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

Kristina M. Horback
University of Southern Mississippi, U.S.A.

Whitney R. Friedman and Christine M. Johnson
University of California San Diego, U.S.A.

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 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 its 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. None of the S-postures observed co-occurred with another visual display (i.e., bubble clouds, open mouth, jaw clap), while only 8% were observed to have co-occurred with an acoustic production by the whales present. The proportion of S-postures displayed by each subject was analyzed for differences in the following 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 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, 1998). 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 et al., 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; Paulos, 2004; Pryor, 1990). The S-posture has

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been observed in several cetacean species (*Stenella frontalis*, Dudzinski, 1998; *Megaptera novaengliae*, Helweg, Bauer, & Herman, 1992; *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 Fig. 1).

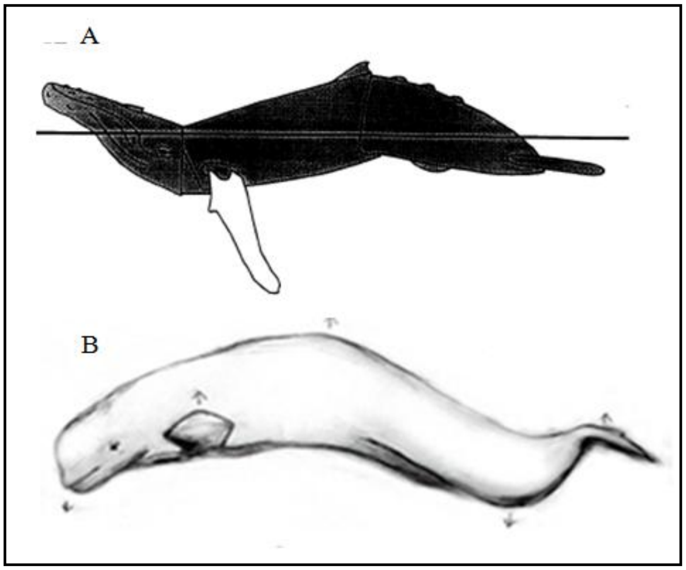

Figure 1. S-posture in a A) humpback whale (illustration reprinted from Figure 1b. in Helweg et al., 1992 with permission from Aquatic Mammals) and B) beluga (illustration by Whitney Friedman).

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, 1977; Dudzinski, 1998; Helweg et al., 1992; Herman & Tavolga, 1980; Puente & Dewsbury, 1976). Johnson and Norris (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 (1992) described 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., 1992). 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., 1992).

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., 1992). 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, 1998): 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, 1998). 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. This intention movement can be effective as a visual threat signal that may preempt a potentially damaging aggressive interaction (Lorenz, 1966; Tinbergen, 1960, 1965). When humpback whales display an S-posture, the raised peduncle could be a potential preparation for a tail strike, and the raised head could be a potential preparation for a head strike (Helweg et al., 1992).

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. S-postures may also increase the apparent size of the cetacean in both horizontal and vertical planes. This study reports on the occurrence and contexts of S-posture display in four captive beluga whales (*Delphinapterus leucas*). S-posture display was analyzed for possible co-occurrence with indicators of high arousal; such as acoustic outbursts and other visual displays (i.e., bubble clouds, jaw claps). Three contexts in which S-posture display occurred was analyze: the state (open or 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. All three contexts are hypothesized to be highly arousing, as they reduce the personal space of each individual.

Method

Facility

Beluga behavior was filmed at the Wild Arctic exhibit, at SeaWorld San Diego, California. The beluga enclosure is comprised of a front viewing pool (96 ft in width, 61 ft in length, and 18 ft 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 (Allua, age 23; Muktuk, age 42; Ruby, age 29), and one male (Ferdinand, age 37) comprised the subjects for this study. Muktuk and Ruby have been housed at SeaWorld San Diego since 2000. Ferdinand was transferred to Sea World San Diego in the summer of 2004, and Allua was transferred in August 2005.

