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Perspectives on the Function of Behaviors Synchronized with Calling in Female Killer Whales, *Orcinus orca*: Patterns of Bubbling and Nodding in Bouts

Ann E. Bowles[1], Whitney B. Musser[1], Kelly Flaherty Clark[2], Samuel L. Denes[3], and Dawn M. Grebner[4]

[1]*Hubbs-SeaWorld Research Institute, U.S.A.*
[2]*SeaWorld Orlando, U.S.A.*
[3]*Syracuse University, U.S.A*
[4]*Bioacoustician, U.S.A.*

In odontocetes, synchronous visible displays accompany a small proportion of vocalizations but the function of these multimodal signals is still unclear. Bouts of stereotyped pulsed calls were collected from two adult female killer whales (*Orcinus orca*) concurrently with behavioral observations and the incidence of two types of synchronous behaviors measured (bubble formations and nodding). Thirty-four hours of focal individual data were collected in the presence of dependent calves in 1993 and 1994. Overall, 471 pulsed calls were attributed to the two subjects using synchronous behaviors or independent cues (proximity, localization by ear in air). Both subjects used the same stereotyped pulsed call repertoire and they ordered calls within bouts similarly, despite dissimilar previous histories. Bubble streams and nodding were disproportionately associated with a subset of stereotyped pulsed calls, but the subset was different for the two behaviors. General linear model analysis was used to predict relative odds (a ratio of probabilities reflecting likelihood) that subjects would be swimming with calves given call class and attribution cue. Bubbling was not associated with significant odds that a subject would be swimming with one or more calves, but nodding was associated with significantly higher odds and resting calls with lower odds. Given these observations, synchronous behaviors in the presence of calves could function in one or more of the following ways: altering the signal value of calls, emphasizing social context, and facilitating learning. All are possibilities at the interface between cognition and communication that would have interested Stan Kuczaj.

Although Stan Kuczaj's research interests were focused on cetacean cognition, he understood the interaction between communicative behaviors and cognitive capabilities very well. Over the course of his career he was involved in a number of studies of vocal behavior. Although Stan was famous for conducting critical experiments—an elegant example can be found in one of his last publications (Kuczaj, Eskelinen, Jones, & Borger-Turner, 2015)—he took a more patient approach to the complex vocal behavior of social odontocetes because good data are so difficult to obtain (e.g., Hernandez, Solangi, & Kuczaj, 2010; Simard et al., 2011). The study reported here pays homage to his legacy by focusing on an example of odontocete multimodal social communication that has implications for cognition.

Many terrestrial species (e.g., birds and primates) produce distinct movements when they vocalize, such as opening the mouth, raising the head, or vibrating the trachea (Hauser, Evans, & Marler, 1993; Hinde & Rowell, 1962; Ghazanfar & Logothetis, 2003; Wild, Goller, & Suthers, 1998). These movements may result from motions required to produce the sounds, but vocalizations may also be synchronous visual displays (e.g., Patricelli, Uy, & Borgia, 2004). Such distinct movements enable terrestrial observers to both attribute calls to individual callers and study multimodal signals in varying behavioral and social contexts. Unfortunately, such movements are of comparatively limited use in an environment with poor visibility, such as underwater, and

Please send correspondence to Dr. Ann E. Bowles, Hubbs-SeaWorld Research Institute, U.S.A. (Email: abowles@hswri.org)
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where anatomical specializations may restrict expressive movements (e.g., fusiform body structure). Thus, it is not surprising that odontocete cetaceans usually vocalize without obvious physical movements identifying the vocalizer (Pryor, 1990; Tyack & Miller, 2002).

In smaller social odontocetes, a few discrete behaviors, particularly bubble formations, have been observed synchronously with vocal behaviors. Bubbles can be emitted in more than one stereotyped formation; they may be visible or audible; and they may be observable using echolocation (Pryor, 1990). Thus, they have great potential to be highly salient gestures underwater. However, various functions of bubble formations are possible in addition to signaling. For example, odontocetes may be able to exploit nonlinear acoustic features when detecting targets in complex, bubble-filled environments (Leighton, Finfer, & White, 2005; Norris, Prescott, Asa-Dorian, & Perkins, 1961), which might be a benefit of emitting bubbles. Killer whales (*Orcinus orca*), bottlenose dolphins (*Tursiops* spp.) and spotted dolphins (*Stenella* spp.) can actively generate bubbles to facilitate cooperative or coordinated feeding (Fertl & Wilson, 1997; Fertl & Würsig, 1995; Simila & Ugarte, 1993).

Surprisingly, systematic efforts to explore the use of bubble formations in social communication have been limited, although the basic characteristics have been described in spotted and bottlenose dolphins (Beard, 2007; Dudzinski, 1996; Herzing, 1996; Pryor, 1990; Pryor & Schallenberger, 1991). Several types of bubble formations have been reported, bubble bursts, bubble rings or other complex shapes, and bubble streams. Bubble bursts are amorphous, roughly spherical masses of large bubbles emitted abruptly, with a roiling sound detectable at close range (Delfour & Aulagnier, 1997; Herzing, 1996; Pryor, 1990; Pryor & Schallenberger, 1991). Bubble bursts are rarely or never emitted synchronously with vocalizations, although the roiling sound could have a signal function. In one study of a larger species, the beluga (*Delphinapterus leucas*), bubble bursts were used in the context of maternal protection of calves and when animals were surprised (Hill, Kahn, Brilliott, Roberts, & Gutierrez, 2011); they occurred secondarily in the context of play.

Bubble rings or other complex shapes can be produced in the presence of vocalizations, but synchronous emission with vocalizations is rare. These formations have been reported most often in the context of play (e.g., Delfour & Aulagnier, 1997; Gewalt, 1989; McCowan, Marino, Vance, Walke, & Reiss, 2000; Pace, 2000; Pryor & Kang, 1980). Under controlled conditions, odontocetes have been trained to produce a variety of bubble structures, highlighting their control and ingenuity (Kuczaj, Makecha, Trone, Paulos & Ramos, 2006; Marten, Shariff, Psarakos, & White, 1996). This ingenuity was a source of fascination for Stan Kuczaj, especially after he found evidence that cetaceans could mimic one another's bubble behaviors (Jones & Kuczaj, 2014). Much of the interest in bubbling behavior historically has been drawn by the sophistication and control exhibited by cetaceans in producing and interacting with these bubble formations and the cognitive capabilities that such flexible behaviors imply.

Although more stereotyped, the use of bubbling behaviors in complex social communication may require similar or greater physical control (perhaps explaining the availability for play). Bubble streams, also called bubble trails and whistle trails (Pryor, 1990), are uniform, small to mid-sized streams of bubbles emitted in a long sequence, producing a highly visible, linear display that clearly indicates the caller and direction of travel. Streams are the bubble formations most associated with vocalizations and may be interrupted if the vocalization is interrupted (Pryor, 1990). From a physical point of view the behavior requires impressive control because the animal must pass a large volume of air out the blowhole at the same time that it is passing air under pressure through its dorsal bursae to produce a vocalization. In the killer whale, examination of a complex, biphonic vocalization produced with and without bubble streams showed no evidence that callers had difficulty with this coordination (Bowles, Grebner, Musser, Nash, & Crance, 2015).

