for detecting motion, and one type of cone receptor for detail and contrast (Herman & Tavolga, 1980; Madsen & Herman, 1980; Mobley & Helweg, 1990). In addition, Mobley (1984) has found that bottlenose dolphins are excellent at estimating the relative distance to an object using vision alone. This heightened ability to detect moving visual stimuli, and the ability to distinguish the personal space separating individuals, is perhaps what allows visual signals to be effective in proximal social interactions for cetaceans. Therefore, it is possible that the stark contrast between the belugas' white skin and their natural environment in the dark arctic sea, coupled with a flexible neck (O'Corry-Crowe, 2002) and visual system geared toward motion, may allow for the development and use of a gestural communication system (see Suzuki, 2007).

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