Video data collection

Data were collected from July 12 - August 24, 2006, for a total of 25 days. Behavior was 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.

Figure 2. Ruby displays an S-posture at the surface while Muktuk looks on.

Video coding

Roughly one hour observed from each day was analyzed. Behavioral data was collected using an all-occurrence sampling method (Altmann, 1974), which consisted of creating a separate observation line for each visual display observed or a change in context. Video data was scanned and coded by two observers (Cohen's Kappa κ = 0.88) using a specifically constructed Excel® database. 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 individual S-posture display rate. These rates were calculated by dividing the number of S-postures each individual displayed during each context by the total number of minutes each individual was recorded in that context. These contexts include the state of the rear gate leading to a separate handling pool, the presence of cohabitant seals, and the number of belugas present in the front pool. The state of the gate (open or closed) was recorded for each segment in view of the fact that the closed gate would prevent exiting or entering the front pool. Thus, the gate influenced the number of individuals occupying one or two different pools (i.e., personal space). The presence of harbor seals (yes or no) was recorded for the entire segment due to the lack of reliability in identifying each seal's position in the tank. Onscreen time for each beluga was recorded in order to weigh the amount of time each individual was observed in each context, as well as to monitor the number of belugas in the same pool. All chi-square and 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 *open* or *closed* throughout a single segment.
Seals	Marked as either *present* or *not present* 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 16 kHz. The hydrophone fed directly into the JVC camcorder, providing simultaneous recordings of videographic and acoustic data. Under these conditions, the beluga producing each sound was not identifiable. To verify the presence of jaw claps or phonations, acoustic data was extracted from movie data files, and analyzed with 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 as to determine any pattern 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 were identified as a sequence of short (duration), broadband pulses.

Results

Out of the total 1604 mins and 37 s of video data coded, Allua was visible 80% of the time ($n \approx 1280$ mins), Ferdinand was visible 50% of the time ($n \approx 788$ mins), Muktuk was visible 92% of the time ($n \approx 1472$ mins), and Ruby was visible 80% of the time ($n \approx 1283$ mins). There were considerable individual differences in S-posture display, with a total of 174 S-postures observed (Allua = 81 S-postures, Ferdinand = 46 S-postures, and Ruby = 47 S-postures). Interestingly, Muktuk was observed 92% of the time, and yet did not display a single S-posture.

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 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.

Contextual analysis was split into two categories: gate and seals combined, and number of whales. This was done because each category was not represented in the data (i.e., no footage of 2 whales out, while the gate was closed and the seals were out). In addition, chi-square tests would be invalid due to the very limited sample size in each category (i.e., violating an assumption that $n > 20$).

Gate and Seals

For both Allua and Ferdinand the state of the rear gate and the presence of the seals had a significant effect on S-posture display (Allua, χ^2 $(3, N = 81) = 28.3$, $p < 0.01$; Ferdinand, χ^2 $(3, N = 46) = 19.3$ $p < 0.01$). Ruby, however, did not significantly differ in her S-posture display when combining the contexts (χ^2 $(3, N = 47) = 2.9$, $p = 0.4$). Allua and Ferdinand both displayed their highest S-posture rates (8.5 and 8.6/hr) when the rear gate was closed and the cohabitant seals were present. Ruby's highest S-posture rate (2.8/hr) occurred when the gate was open and the seals were present (see Fig. 3).

Because each of the posturing belugas displayed their highest S-posture rate while the seals were present, subsequent binomials were performed for each individual, holding the state of the gate constant. All three posturing belugas displayed significantly more S-postures than expected by chance when the seals were present (Allua, n = 76, $p < 0.01$; Ferdinand, n = 41, $p < 0.05$; and Ruby, n = 41, $p < 0.05$; one-tailed binomial test).