The social function of synchronous bubble streaming has received little study despite being a highly salient behavior. Pryor observed that bubble streams occurred in social interactions to demarcate the signaling individual. However, in studies of free-ranging bottlenose and spotted dolphins, bubble streams have been relatively uncommon and primarily associated with highly active social interactions (Dudzinski, 1996; Herzing, 1996; Pryor & Shallenberger, 1991). Blomqvist and Amundin (2004) suggested that bubble streams were an indicator of affiliative intent. They do not appear to occur in contexts that are frankly agonistic, where head bobbing, jerking, and gaping (including abrupt gapes associated with jaw claps) are the salient gestures sometimes associated with sound production (Herzing, 1996; Pryor, 1990; Pryor & Shallenberger, 1991). However, the incidence of bubble streams is low enough that they cannot simply signal affiliative state in a general way—they must have some additional signal content.

The relationship between bubble streams and specific vocalization types has been a matter of debate. Bubble streams have been used to attribute calls to callers under both controlled and free-ranging conditions (Bowles, Young, & Asper, 1988; Caldwell, Caldwell, & Tyack, 1990; Herzing, 1996; McCowan, 1995; McCowan & Reiss, 1995a, 1995b; Pryor, 1990), but bias in the types and incidence of vocalizations with bubbling may complicate their use as a cue. McCowan (1995) found no significant difference in the rate of whistle types produced with *vs*. without bubble streams in bottlenose dolphins under controlled conditions, but Fripp (2005) reported a bias with vocalization type and among behavioral states from another facility. Given the small percentage of vocalizations that are bubbled (Tyack, 2000) and the potential for biases in production, there is a need for further study, especially with vocalizations attributed using other methods (Beard, 2007; Fripp, 2005; Herzing, 1996; Miksis, Tyack, & Buck, 2002).

Gaps and inconsistencies in the literature are a measure of the difficulty of localizing callers without synchronous behavior. Subjects may be localized by the human ear using movements and sounds projected by the caller at the water's surface (Caldwell et al., 1990). A multi-channel mobile video/acoustic system may be deployed by a diver (Dudzinski, Clark, & Würsig, 1995), permitting localization when callers are well separated. Recording devices may be attached using a suction cup (Fripp et al., 2005; Tyack, 1986). They can collect many hours of acoustic data, but vocalizations may be difficult to attribute to individuals when vocally active social partners are at close range (Parks et al., 2011; Sayigh, Quick, & Hastie, 2013). Also, the instruments have not been maintained on animals long-term. Hydrophone arrays can localize calls with high accuracy (Brensing, Linke, & Todt, 2001; Freitag & Tyack, 1993; Grebner et al., 2011; Thomas, Fristrup, & Tyack, 2002), but have not yet been linked to long-term, high-resolution underwater visual observations allowing bubbling rates to be associated with specific vocalizations and behavioral contexts.

Comparative observations from a delphinid with a large repertoire of stereotyped vocalizations might shed light on the function of bubble streams and other behaviors synchronized with vocalizations. The larger species (small whales) have vocal repertoires that differ from those of intensively studied bottlenose dolphins. However, the only study of communicative bubbling in these species focused on a formation that is not usually synchronized with vocalizations, the bubble burst (Hill et al., 2011).

The killer whale is a good model species because it appears to have a stable social structure (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990) that contrasts with the fission-fusion societies of bottlenose and spotted dolphins (Connor, Wells, Mann, & Read, 2000). Killer whales produce a large repertoire of discrete, stereotyped pulsed vocalizations (call types) that have been characterized as a dialect, in addition to whistles, clicks and burst-pulse vocalizations (Ford 1989, 1991). Bubble streams and other behaviors synchronized with vocalizations have not yet been explored in a social context for this species.

Here we describe stereotyped pulsed calls and synchronous behaviors of two killer whales observed under controlled conditions in the presence of dependent calves. The data were part of a series of observations collected in several facilities from 1986 to 2012 to study the development and behavioral context of killer whale vocal repertoires (Crance, Bowles, & Garver, 2014; Musser, Bowles, Grebner, & Crance, 2014).

Method

Subjects

The two subjects were adult female killer whales (F2 and F9) recorded in the period surrounding two births. Although their histories differed, at the time of the recordings the subjects shared a common discrete, stereotyped pulsed call repertoire of Icelandic origin (Figure 1). F2 had lived with bottlenose dolphins intermittently over a 10-yr period prior to transfer to the study facility, where she had been for two years before recordings were collected. F9 had been housed in the facility with other killer whales since she was a juvenile. The whales where closely associated based on the proportion of time spent swimming within one body length of one another (Crance et al., 2014).

The females were housed with other killer whales ranging from juveniles to adults of both sexes. One was the non-dependent juvenile calf of F2. However, the data for the present study were collected when the subjects were together with one or both of their dependent calves in a pool instrumented with an underwater video camera. Only the vocalizations attributed to the two adults were included in the study. Vocalizations of young killer whale calves are distinctive from those of adults (Bowles et al., 1988) and were excluded on that basis as well as using the cues described below.

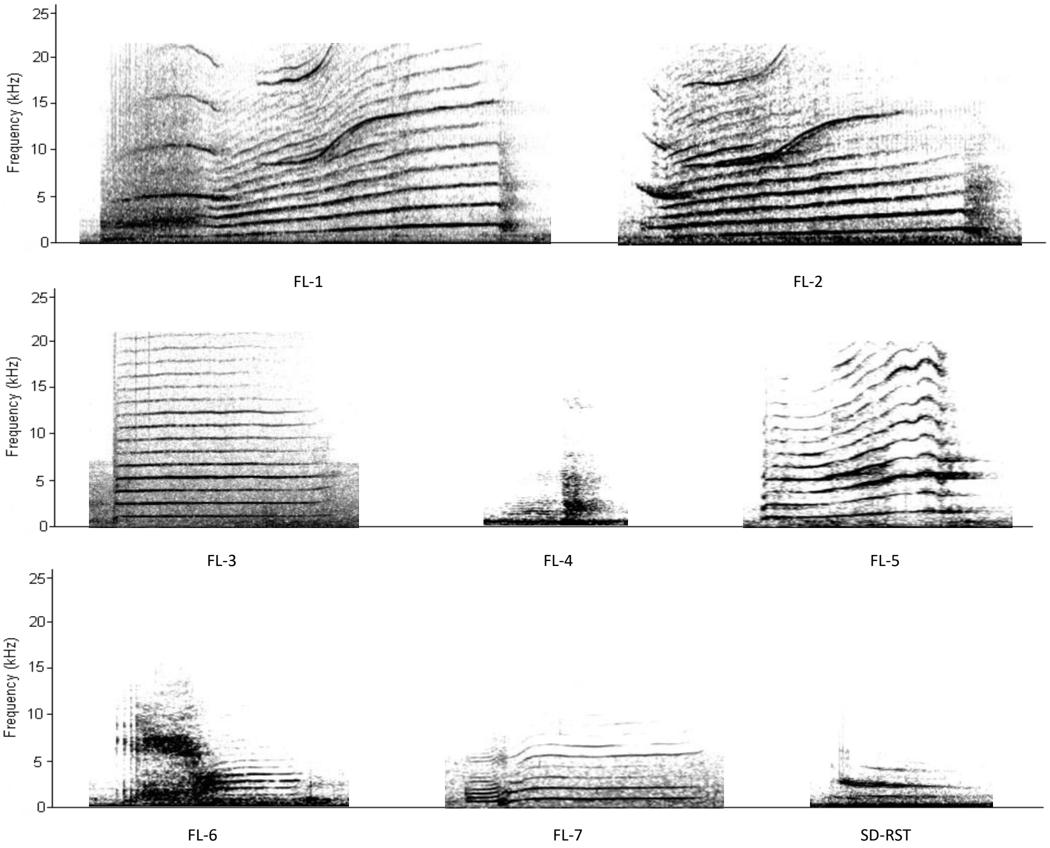

Figure 1. **Spectrograms of the eight stereotyped pulsed calls shared by killer whales F2 and F9.**

