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Short Note

A Giant's Dance: Underwater Social and Vocal Behavior of Humpback Whales (*Megaptera novaeangliae*) Recorded on the Northern Coast of Ecuador

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Humpback whales (*Megaptera novaeangliae*) produce an array of social behaviors on their tropical breeding grounds. The most commonly reported behaviors are surface active displays, which include tail, pectoral, or full body slapping events (Kavanagh et al., 2017). Social interactions also comprise a diverse range of subsurface behaviors that include calls (Dunlop et al., 2007; Zoidis et al., 2008; Seger, 2016). The function of most social behaviors within humpback whale groups remains unclear; whales spend most of their time underwater, and their behavioral repertoire is, thus, obscured due to inherent difficulties in documentation in this environment. For example, synchronized movements and tactile signals occur underwater during social group interactions (e.g., between mothers and calves or within competitive groups), and these behaviors may play an important role in their social lives and communication (Darling & Bérubé, 2001; Zoidis et al., 2008, 2014). As such, multiple functions have been proposed, and the significance of social behaviors, including underwater displays, are still debated for humpback whales and most marine mammal species (Dudzinski et al., 2009).

Humpback whales produce vocalizations named *social calls* (Silber, 1986), and these are considered to be emitted by individuals of all ages and sexes (females/males/calves; Zoidis et al., 2008). Some social calls can also be units as part of the male song display (Rekdahl et al., 2013). Social calls are vocalized as opposed to social sonances, which occur during surface activity and are made by the percussive nature of a body part hitting the water surface (Dunlop et al., 2008; Seger, 2016). Social calls can be short (tenths of a second) or long (multiple seconds) and can be emitted once or arranged into bouts (Dunlop et al., 2007; Zoidis et al., 2008; Rekdahl et al., 2015). For instance, social calls in mother–calf groups are often accompanied by bodily contact between the mother and calf, and are considered an important communication component in maternal care (Zoidis et al., 2008; Zoidis & Lomac-MacNair, 2017). Also, social calls have been recorded during agonistic behavioral interactions in competitive groups (Herman et al., 2008). The importance and function of social calls during different stages of a humpback whale's life are poorly understood, as is the role of these calls within the diverse and complex range of marine mammal social interactions.

Behavioral studies have used new underwater technologies to provide important information about the humpback whale mating system and social structure of transient/fluid (competitive group or dyad) or stable (mother–calf pair) social groups on their tropical breeding grounds (e.g., Herman et al., 2008; Andriolo et al., 2014; Zoidis & Lomac-MacNair, 2017). Herein, we describe a series of interactions between members of a whale triad that included social calls, likely bodily contact, and simultaneous or synchronous underwater movements. To our knowledge, this is the first documentation of underwater humpback whale social behavior from the Ecuadorian coast. Our findings are also applicable to the broader understanding of humpback whale associations, and we discuss the possible function(s) of this behavior for socio-sexual conduct and/or social play in a wider behavioral context (Paulos et al., 2010; Pack et al., 2012; Hill & Ramirez, 2014).

Data were collected in the Galera-San Francisco Marine Reserve, located on the northern coast of Ecuador (between 0° 49' 43.9" N, 80° 02' 55.2" W and 0° 37' 18.5" N, 80° 03' 17.6" W). This area has sea surface temperatures that range between 24 and 28ºC, and a seabed composed of sand and rocks. The reserve has a size of 54,604 ha with a coastline stretching approximately 23 km alongshore and extending 11.7 km offshore with the depth ranging from 10 to 200 m (Ministerio de Ambiente [MAE], 2015).

During the austral winter breeding season of 2015, a total of 30 field surveys were conducted from an 8-m fiberglass boat; these included acoustic, visual, and underwater video recordings of humpback whales. Field surveys lasted 4 to 5 h each day, resulting in 91 h of visual observation, 5 h 57 min of acoustic recordings, and 12 min 46 s of underwater video effort (Table 1). All field data were collected in accordance with the guidelines for humpback whale research in Ecuadorian waters (Félix, 2015) and the Universidad San Francisco de Quito Ethics Committee.

The 16 video recordings were collected using a modification of the approach techniques described in Stimpert et al. (2012) and Zoidis & Lomac-MacNair (2017). The boat slowly approached the humpback whales and was stationed 100 m away with the engine off, waiting for the whales to approach the boat. The videographer (MN), equipped with a recording device (GoPro Hero 4, Silver version) and a 1-m-long pole, lowered the camera over the side of the boat into the water while the whales remained between 5 to 20 m from the boat, always visible from the surface (see also Zoidis & Lomac-MacNair, 2017).