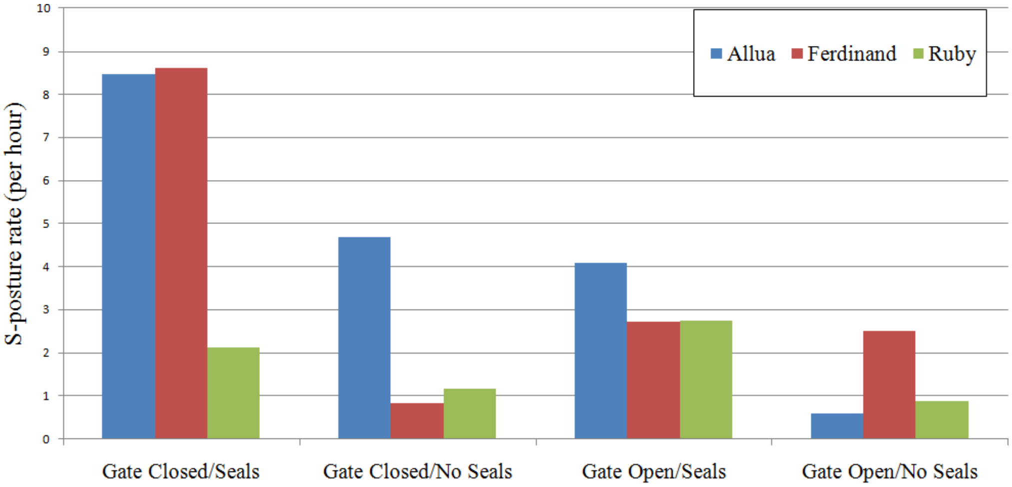

Figure 3. S-posture display rate (per hour) for each of the posturing belugas given the combined context of the state (open or closed) and the presence of cohabitant harbor seals.

Number of Belugas

Allua did not display while she was in the front pool alone for only 31 s. She was present with one other beluga roughly 14% of the time ($n \approx$ 180 mins) and performed 5 S-postures. Allua displayed 22 S-postures while when she was with two other belugas 27% ($n \approx$ 345 mins), and 54 S-postures with all three other belugas 58% ($n \approx$ 742 mins) of her onscreen time. A chi-square test resulted in no significant difference in the proportion of Allua's S-postures given the changing number of belugas in the front pool (χ^2 (2, N = 47) = 4.5, p = 0.1). Allua displayed her highest rate of S-postures (7/hr) when all three other belugas were also present in the same pool.

Ferdinand also did not display while he was alone in the front pool for approximately 1 min 20 s. He was recorded with one other beluga approximately 5.3% of his time onscreen ($n \approx$ 42 mins) and displayed one S-posture. He was recorded with two other belugas present 15.2% of his onscreen time ($n \approx$ 120 mins) and displayed 20 S-postures. Ferdinand was recorded with all other belugas present 79% of his onscreen time ($n \approx 622$ mins) and displayed 24 S-postures during these minutes. The results indicate that Ferdinand displayed a significantly different proportion of S-postures when the number of other belugas changed (χ^2 (3, $N = 46$) = 32.2, $p < 0.001$). Ferdinand displayed his highest rate of S-postures (10.5/hr) for this analysis was when he shared the front pool with two other belugas.

Only 23 s of video data contains Ruby alone in the front pool, and she did not display an S-posture during these few seconds. She was recorded with another beluga 22% of her time onscreen ($n \approx 282$ mins) and displayed 2 S-postures, with two other belugas 28% ($n \approx 363$ mins) and displayed 18 S-postures, and with all three other belugas 48% of the time ($n \approx 615$ mins) and performed 27 S-postures. Ruby also displayed a significant different proportion of S-postures given the changing context of the number of other belugas in the same pool (χ^2 (2, $N = 46$) = 9.2, $p = 0.01$). Like Ferdinand, Ruby displayed her high rate of S-postures (3/hr) for this analysis was when she shared the front pool with two other belugas.