Data Collection

Acoustic recordings were collected with a single ITC 6050C hydrophone (International Transducer Corporation, Goleta, CA) deployed from the surface in a protected gateway, with the hydrophone placed midway down in the water column and at least 1.25 m from the nearest surface or wall. The gateway was immediately adjacent to the pool occupied by one or both of the focal whales. Sound traveled freely across the barrier between the hydrophone and the pool through a gate with apertures > 20 cm. Attribution cues are discussed below. The calls entered into the dataset had high signal-to-noise ratio (SNR), low distortion due to reverberation, and high frequency energy characteristic of signals projected near and in the direction of the hydrophone (Branstetter, Moore, Finneran, Torney, & Aihara, 2012).

Observations of behavior were spoken onto one stereo channel of a Sony EVO9500 VHS video recorder (Sony Electronics Inc., Minato, Japan), while the signal from the hydrophone was recorded onto the other (system bandwidth 50 Hz – 16 kHz). Video was collected using a CCD camera (Princeton Instruments, Trenton, NJ) in an underwater housing. The camera was mounted in the wall of the pool across from the gate and had a view of the gate and one third of the pool. Water clarity was high, so behaviors of whales in the vicinity of the hydrophone could be scored reliably.

Description of Dataset

The study dataset was compiled to examine the relationship between behavioral state, attribution cue, and classes of call types in the period that Fripp (2005) had identified as having the highest bubbling rates in bottlenose dolphins. Data were collected from F2 and F9 by author AEB and processed by author WBM. Recordings were collected in nine 1.5 hr-time blocks from 4 October 1993 to 31 December 1994. F9 had a dependent calf throughout the recording period. F2 had a non-dependent juvenile calf that was not a focal subject and gave birth to a calf in December of 1993.

Vocalizations were attributed using three methods: (1) synchronous behaviors (nodding and bubble streams), (2) calls localized by the observer by ear at the surface close to the whales, and (3) calls produced when the subjects were separated and close to the receiving hydrophone. Above-water behavioral data were collected from a platform over the gate channel and along the margin of the test pool. The observer provided in-air attributions of vocalizations from focal subjects, whale locations, general descriptions of behavior in the vicinity of the hydrophone, and information about human activities. The voice track was recorded with a wireless microphone system so the observer could move short distances along the pool boundary to maintain proximity to the focal whale. Underwater video was used to score behaviors.

The video camera covered a part of the pool used frequently by the whales. Every effort was made to attribute complete bouts of calling with synchronous behaviors when whales were close to the observer. Calls within bouts were typically separated by less than 3 s. Bouts were differentiated by silences lasting more than 5 s. Attribution by behavioral cue was assigned only to calls beginning within about 100 ms of the onset of the behavior regardless of whether the call was part of a bout. That is, attribution cue was not assigned to calls in a bout unless they were synchronous with a behavior.

Attribution Cues

Behavioral cues. In adults, bubble streams were reliably associated with vocalizations, although the proportion of calls synchronous with bubble streams could be small. Bubble streams could be detected regardless of the position of the focal whale relative to the camera.

Calves produced bubble streams in the absence of detectable vocalizations frequently. They could have been bubbling silently, but it was also possible that they were emitting whistles exceeding the upper frequency limit of the recording system (Bowles et al., 1988). Therefore, calf vocalizations were not included in the dataset.

Observers had previously identified several other behavioral cues that could have been associated with vocalizations. Gaping has long been associated with jaw claps, although the sound and behavior may not be tightly linked (Cranford, Takaki, Hudson, & Ramirez, 1993). Killer whales can bob or jerk the head repeatedly in agonistic contexts. These behaviors correspond to *head bobbing* in Jacobsen’s (1986) ethogram, drawn from observations under controlled conditions by Martinez and Klinghammer (1978). Jacobsen (1986) could not see the behavior reliably from a surface-based platform, but Martinez and Klinghammer (1978) described a behavior akin to rapid head jerking described for the bottlenose dolphin (Dudzinski, 1996), sometimes associated with pulse bursts. In the present dataset, the behavior was dubbed *nodding* (described in more detail in the Results section). It could be detected reliably from above water when the subject was close to the surface (e.g., in the gateway), but less so in underwater video if the subject was oriented directly away from the camera.

Proximity cue. When a subject was separated from other whales and in close proximity to the hydrophone, vocalizations could be attributed reliably. Cues for proximity included substantially greater SNR, minimal reverberation, and presence of higher frequencies in spectra (Branstetter et al., 2012). This attribution cue was unbiased with respect to vocalization types, but not with respect to behavioral state. It required the subject to be near the recording hydrophone and well separated from other individuals. Under these conditions, whales were often relatively inactive.

Localization by ear. Vocalizations could be localized by ear when whales were at or close to the surface of the water. This attribution cue required the subject to be well separated from other animals (> 3 BL), alone at the surface, and close to the observer. However, when these criteria were met, it was a reliable cue and more effective in multiple behavioral contexts than proximity.

All the attribution cues had limitations. However, they could be used over long periods without interfering with the subjects or facility operations. Data collected by ear and using proximity/separation cues were pooled to form a reference sample. It provided a point of comparison for the samples of vocalizations attributed behaviorally.

Categorization and Classification of Vocalizations

All attributed vocalizations were grouped initially into broad categories, stereotyped pulsed calls, variable pulsed calls, clicks, burst-pulse sounds and whistles. Stereotyped discrete pulsed calls were then classified into call types by experienced observers (AEB and WBM). Samples were compared by eye and ear with reference to an ethogram of spectrograms and type specimen recordings (Figure 1). Based on trials with naïve observers and a larger pool of animals, Crance (2008) found that stereotyped calls could be classified correctly by naïve observers with 95% agreement, including calls with variable modulated endings (i.e., the excitement or aberrant calls described by Ford, 1984). Here, the dataset was limited to classifications that both AEB and WBM agreed on. All other pulsed calls were encoded as variable (VAR). Only non-overlapping vocalizations were included in the dataset.