From the ~13 min of underwater video recorded, we focused on a 2.06-min-long segment recorded on 29 July, which was rich in concurrent social calls and behaviors. This section contained the highest-quality resolution of social behaviors, allowing a detailed description of both visual and acoustic components. All other video data were inspected for behaviors but were not included due to low resolution. Regrettably, the routine acoustic survey (using a H2a-XLR omnidirectional hydrophone and Tascam DR-40 digital recorder as .wav files, 16 bit, and 44.1 kHz sampling rate) was not deployed and, thus, did not acoustically capture this underwater behavioral interaction. The underwater behavior and extraction of images of each frame from the 2.06-min-long segment were analyzed and transcribed by JO using the *Behavioral Observation Research Interactive Software* (*BORIS*), Version 5.1.3 (Friard & Gamba, 2016). The audio for acoustic analyses presented herein was extracted from the underwater video material as uncompressed .wav files using *WinX HD Video Converter Deluxe*, Version 5.8.9.

Furthermore, underwater movements were considered *associations* when the same behavioral state was displayed by two or more humpback whales within 30 m of each other; these associations were noted as social interaction events, while social calls were classified as acoustic events (Whitehead & Van Parijs, 2010). We defined *behaviors* as *simultaneous* when different actions occurred concurrently by individual group members (without coordination, i.e., not the same behavior) and *synchronous* when the movements of two or more individuals appeared to be coordinated in behavior and timing (e.g., the same action at the same time) (Connor et al., 2006; Senigagli & Whitehead, 2012; Hill et al., 2015).

Calls were analyzed visually and aurally in collaboration with the ongoing Humpback Whale Social Call International Working Group (Seger, 2016). Spectrograms were viewed either in the custom *MATLAB* software *Ulysses* (written by Drs. Aaron Thode and Jit Sarkar) with a 1,026 Nfft, 90% overlap, and Hanning window (KS), or *Raven Pro*, Version 1.4, with a 2,048 FFT, 75% overlap, 33 Hz resolution, and Hanning window (ECG). These parameters were adjusted accordingly for clarity when zooming into smaller bandwidths. Given that most humpback whale calls are below 15 kHz (Dunlop et al., 2007), the GoPro's audio equipment roll-off above 15 kHz was not an issue. All sounds were categorized qualitatively

Table 1. Survey effort in Galera-San Francisco Marine Reserve, Ecuador, to collect visual, acoustic, and underwater video data, 2015

Survey period	Survey type	Duration (d)	No. of sightings/ recordings	Total data recorded (h:min:s)
6 June to 3 August	Visual	30	159	91:00:00
22 June to 31 July	Acoustic	13	35	05:57:00
22 June to 31 July	Underwater video	4	16	00:12:46

according to the international catalog of social calls largely compiled from humpback whales recorded off Los Cabos, Mexico (Seger, 2016), Alaska, USA (Fournet et al., 2015, 2018a, 2018b), Hawaii, USA (Zoidis et al., 2008), and the east coast of Australia (Dunlop et al., 2007). Given the paucity of social calls ($N = 46$), which precluded statistical analyses, all sounds were classified by consensus between two experienced humpback whale vocalization classifiers (KS and ECG).

From the 2.06-min-long video recorded in a routine visual and acoustic survey, a time series of underwater social behaviors and concurrent calls was classified from an encounter involving a pod of three adult humpback whales (see Supplemental Material; the Supplemental Material is in the Supplemental Material section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Just prior to this 2-min recording, another short video recording (00:27:00 s) showed the three whales moving calmly underwater. In the focal 2-min video, the group of three whales dove, and two individuals (the focal whales, labelled A and B) started the simultaneous behaviors described herein (Figure 1; see Supplemental Material for full behavioral sequence). The sequence starts with two of the whales (A and B) submerged for a period of > 6 s, at at least 3 m, and facing the same direction. Whale A positioned its body with the ventral side facing up to the surface in a back-to-back position with whale B (Figure 1d). Facing the same direction and moving at the same speed, both bodies stayed parallel to the surface. Then, the two whales synchronously swam in a back-to-back position with their pectoral fins outstretched (Figure 1c). At this time, the third whale (C) swam below the focal pair (A and B) and moved in the same direction as the other two, maintaining the same parallel position to the surface (Figure 1b-d). During