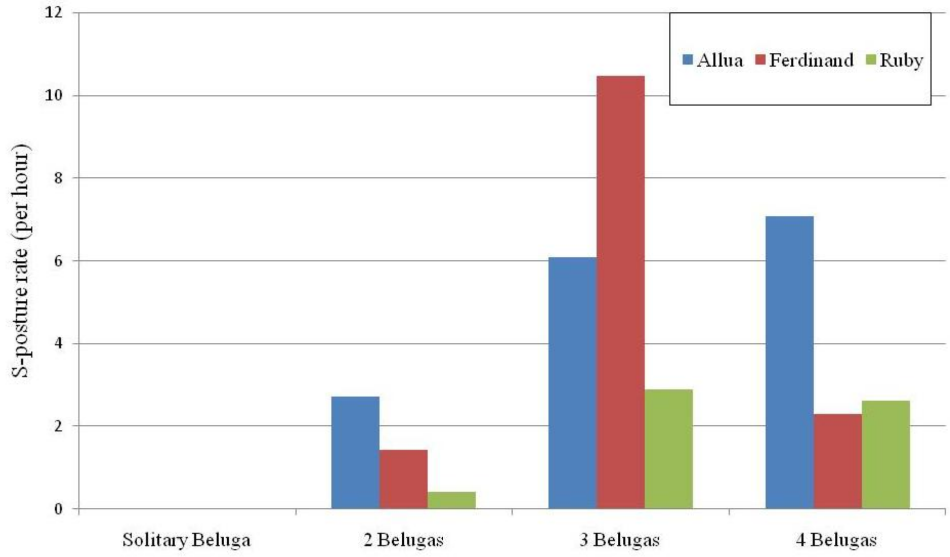

Figure 4. S-posture display rate (per hour) for each of the posturing belugas given the context of the number of other belugas also present in the same pool.

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. The lack of S-posture production by Muktuk could be due to her age (42 years) and rank in the dominance hierarchy. Based on anecdotal observations from the training staff and a separate study on the use of social space by these belugas (Suzuki, 2007), Muktuk was assumed to be the least dominant individual of this group. The three younger belugas had a more ambiguous social hierarchy.

Surprisingly, not one of the S-postures observed co-occurred with another visual display (i.e., bubble clouds, open mouth, jaw clap), while only 8% were observed to have co-occurred with an acoustic production by the whales present. 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., 1992; Herman & Tavolga, 1980; Johnson & Norris, 1994; Overstrom, 1983). In addition, a majority (66%) of the S-postures occurred while the individual was resting at the surface, indicating that these S-postures are most likely not a by-product of physically altering a swim path.

When the rear gate was closed, and the seals were present in the same pool, Allua and Ferdinand displayed their highest S-posture rates. In addition, the rates of S-posture display for Ferdinand and Ruby were greater than expected by chance when all four belugas were present in the same pool. These contexts greatly reduce the personal space of each individual, and therefore can be suggested to be highly arousing. Conversely, all three posturing belugas displayed significantly fewer S-postures than chance alone 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 in reduced.

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 (see Suzuki, 2007), or a simple reaction to a highly arousing context.

Interestingly, all three posturing belugas displayed significantly more S-postures then expected by chance when the harbor seals were present. Not only did the cohabitant seals constantly move at a speed greater than the belugas, but they sometimes physically collided 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 of the present study also indicate that cohabitant harbor seals have the potential to greatly affect the behavioral state of captive belugas (i.e., increase in S-posture rates).

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., 1992) 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 suggested that both captive and free-ranging belugas decrease vocalizations during high arousal contexts (i.e., during a capture, in close proximity to boats, etc.) (Azorín, Castellote, & Esteban, 2007; Castellote & Fossa, 2006; Lésage, Barrette, Kingsley, & Sjare, 1999; Karlsen, Bisther, Lydersen, Haug, & Kovacs, 2002; Morgan, 1979; Van Parijs, Lydrsen, & Kovacs, 2003). This reduction in acoustic production during such threatening contexts can be interpreted as a survival strategy to avoid detection by predators. Belugas may respond to high arousal situations (e.g., decrease of personal space) by reducing their acoustic production, and in turn compensating with silent visual signals, like the S-posture.

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