Categorization of Behaviors

Bubbling and nodding were linked to vocalizations only when they overlapped with them. Bubble formations were categorized into two types: bubble bursts and streams (no bubble rings were observed). Bursts and streams could be distinguished easily. Two types of bubble streams were identified, highly visible streams composed of bubbles with diameters generally in the 1-5 cm range; and threads, composed of bubbles only a few millimeters in diameter. Bubble threads were rarely emitted by the adult whales. Only highly visible streams were scored.

All behavioral events and states were encoded for the two whales separately. Rates of events were quantified as the number of behaviors by individual whales per hour (whale-hr).

Killer whale cows with dependent calves swam persistently within a body length of their calves a high proportion of the time, with irregular bouts of nursing interspersed. The study subjects swam with one or more of the calves for approximately half the observation period. Their behaviors were pooled into two states, swimming within a body length of one or both calves (SWCA) and other (NCA). Unfortunately, the camera view was not sufficiently detailed nor the dataset large enough to break behaviors into more detailed categories. In particular, nursing bouts were short and success difficult to evaluate in the camera view; nursing bouts were pooled within the SWCA state.

Analysis

Video recordings were digitized using Adobe premiere software (Adobe Systems Inc., San Jose, CA) through a Canopus ADVC110 digital video converter (Belden/Grass Valley, Grass Valley, CA). The audio track was extracted from digitized video and processed separately. Oscillograms and spectrograms of vocalizations were prepared and quantified in Raven pro 1.4 (Cornell Laboratory of Ornithology, Cornell, NY).

Bubbling and nodding were encoded as BUB and NOD, and compared with the reference pool of independently attributed pulsed calls (REF). Call types were classed by pooling the seven non-resting FL call types (Figure 1) into one category (FL), to be compared with the resting call (SD-RST), and all other vocalization types (OTHER). SD-RST had been identified initially in killer whales of Icelandic origin from another facility (Crance et al., 2014). It was comparable in structure to the N3 resting call identified by Ford (1984) from the Northern Resident community in that it contained a downsweep with complex modulation between the two independent vocal sources. However, it lacked an initial pulse burst and had a somewhat different timbre to the human ear. Although stereotyped, SD-RST was not automatically pooled with FL calls because resting calls have been associated with a specific activity state, group resting, in free ranging whales (Ford, 1984).

We did not have baseline data from periods when neither whale had a calf, but repertoire use and synchronous behaviors while swimming within a body length of one or both of the dependent calves (SWCA) could be compared with those in other behavioral states (NCA).

Statistical analyses were conducted in the R programming environment (Version 2.12.1, R Development Core Team, University of Aukland, NZ). Generalized linear model (GLM) analysis (Venables & Ripley, 2002) was used to test the likelihood that calls would be attributed in the two behavioral states (SWCA and NCA) given the two predictor variables (attribution cue and call class) using the *glm* function (R Core Team, Version 2.15.2).

There were large individual differences between the two whales in behavior patterns. Analysis was first conducted with the data pooled and then for the two whales separately. The data were not sufficient to test a full model with interactions among all factors, so odds were calculated based on relative likelihood of a given attribution cue or call class. Bubbling (BUB) was the default attribution cue and FL was the default call class. Odds ratios for factors of interest were predicted post hoc from the best-fit GLM model using *exp*(Estimate). The confidence interval around this ratio (2.5 to 97.5%) was calculated using a resampling procedure. Odds ratios were interpreted as the odds that an attributed call would be detected in the NCA behavior state relative to the odds that it would be detected in the SWCA state given the default factors.

Results

Killer whale subjects emitted two types of bubble formations, bursts and streams. Bubble bursts were uncommon; one was detected in the study dataset and not emitted synchronously with a vocalization. Bubble streams were emitted regularly, but the absolute proportion of vocalizations that were bubbled could not be estimated because many calls were not attributed to a given individual. When observed, bubble streams were initiated within about 100 ms of the start of a vocalization. There was a break in emission if multiple calls were bubbled.

The other behaviors synchronized with vocalizations were gaping and nodding. Gaping (opening the jaws) was observed synchronously with a vocalization (jaw clap), but jaw clapping was rare in the dataset and gaping could not be detected reliably. Only two instances of gaping were observed, one an abrupt opening of the mouth associated with a jaw clap and the other a more prolonged open mouth gesture not associated with any vocalization.

Nodding has not been described previously as a behavior synchronous with vocalizations in the killer whale. Initially it was classed with other head movements, but once the association with vocalizations started to become clear, the stereotyped nodding gesture was readily distinguished. A nodding whale raised and lowered the head deliberately, typically once or twice, within a few hundred milliseconds of call onset. We assigned it a new behavior category, *nodding*. In the combined dataset, the whales nodded synchronously with pulsed calls nearly as often as with bubble streams, despite the fact that nodding was more difficult to detect.

A total of 507 vocalizations were attributed in 34.2 whale-hr of observations. Roughly equal samples were attributed to the two whales (246 to F2, 261 to F9), but F2 produced all the whistles (4), jaw claps (5), and click trains (27).

Of the sample, 471 were pulsed calls (93%), including 12 variable pulsed calls (VAR) and 54 resting calls (SD-RST). Pulsed calls accounted for 81 and 97% of the sample for F2 and F9, respectively. Of these, 190 (40%) were emitted synchronously with bubble streams, and another 221 (47%) were nodded. The rest were attributed in air and by proximity (13%).

Both whales used the same repertoire of stereotyped pulsed calls (Figure 1), FL-1 to FL-7 and the resting call, SD-RST (Table 1). Of the stereotyped pulsed calls, both F2 and F9 used FL-1 most often (26 and 23%, respectively), and they emitted similar proportions of SD-RST calls (12 and 11%, respectively). However, they produced somewhat dissimilar proportions of other call types (Tables 2 - 5). The largest relative differences were in the use of FL-5 to FL-7, and in VAR pulsed calls, of which 11 of 12 were emitted by F2.

Table 1

Summary of Attributed Calls Emitted with Synchronous Behaviors while Subjects F2 and F9 were Swimming with and without Calves

		Synchronous Behavior			
State/Whale	Call Category	Bubbled	Nodded	None‡	Total
With calf*					
F2	All	64 (50%)	60 (48%)	2 (2%)	126
	FL pulsed	49 (51%)	46 (47%)	2 (2%)	97
	Resting	0	12 (100%)	0	12
F9	All	66 (33%)	126 (63%)	8 (4%)	200
	FL pulsed	65 (37%)	107 (60%)	6 (3%)	178
	Resting	0 (0%)	19 (90%)	2 (10%)	21
Without calf					
F2	All	57 (47%)	13 (11%)	50 (42%)	120
	FL pulsed	38 (50%)	10 (13%)	28 (37%)	76
	Resting	0	3 (21%)	11 (79%)	14
F9	All	30 (49%)	23 (38%)	8 (13%)	61
	FL pulsed	29 (54%)	17 (31%)	8 (15%)	54
	Resting	1 (14%)	6 (86%)	0	7

Note. *Swimming within a body length of one or both calves. The whales tended to swim constantly in this state, but engaged in a range of activities when calves were at greater distances. ‡ The reference attribution cue - attributed without synchronous behaviors.