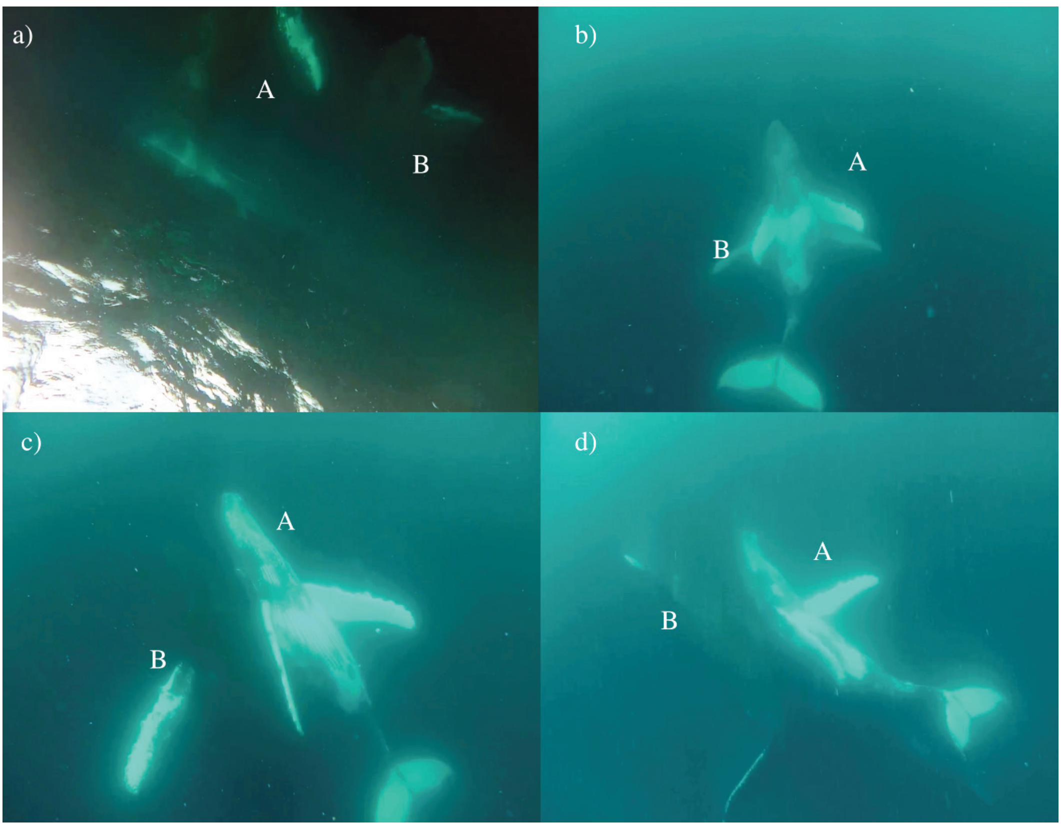

Figure 1. Simultaneous subsurface behavior off the coast of Esmeraldas, Ecuador, observed between two humpback whales (*Megaptera novaeangliae*) (A and B) with a third whale nearby (but not pictured): (a) dive, (b) simultaneous subsurface swimming of the pair in a back-to-back position, (c) synchronous subsurface swim in a back-to-back position with pectoral fins extended, and (d) simultaneous subsurface swimming with presumed dorsal contact (see Supplemental Material for full list of behaviors displayed).

this behavior, the dorsal surfaces of the focal pair may have been in contact with one another while they were moving synchronously in the same direction. The subsurface social association ended when the two focal whales (A and B) returned simultaneously to the surface, keeping the same parallel position, and moved gradually forward, with whale A's body still in a belly-up position (see Supplemental Material).

Social calls, including single calls and others arranged into bouts, were recorded 18 s after the humpback whales submerged during the back-to-back position (see Figure 2 & Table 2 for a social call list). At this stage, whales A and B slowly and simultaneously moved forward and then stayed immobile at a depth of approximately one and a half whale body lengths from the surface. Their bodies remained parallel while vocalizations were recorded. The complete social interaction occurred throughout the 2.06-min recording, but the simultaneous and synchronous back-to-back movements occurred in the last ~12 s, from 01:17.88 to 01:29.93. From minute 0:42 to 2:02, social calls were recorded with sufficient intensity to be assigned to the focal whales rather than to any other whale in the area (the closest whales observed in the area were 800 m away and, therefore, unlikely to be close enough to produce such clear audio samples).