In the dataset, 249 sequences of vocalizations met the criterion for a bout (separated by more than 5 s), of which 41% were single calls (Figure 2). The rest were bouts of up to 7 calls, with counts of 2-3 most common (54%). Call order was not random, but sequences were sufficiently variable that they could not be pooled as complex stereotyped calls composed of multiple call units. Both whales most often produced FL-1 first, whether or not other calls followed. Of the 147 bouts with multiple calls, the sequence FL-1/FL-2 occurred most often (28 bouts), followed by FL-1/FL-2/FL-3 (16 bouts). FL-5 occurred in the initial position relatively often as well, with FL-5/FL-6/FL-7 occurring as a triplet (15 bouts).

Resting calls were rarely emitted in bouts with FL calls. Bouts of one to three SD-RST calls were attributed in the dataset (35% >1 call). These attributed bouts probably underestimated the potential maximum length because sequences of up to 10 resting calls met the criterion for a bout. However, only a subset of these calls could be attributed to a caller. With one exception (attributed to F9), SD-RST calls were not bubbled.

Bubbling was always accompanied by a vocalization in the focal whales. F2 bubbled 49% of her sample overall (Table 1), while F9 bubbled 37% (Table 2 – 5, Figure 2). These rates should not be considered absolute due to the difficulty of attributing calls without synchronous behaviors. However, multiple attribution cues made it possible to compare relative use.

Within the bubbled sample, one call type, FL-1, predominated. For F9, FL-1 comprised 90% of bubbled single calls and 84% of the calls in bouts (Figure 2b). The proportions were slightly lower for F2 (Figure 2a), but still high (74 and 78%).

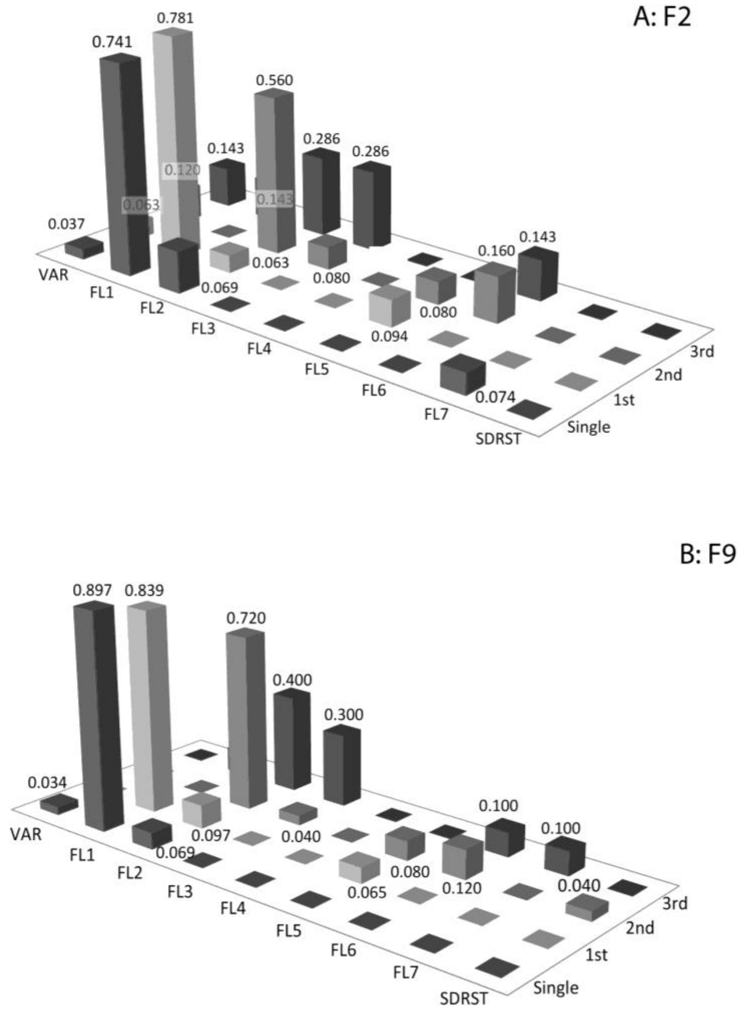

Figure 2. **Relative proportions of call types emitted with bubble streams singly and in bouts, (A) F2 and (B) F9.** The first row indicates calls emitted singly. The remaining rows indicate proportions in the first to third call of a bout (bout lengths of 4 or greater were rare). Numbers on the bars indicate proportions greater than zero. Those that are shaded indicate the value for a hidden bar.

Nodding was always synchronous with pulsed calls and all but two nodded calls were stereotyped. Nodding proportions were 33% and 57% for F2 and F9, respectively. F9 produced 67% of the nodded sample (149 nodded calls F9 vs. 72 calls F2). The large relative difference suggested that F9 was more likely to nod her calls, but it could have been explained by differences in activity budget, as F9 spent 82% of her time swimming with calves but F2 only 52%. However, other lines of evidence suggested that at least some of the difference was typical of F9. Both whales nodded resting calls at similar rates (7% and 10% for F2 and F9, respectively), but F9 nodded a substantially higher proportion of FL calls (47% vs. 25%). With one exception, neither whale nodded the two calls that were most commonly bubbled, FL-1 and FL-2 (F2 nodded a single FL-2 call). Both most often nodded calls that were never or rarely bubbled, FL-4 to FL-7 and SD-RST. F2 nodded 50-83% of these call types, and F9 nodded 80-100%.

Table 2
Pulsed Calls in Bout Sequences Attributed to Whale F2

	Count Pulsed Calls (% of Total)									
Behavior*	VAR	FL-1	FL-2	FL-3	FL-4	FL-5	FL-6	FL-7	SD-RST	Total count (%)
Total calls	12	57	34	30	20	19	14	8	26	210 (45%)
BUB	7 (63%)	46 (82%)	24 (71%)	4 (17%)	0 (0%)	5 (26%)	5 (36%)	3 (38%)	0 (0%)	94 (49%)
NOD	1 (9%)	3 (5%)	3 (9%)	12 (50%)	15 (83%)	11 (58%)	8 (57%)	4 (50%)	15 (58%)	72 (33%)

Note. *Total count of the given call type, followed by counts bubbled and nodded. Cells give the count by call type. The percentage in the last column indicates the proportion of the total for both whales (compare with Table 4). Percentages in the rows are calculated based on the column total. They do not total 100% because some calls were emitted without synchronous behaviors. VAR indicates variable pulsed calls; FL[#] refer to stereotyped pulsed call types (Figure 1). SD-RST indicates the resting call.

Table 3
Ordering of Pulsed Calls in Bouts, F2

	Count (Percentage Bubbled)									Total count (%)
Order	VAR	FL-1	FL-2	FL-3	FL-4	FL-5	FL-6	FL-7	SD-RST	
1st	6 (27%)	54 (80%)	9 (18%)	3 (0%)	11 (0%)	9 (16%)	1 (0%)	3 (25%)	18 (0%)	114 (46%)
2nd	3 (27%)	0 -	20 (41%)	8 (8%)	5 (0%)	9 (11%)	7 (29%)	0 -	7 (0%)	59 (41%)
3rd	2 (9%)	1 (2%)	2 (6%)	10 (8%)	1 (0%)	1 (0%)	6 (7%)	3 (0%)	1 (0%)	27 (41%)
4th	0 -	0 -	2 (6%)	2 (0%)	0 -	0 -	0 -	2 (12%)	0 -	6 (60%)
5th	0 -	0 -	1 (0%)	0 -	0 -	0 -	0 -	0 -	0 -	2 (50%)
6th	0 -	0 -	0 -	0 -	1 (0%)	0 -	0 -	0 -	0 -	1 (50%)
7th	0 -	0 -	0 -	1 (0%)	0 -	0 -	0 -	0 -	0 -	1 (100%)

Note. The numbers in each cell are counts in the given bout order. Percentages indicate the proportion bubbled. Percentages in the right column are relative to all calls for both whales in bout order. Percentages in the columns are of all calls of the given type.

Table 4

Pulsed Calls in Bout Sequences Attributed to Whale F9

	Count Pulsed Calls (% of Total)									Total Count (%)
Behavior*	VAR	FL-1	FL-2	FL-3	FL-4	FL-5	FL-6	FL-7	SD-RST	
All	1	59	37	15	19	49	27	27	28	262 (55%)
BUB	1 (100%)	53 (90%)	28 (76%)	4 (27%)	0 (0%)	4 (8%)	4 (15%)	1 (4%)	1 (4%)	96 (51%)
NOD	0 (0%)	0 (0%)	4 (11%)	9 (60%)	19 (100%)	45 (92%)	22 (82%)	25 (92%)	25 (89%)	149 (67%)

Note. *Total count of the given call type, followed by counts bubbled and nodded. Cells give the count by call type. The percentage in the last column indicates the proportion of the total for both whales (compare with Table 2). Percentages in the rows are calculated based on the column total. They do not total 100% because some calls were emitted without synchronous behaviors. VAR indicates variable pulsed calls; FL[#] refer to stereotyped pulsed call types (Figure 1). SD-RST indicates the resting call.

Table 5

Ordering of Pulsed Calls in Bouts, F9

	Count (Percentage Bubbled)									Total Count (%)
Order	VAR	FL-1	FL-2	FL-3	FL-4	FL-5	FL-6	FL-7	SD-RST	
1st	1 (100%)	57 (91%)	6 (14%)	0 -	19 (0%)	27 (4%)	0 -	6 (0%)	17 (0%)	133 (54%)
2nd	0 -	1 (0%)	26 (50%)	6 (7%)	0 -	20 (4%)	17 (17%)	3 (0%)	10 (4%)	83 (58%)
3rd	0 -	1 (2%)	4 (11%)	9 (20%)	0 -	0 -	7 (4%)	16 (4%)	1 (0%)	38 (58%)
4th	0 -	0 -	1 (3%)	0 -	0 -	2 (0%)	0 -	1 (0%)	0 -	4 (40%)
5th	0 -	0 -	0 -	0 -	0 -	0 -	2 (0%)	0 -	0 -	2 (50%)
6th	0 -	0 -	0 -	0 -	0 -	0 -	0 -	1 (0%)	0 -	1 (50%)
7th	0 -	0 -	0 -	0 -	0 -	0 -	0 -	0 -	0 -	0 -

Note. The numbers in each cell are counts in the given bout order. Percentages indicate the proportion bubbled. Percentages in the right column are relative to all calls for both whales in bout order. Percentages in the columns are of all calls of the given type.

Of F2’s vocalizations, 126 (51%) of were attributed in the SWCA state (Table 1), while the count for F9 was 200 (77%). For F2, the proportion of calls bubbled in the SWCA state was roughly equal to the proportion bubbled in the NCA state, but in F9’s case the proportion bubbled in the NCA state was somewhat higher (49% vs. 33%). Both whales nodded substantially more calls in the SWCA state. F2 nodded 48% of her SWCA samples, but only 11% in the NCA state, while F9 nodded 63% and 38% respectively.

When broken down by whale, attribution cue, and call class imbalances in the sample were large enough that a fully saturated GLM model could not be tested. There was a large difference between the subjects in effort by behavioral state, and hence potentially attributions in the SWCA state. Reference attributions were low for both whales while swimming with calves due to the difficulty of isolating their calls. Also, F2 did not have a young calf during the first six observations. As a result, reference attributions were rare in F9's sample, but comprised 42% of F2's sample in the NCA state, largely collected at the surface in the gateway with her attention apparently focused on other whales.

Table 6

Results of the General Linear Model Analysis for Both Whales

Factor	*df*	Difference (deviance-residual)	*df* residual	Residual deviation	$p\ (> \chi^2)$
NULL	6	66.96			
Call Class	2	15.52	4	51.44	$p < 0.001$
Attribution Cue	2	45.26	2	6.18	$p < 0.001$
Call x Attribution Interaction	2	6.18	0	0.00	$p < 0.001$

Note. Table gives the likelihood that calls would be attributed in one of two social states (swimming with calf [SWCA] and not with calf [NCA]) given pulsed call class (FL, RST, Other) and attribution cue (BUB, NOD, OTHER).

* $p < 0.05$. ** $p < 0.01$.

Table 7

Best-fit Model with Interactions for Both Whales

Factor	Best fit estimate	*SE*	*z*	$p\ (> \lvert z \rvert)$
(Intercept)	-0.64	0.165	3.863	$p < 0.001$
Call-OTHER	0.71	0.407	1.739	0.082
Call-RST	1.48	0.540	2.743	0.006**
Att-NOD	-1.42	0.374	3.783	$p < 0.001$
Att-REF	0.26	0.227	1.131	0.258
Call-OTHER x Att-NOD	NA	NA	NA	NA
Call-RST x Att-NOD	-0.97	0.779	-1.241	0.215
Call-OTHER x Att-REF	2.07	1.132	1.831	0.067
Call-RST x Att-REF	NA	NA	NA	NA

Note. Best-fit model including interactions, with call category FL and attribution type BUB taken as the default types. The model included as factors two call categories (RST, OTHER), and two attribution cues (NOD, REF). Significance indicated by bold type. For clarity, factors of the variables call category and attribution cue are preceded by a code indicating the variable (Call, Att). An 'x' between the factors indicates a test for interaction.

Table 8

Odds Calculated from the Best-fit Model for Both Whales

Factor	Odds NCA - Pooled	Lower – Upper CI (2.5% - 97.5%)	Inverse - Odds SWCA Pooled
Call-OTHER:FL	2.0	0.91 - 4.50	0.5
Call-RST:FL	4.4	1.53 - 12.64	0.2
Att-NOD:BUB	0.2	0.12 -0.51	4.1
Att-REF:BUB	1.3	0.83 -2.02	0.8
Call-RST&Att-NOD: Call-FL &Att-BUB	0.4	0.08 -1.75	2.6
Call-OTHER&Att-REF: Call-FL &Att-BUB	7.9	0.86 - 72.96	0.1

Note. Table indicates relative odds of detecting calls calculated from the best-fit model. Odds were calculated from the model estimates for the two social states, NCA and SWCA, using exp(Estimate). Confidence intervals (CI) shown for NCA. The last column gives the odds for the complement (SWCA). Boxes with gray shading indicate significance (that the CI range for the odds ratio did not include 1:1). For clarity, factors of the variables call category and attribution cue are preceded by a code indicating the variable (Call, Att). A colon indicates the comparison being made by the odds ratio.