In the acoustic analysis, a total of 15 call types (Table 2) were identified, with 13 single call types and two composite calls (composed of two call types that were not separated by silence and denoted in nomenclature by a dash [–]; Seger, 2016). These sounds were grouped into six call bouts, where a *bout* was defined as groups of calls within 1 s of each other (where all calls could be identified). Of these, three were pure bouts (repetition of the same call type) and three were mixed bouts (containing more than one call type). The three pure bouts were comprised of four snorts and three n-shaped cries or squeaks, while the mixed bouts contained 15 or three individual call types (see Table 2). The 15-sound mixed bout began at minute 1:24.5, and the individual call types were an n-shaped shriek, three ascending shrieks, three squelches, a grunt, a short moan, a bark, a squelch, a squeak, a short moan, and two snorts (see Figure 2 for some examples).

From our qualitative classification and comparison with the literature, we determined that, out of the 15 identified call types, 11 were previously identified in Australia (Dunlop et al., 2007), five in

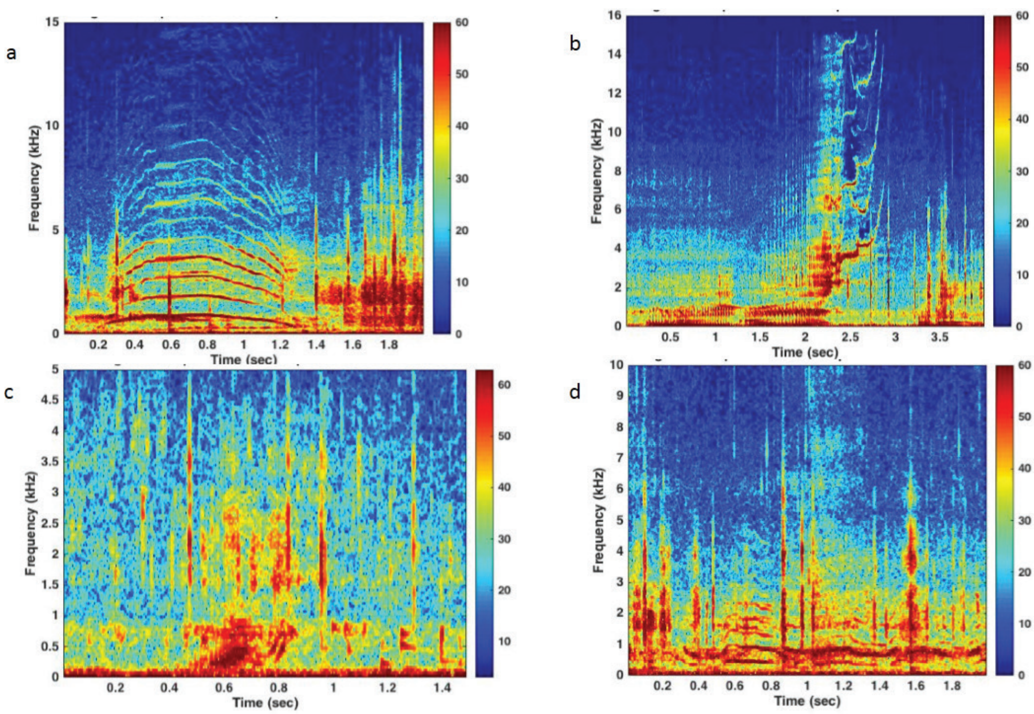

Figure 2. Four of the call types recorded during the underwater social interaction (physical contact and social call display): (a) n-shaped cry, (b) purr-ascending shriek, (c) bark, and (d) modulated moan. Sound intensity units (color scale) are in decibels re 1 micropascal (dB re 1 µPa). Spectrograms were produced in *Ulysses* with a 1,026 Nfft, 90% overlap, and Hanning window.

Table 2. Social calls identified in the video recording; time corresponds to full video sequence analyzed.

Time (min:s)	Call types	Bout
0:43	N-shaped cry, n-shaped cry, n-shaped cry	3-call pure bout
0:46	Unclear high frequency call, n-shaped whistle	--
0:48	Snort, snort, snort, snort	4-call pure bout
0:54	Squeak, unclear social call	--
1:03	Ascending moan	--
1:10	N-shaped cry	--
1:17	Long purr-ascending shriek, purr, purr-ascending shriek	3-call mixed bout
1:24	N-shaped shriek, ascending shriek, ascending shriek, ascending shriek, squelch, squelch, squelch, grunt, short moan, bark, squelch, squeak, short moan, snort, snort	15-call mixed bout
1:35	Bark	--
1:38	Squeak	--
1:41	Squeak, squeak, squeak	3-call pure bout
1:43	Unclear social call, ascending shriek	--
1:46	Modulated moan	--
1:49	Unclear social call, unclear social call, unclear social call	--
1:52	N-shaped moan, modulated moan, squeak	3-call mixed bout
2:03	Purr-ascending shriek	--