The GLM analysis was conducted as follows. Data were pooled for both whales (Table 6 – 8) and the model designed to examine the influence of pulsed call class (FL, RST, OTHER) and attribution cue (BUB, NOD, REF) on the relative likelihood of counting a call in each social state (SWCA vs. NCA). The analysis could not be repeated including whale as a factor, but there were sufficient data to make the comparison for F2 separately (Table 9 – 11).

The pooled model showed that both call class and attribution cue were significant predictors of calling in a given behavioral state (Table 6), but they interacted significantly. When interactions among factors were broken out and tested (Table 7), the SD-RST class and NOD attribution were significant predictors of the likelihood of calling by comparison with the FL class and BUB attribution. The interaction effect disappeared once degenerate interactions (those with insufficient data) were accounted for (NA in Table 4b).

Based on this model, the odds of a whale being in either behavioral state could be calculated given attribution cue and call class (Table 8). In two cases, the odds ratio was significantly different from 1:1. For clarity, these are expressed as ratios greater than 1:1. Confidence intervals are shown only relative to the NCA state (the odds ratio for the SWCA state was its complement). For the pooled analysis, odds of being in the SWCA state were 4.1 times higher when a call was attributed by nodding than in the NCA state (with likelihood of FL calls and BUB attribution as points of reference). The difference was probably explained by F9's tendency to nod calls in the SWCA state (Table 1). The odds of being in the NCA state were 4.4 times higher than in the SWCA state if a resting call was attributed.

When the data for F2 were analyzed separately (Tables 9 – 11), it became clear that F2 and F9 had different influences on the dataset, consistent with Table 1. F2's overall GLM model was significant, again including the interaction terms. However, odds of being in either of the two behavior states were not significantly different if a call was nodded relative to bubbled. Call type had a strong impact, however. The odds of being in the NCA state were 12.6 times higher if a resting call was attributed, or three times the ratio for both whales combined (Table 11). It may have been relevant that F2 was nearly always swimming with F9 when in the SWCA state, but the influence of swimming partner could not be tested.

Table 9

Results of the General Linear Model Analysis for F2

Factor	*df*	Difference (deviance-residual)	*df* residual	Residual deviation	*p* (> χ^2)
NULL	6	31.06			
Call Class	2	7.05	4	24.01	0.029*
Attribution Cue	2	15.35	2	8.66	< 0.001
Interaction Call x Attribution	2	8.66	0	0.00	0.011*

Note. Table gives the likelihood that calls would be attributed in one of two social states (swimming with calf [SWCA] and not with calf [NCA]) given pulsed call class (FL, RST, Other) and attribution cue (BUB, NOD, OTHER).

* $p < 0.05$. ** $p < 0.01$.

Table 10

Best-fit Model with Interactions, F2

Factor	Best fit estimate	*SE*	*z*	*p* (> |*z*|)
(Intercept)	-0.30	0.23	-1.34	0.118
Call-OTHER	0.44	0.44	1.01	0.313
Call-RST	2.53	1.07	2.38	0.018*
Att-NOD	-0.88	0.62	-1.42	0.154
Att-REF	0.17	0.31	0.54	0.586
Call-OTHER x Att-NOD	NA	NA	NA	NA
Call-RST x Att-NOD	-2.65	1.37	-1.93	0.050
Call-OTHER x Att-REF	2.09	1.15	1.81	0.070
Call-RST x Att-REF	NA	NA	NA	NA

Note. Best-fit model including interactions, with call category FL and attribution type BUB taken as the default types. The model included as factors two call categories (RST, OTHER), and two attribution cues (NOD, REF). Significance indicated by bold type. For clarity, factors of the variables call category and attribution cue are preceded by a code indicating the variable (Call, Att). An ’x’ between the factors indicates a test for interaction.

Table 11
Odds Calculated from the Best-fit Model for F2

Factor	Odds NCA - Pooled	Lower – Upper CI (2.5% - 97.5%)	Inverse - Odds SWCA Pooled
Call-OTHER:FL	1.5	0.66 - 3.71	0.6
Call-RST:FL	12.6	1.56 - 101.50	0.1
Att-NOD:BUB	0.4	0.12 - 1.39	2.4
Att-REF:BUB	1.2	0.65- 2.17	0.8
Call-RST&Att-NOD: Call-FL &Att-BUB	0.1	0.00 - 1.04	14.0
Call-OTHER&Att-REF: Call-FL &Att-BUB	8.1	0.84 - 77.22	0.1

Note. Table indicates relative odds of detecting calls calculated from the best-fit model. Odds were calculated from the model estimates for the two social states, NCA and SWCA, using exp(Estimate). Confidence intervals (CI) shown for NCA. The last column gives the odds for the complement (SWCA). Boxes with gray shading indicate significance (that the CI range for the odds ratio did not include 1:1). For clarity, factors of the variables call category and attribution cue are preceded by a code indicating the variable (Call, Att). A colon indicates the comparison being made by the odds ratio.

Discussion

Observers of small delphinids, primarily bottlenose and spotted dolphins, historically have treated bubble streams as social signals drawing attention to the caller (Pryor, 1990), that is as generalized signals not associated with particular vocalizations, individuals, age/sex classes, or social contexts. However, some recent evidence has suggested that bubble streams are emitted with specific vocalization types in specific contexts and by some age/sex classes more than others (Beard, 2007; Harley, 2008; Fripp, 2005; Tyack, 2000). Although vocalizations paired with bubble streams occur with low probability (Fripp, 2005; Tyack, 2000), they have been reported most often in highly active states (highly-active social interactions, play, chases) and mother/calf interactions (Fripp, 2005; Pryor & Kang, 1980; Smolker, Mann, & Smuts, 1993; Tyack & Whitehead, 1983; Wood, 1953). Blomqvist and Amundin (2004) concluded that the behavior was associated with affiliative interactions, but it has been less clear how uncommon bubble streams relate to this broadly-defined behavioral state.

Difficulties with attributing vocalizations to individuals have slowed efforts to study individual use of synchronous behaviors. In general, investigators have not attempted independent methods of attribution (Herzing, 1996) or restricted themselves to vocalizations emitted when individuals were separated (Caldwell et al., 1990), a context that introduces other biases (Harley, 2008). Where synchronous bubbling has been the primary attribution method (McCowan & Reiss, 1995a, 1995b) concerns about uncontrolled bias have arisen (Fripp, 2005).

Although attribution challenges were significant in this study as well, the availability of two additional points of reference made it possible to show that synchronous behaviors were used preferentially with specific calls and at specific points within a bout of calls. First, two different behaviors were found to be reliably synchronized with vocalizations, making direct comparisons possible. Second, although small, there was a sample of reference calls attributed by other methods. With these points of reference, it was possible to compare the incidence of synchronous behaviors with elements of the vocal repertoire and to a lesser degree across behavioral states.

The use of synchronous behaviors by the two whales was strikingly similar. Both disproportionately bubbled the same two of eight pulsed calls (FL-1 & FL-2), and nodded call types that were never or infrequently bubbled (FL-4 to FL-7, SD-RST). The association of stereotyped calls with particular synchronous behaviors suggested two possibilities. First, the behaviors might be modifiers, analogous to vocal modifiers that alter the signal content of calls in primates (Lemasson & Hausberger, 2011). Second, they might have been meta-communicative signals (Lemasson, Remeuf, Rossard, & Zimmerman, 2012) added to the calls for emphasis or to acknowledge social context, in the same way that a human might gesture or speak loudly to indicate emotional intensity.

The dataset was not adequate to examine the use of synchronous behaviors across behavioral contexts in any detail. Although Fripp (2005) provided evidence that female bottlenose dolphins bubbled more often when they had dependent calves, she did not compare bubbling rate in particular behavior states, such as swimming with or without their calves, nor was she able to distinguish the functional vocalization types that might have been bubbled differentially (e.g., signature whistles, calls of calves vs. adults). In the present dataset, bubbling was not significantly associated with swimming with calves.

Stereotyped nodding with vocalizations has not been studied systematically in bottlenose dolphins or other small odontocetes, so there is no comparative point of reference for this killer whale behavior. In the present study, the odds of nodding attributions were statistically more likely while swimming with calves (both in the pooled case and for F2 alone). However, the whales were less likely to emit resting calls. F2 had substantially higher odds (12.6) of emitting resting calls relative to FL calls when not swimming with calves, likely explaining the difference, but biases in the dataset must be considered. It is unclear whether the difference in the odds of detecting resting calls was related to swimming with calves per se. The pattern could have resulted from interactions between F2 and other whales and/or the challenges of attributing resting calls while swimming with calves. However, since the chances of detecting nodding were higher when swimming with calves and since resting calls were likely to be nodded, the direction of the hypothetical bias is the opposite of what would be expected. This suggests that some of F2's tendency to produce resting calls when not swimming with calves was believable.

Differential use of vocalizations based on behavioral context has precedents in killer whale vocal communication. Ford found that resting calls were more common in his 'group resting' state (Ford, 1989). Unstereotyped variable pulsed calls and 'excitement' calls (usually stereotyped pulsed calls with warbled terminal components) are used preferentially in highly-active social contexts (Rehn, Teichert, & Thomsen, 2007; Rehn, Filatova, Durban, & Foote, 2011). In the case of excitement calls, the behavior is probably meta-communicative because the pattern appears to be common to all killer whale vocal repertoires.

Of the two behaviors synchronous with vocalizations presented here, bubbling did not appear to be tightly linked to either of the two behavioral states, but rather was associated strongly with specific call types. Both FL1 and FL2 had strongly divergent biphonic components (Figure 1), which have been associated with bubble streams in killer whales at other facilities (Bowles et al., 2015). The tight association between bubble streams and calls with a particular feature is more suggestive of an addition or alteration to the signal content of calls (Lemasson & Hausberger, 2011), either as opposed to or in addition to meta-communicative emphasis. The evidence for behavioral context was stronger in the case of nodding.

Not only were there strong associations between call types and synchronous behaviors, but our data support the hypothesis that killer whales can organize calls sequentially in bouts. The behavior has been suggested for free-ranging killer whales (Riesch, Ford, & Thomsen, 2008). Riesch et al. (2008) could not attribute vocalizations to individuals, but found that there were stereotyped sequences in the ensembles of calls from groups. They concluded that the sequences were complex signal series and further that they were probably emitted by single individuals. The data collected here support their claim, as do Sayigh et al. (2013) for the short-finned pilot whale. Our data suggest further that sequences may be modified or emphasized by synchronous behaviors.

Stan Kuczaj would have appreciated hypotheses about complex killer whale communication made up of sequences of stereotyped elements, sometimes emphasized with multimodal signals. However, he would have criticized sternly any suggestion that they might form a proto-language (Kuczaj, 2013).

An unexpected similarity between the whales also would have interested Stan because it provided indirect evidence of learning. There was complete overlap in the stereotyped pulsed call repertoire of the two females. F2 had lived separately from F9 with bottlenose dolphins prior to transfer to the study facility and vestiges of her vocal history were present in her repertoire (Musser et al., 2014). She produced all the whistles, jaw claps, and click trains in the present dataset, vocalizations that are highly typical of bottlenose dolphin vocal interactions. Nevertheless, she and F9 had stereotyped pulsed call repertoires that overlapped completely. Their close association may have driven a convergence in repertoire, as has been seen in another young female (Bain, 1986) and two young male killer whales (Crance et al., 2014). Unfortunately, convergence could not be quantified with the available data, but the overlap was striking given the different histories of the two whales.

The question of convergence is interesting from a comparative perspective. Previous workers have characterized the repertoire of killer whales as a social dialect, a group-specific repertoire (Deecke, Ford, & Spong, 2000; Ford, 1991). However, smaller delphinids are characterized as having individually-distinctive stereotyped *signature* whistles (Harley, 2008; Janik & Sayigh, 2013; Sayigh et al., 2013). Since signature whistles are imitated by others (King, Sayigh, Wells, Fellner, & Janik, 2013) and groups can converge in features (McCowan & Reiss, 1995a), the contrast between the two types of stereotyped vocalizations may not be as great as the literature suggests. Stan would have asked if the dichotomy was real and suggested a straightforward approach: gathering more information on individual development and use of stereotyped vocal repertoires across a range of species.

In this study, the stereotyped pulsed call repertoire and pattern of usage were strikingly similar for two whales associating closely when both were rearing calves, even though the bond was formed for the first time as adults. The only difference in their stereotyped repertoires was relative usage of a subset of call types (e.g., F2 produced more FL5-FL7 calls). The subjects' behaviors supported the hypothesis that killer whale group-specific repertoires are the result of repertoire convergence over time (Deecke et al., 2000). There was no evidence that convergence was the result of simple mimicry or matching on a call-by-call basis (Miller, Shapiro, Tyack, & Solow, 2004). Instead, both independently used the same repertoire and largely shared usage patterns. There is evidence that convergence in repertoire of bottlenose dolphins is affected by positive social context (Hooper, Reiss, Carter, & McCowan, 2006), so it is possible that other strong positive relationships, such as an allomaternal relationship during calf rearing, could similarly reinforce learning.

The vocalizations used differently by the two whales were also the ones least likely to be bubbled and most likely to be nodded by F9. This raises the possibility that elements of the repertoire are marked for emphasis, for instance, by a bubble stream. If so, it is possible that differential use of synchronous behaviors has a function in call learning. Vocalization rates in other odontocetes increase immediately pre-partum and in the presence of calves post-partum (Fripp & Tyack, 2008; Mann & Smuts, 1998; Mello & Amundin, 2005). This has been interpreted as a behavior that facilitates learning. The learning hypothesis would be stronger if vocalizations important to calf survival, such as the mother's signature whistle or primary elements of a group dialect, were emphasized with synchronous behaviors. Unfortunately, research to date has not clearly linked bubbling or other synchronous behaviors with functional vocalization types in any species but the killer whale (Bowles et al., 2015). Stan would have seen this as an opportunity for well designed comparative observations!

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