Alaska (Fournet et al., 2015, 2018a, 2018b), 10 in Hawaii (Zoidis et al., 2008), and 13 in Los Cabos, Mexico (Seger, 2016). However, given multiple research groups' work on calls, consistently naming call types across distinct population segments is challenging. We have endeavored to name call types following the social calls described in a broad range of studies (e.g.. Dunlop et al., 2007; Zoidis et al., 2008; Darling, 2015; Seger, 2016). For example, the grunt identified in the current study may show differences to the "grunt" identified in Zoidis et al. (2008) based on its visual contour and frequency bandwidth but is similar to "grunts" classified in the Australian and Mexican repertoires. Agreement on a standard call-type naming scheme would greatly aid in future broad-scale comparative studies; and as the "grunt" classification is very common across all recorded humpback whale populations, it would be a prime place to start.

Our observations give insight into the occurrence of social interactions accompanied by acoustic displays, with simultaneous (commonly referred to as *synchronous*) behavior and tactile underwater movements that have mainly been studied in toothed whales such as bottlenose dolphins (*Tursiops truncatus*), pilot whales (*Globicephala melas*), and sperm whales (*Physeter macrocephalus*) (Connor et al., 1992a, 1992b, 2006; Whitehead, 1996; Senigagli & Whitehead, 2012). In these species, synchronous behaviors and bodily contact may be used as a signal for social associations inside alliance systems (i.e., cooperative processes such as mating strategies) to reinforce social bonds and alloparental care strategies (Connor et al., 1992a, 1992b, 2006; Whitehead, 1996; Senigagli & Whitehead, 2012; Aoki et al., 2013). However, for mysticete species, data documenting simultaneous acoustic behaviors and bodily contact are scarce but are becoming more available with the increase in underwater video and tagging studies (Friedlaender et al., 2009; Wiley et al., 2011; Goldbogen et al., 2013; Zoidis & Lomac-MacNair, 2017).

The subsurface behavior video-documented herein represents only a portion of an association with subsurface behavioral observations, potentially by a male and a female, representing an example of socio-sexual conduct and/or social play in humpback whales. At the same time, a third whale was moving in the same direction as the focal whale pair (see Supplemental Material), which may potentially be a male if the focal pair were male/female. According to our previous surface sighting of the three whales, they were first sighted as a triad that moved slowly and peacefully on the surface. Such triad forming may have been a short-term association of mixed sexes (e.g., two females and a male or two males and a female) with the focal pair undertaking socio-sexual interactions (e.g., courtship), while the third whale was outcompeted and simply remained close by as all members of the triad are presumed to have recently split from a disaggregated competitive group and formed the triad. Social calls may occur often during temporally mixed associations of variable male numbers around a central female. For example, calls have been commonly recorded in social groups from eight to 25 whales (supergroups) (Dunlop et al., 2008; Darling, 2015; Seger, 2016; Gridley et al., 2018). Social calls have also been reported in solitary whales, pairs of adults, triads, and larger groups (Dunlop et al., 2008). Previous studies have documented that whale pairs can be actively formed by female/male associations (Darling & Bérubé, 2001; Andriolo et al., 2014). Such pairs can present passive behavior with an association period lasting a day or longer in which synchronized dives frequently occur (e.g., Darling et al., 1983). However, apart from female/female associations, male/male pairs can also occur due to the fluid associations on breeding grounds (e.g., associations of only 1 to 5 d in length) during which the whales cooperate in brief surface active interactions or maintain cohesion as a part of competitive groups (Clapham et al., 1992; Darling & Bérubé, 2001; Nicklin et al., 2006; Pomilla & Rosenbaum, 2006; Cypriano-Souza et al., 2010; Pack et al., 2012; Andriolo et al., 2014).

While the visual underwater range and length of temporal observation in the current study was limited, our findings broadly agree with previous subsurface observations taken using underwater crittercam or digital video recording systems (e.g., Herman et al., 2008; Darling, 2015). Such technology has provided important details about competitive groups and their vocal behavior. For example, Herman et al. (2008) registered a possible principal escort and female observed in close proximity that may have engaged in physical contact (e.g., rubbing with pectoral fins) with accompanying social calls. However, given that we were not able to identify the sexes of the individuals, we cannot speculate further about a sexual function. Thereby, we can only assume a short-term association between conspecifics (female/male, male/male, or female/female) that contained potential tactile contact and acoustic signals for communication. Further underwater recordings and video analyses will help improve our understanding of the socio-sexual behaviors of humpback whales.

Another possibility is that our underwater observations may be related to play interactions as shown in some odontocete species. Observations of playful behavior among humpback whale conspecifics is very rare. Play has been reported in humpback calves (Zoidis et al., 2014), and play interactions with objects and other species have been noted (Deakos et al., 2010; Owen et al., 2012). Broadly playful behavior with bodily contact could be associated with any form of social communication and perhaps become an important driver for social bonds (Pryor, 1990). Observational constraints of this synchronous subsurface event (i.e., whale C being out of camera) precluded further robust analysis; however, clear synchrony was observed when the two focal whales swam simultaneously with presumed bodily contact occurrence. Studies by Connor et al. (2006) and Herzing (2015) suggest that vocal and behavioral studies of synchronized behavior within toothed whale associations are important in understanding individual or group coordination in underwater social interactions. Underwater skills during play events—for example, simultaneous/synchronous movements and acoustic interactions—between humpback whale mothers and their calves during foraging and maternal care events may facilitate the calf's early development, increase successful feeding attempts, and reinforce social communication important in adulthood (Edds-Walton, 1997; Tyson et al., 2012; Faria et al., 2013; Zoidis et al., 2014).

Detailed observations of underwater associations and other social behaviors will increase our understanding of the context and function of individual-level humpback whale behavioral ecology (e.g., sexual, social learning, and play behavior) both within and among populations. Our underwater recording system and observations did not allow the assignment of specific calls to each whale because a single device was used; plus, the whales were too close to each other and, thus, time differences of arrival localization strategies were impossible. We assigned the social calls as the "group's" repertoire while discerning the bodily behaviors of each individual within the pair. However, the purr-ascending shriek calls and underwater behavior presented herein appear to be similar to those behaviors noted in Hawaiian waters. For example, an adult pair (unknown/female sex) produced social call bouts or trains as the female circled the other whale while showing the ventral side of her body (Darling, 2015).

The call types recorded during this subsurface interaction are shared with other humpback whale distinct population segments. Purrs, shrieks, and moans are shared with a humpback whale feeding ground located at Frederick Sound, southeast Alaska (Fournet, 2014; Fournet et al., 2015, 2018a, 2018b); cries, snorts, shrieks, moans, purrs, grunts, and barks are shared with the east Australian migratory corridor (Dunlop et al., 2007); squelches, grunts, moans, and shrieks are shared with humpbacks from Los Cabos, Mexico (Seger, 2016); and modulated moans, short moans, purrs, shrieks, whistles, grunts, and squelches are shared with the Main Hawaiian Islands (Zoidis et al., 2017). However, this is not a complete repertoire for the Southeastern Pacific (SP), and we emphasize that additional underwater studies are needed to reveal potential call types that may be unique to the SP humpback whale population.

Some social call types are also present in multiple years and appear to represent a stable social call repertoire (Rekdahl et al., 2013). New or novel social calls may arise due to individual innovation and subsequent imitation (Payne, 1982; Tumer & Brainard, 2007), which could spread through a population through social learning (similar to song; Garland et al., 2011). Recent studies have found common call types among disconnected populations suggesting that such sounds may represent an innate template of social calls (Fournet et al., 2018a, 2018b). Hence, further research incorporating call types from breeding grounds (such as in the current study), migratory corridors, and feeding grounds from multiple ocean basins will assist in understanding the extent of plasticity in humpback whale social call repertoires.

Humpback whale interactions with conspecifics may be particularly sensitive to human perturbations, which have the potential to interfere with the whales' social behavior. Analysis of underwater video data and data obtained from acoustic methods may increase our awareness and understanding of the nature and type of impacts; to what degree animals may habituate; or how impacts may vary based on a whales' behavior, age, or other parameters. Such an analysis may improve our understanding of social interactions among humpback whales and could potentially provide a way to assess how social interactions might change based on varied levels of disturbance. This is a challenging topic to elucidate; however, it would be useful for future analyses. Therefore, we encourage scientists to make available any information about humpback whale social calling behavior to advance the understanding of underwater social behaviors and the general behavioral ecology of this species.

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