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Female Humpback Whale (*Megaptera novaeangliae*) Positions Genital-Mammary Area to Intercept Bubbles Emitted by Males on the Hawaiian Breeding Grounds

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The production and use of bubble streams, nets, bursts, dribbles, and rings by cetaceans are widely documented (see review by Moreno & Macgregor, 2019). Bubbles are produced by the controlled exhalation of air through the blowhole(s) or from bursts of air released from the mouth. Observations indicate that bubble releases are produced in several different contexts, including agonistic, stressful, social, foraging, and sexual. Bubbles play important roles in cetacean social interactions; however, in most circumstances, their specific function has yet to be determined.

Humpback whales (*Megaptera novaeangliae*) are well known for their use of bubbles, especially in a feeding context where lone whales or cooperative groups use a variety of bubble-based tactics to net, trap, herd, and concentrate different prey species (e.g., Jurasz & Jurasz, 1979; Hain et al., 1982; D'Vincent et al.,1985; Sharpe & Dill, 1997; Wiley et al., 2011). Vigorous use of bubbles is also a feature of humpback whale behavior on breeding grounds. The most obvious are the long bubble streams emitted by males, primarily from "principal" escorts during challenges from other males (e.g., Tyack & Whitehead, 1983).

In this paper, we describe a different context for bubble use by humpback whales on the Hawaiian breeding grounds. In contrast to the bubbles produced by competing male humpbacks, we report an anecdotal observation of male production of bubbles directed at the female's genital-mammary region. In this situation, the female tolerates and possibly aids in the reception of the bubbles by situating her body in the bubble stream (Figure 1; see supplemental video; the supplemental video for this paper is available 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). While we have observed this behavior on multiple occasions, usually the observation is not of the length or completeness needed to definitively state that bubbles are directed at the female (vs at other males in the group) or, if bubbles do reach the female, whether it is intentional or not.

This observation occurred ~20 y ago and was videotaped. Field notes of the encounter have not been located; however, the 14-min video recording clearly illustrates a different context for bubble use and strongly suggests that bubbles play a role in male–female interactions during the breeding season.

The encounter occurred in February or March between 2000 and 2003 in the Au'au Channel off West Maui, Hawaii (approx. 20.85° N, 156.73° W). On this day, our research team encountered a multiple male–single female adult group milling at the surface. The female in this group was motionless or moving very slowly, with three males circling around her. We immediately noticed bubble streams and clouds rising to the surface and that there was no apparent agonistic behavior between the males. As such, CPN entered the water to provide further behavioral context for the surface observations.

Video Observations

The entire 14-min video and the "Supplementary Video Descriptions" file are included in the supplemental materials (also see Figure 1A-D). The main observations are summarized below.

Group Composition

The group was comprised of one adult female and three adult males. The female's sex was confirmed by the presence of the hemispherical lobe (Figure 1C). Male sex was presumed by behavior, including that multiple female groups are not seen together on breeding grounds (Jones, 2010), and multiple male groups typically form around a female (Tyack & Whitehead, 1983). Three of the four individuals seen on the video are clearly identifiable by individual natural markings (see

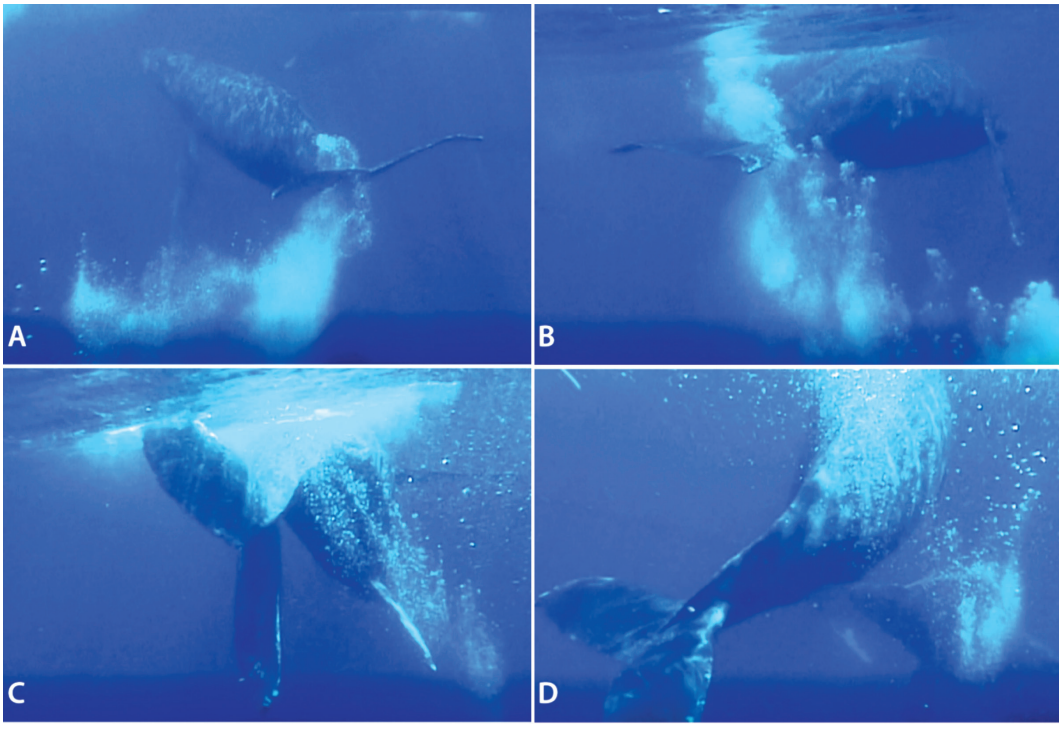

Figure 1. Examples of humpback whale (*Megaptera novaeangliae*) male production and female reception of bubbles (see supplemental video): (A) & (B) show the stationary female slightly lifting her flukes (A) and sliding her tail stock over the bubble releases (B). (C) shows the female rolling toward the bubbles, revealing the hemispherical lobe and swollen genital area. In (D), the female slides her flukes and rear body from left to right over the bubble stream below. Another male with white pectoral fins can be seen deeper and toward the front of the female. (*Photo/video credit:* Charles P. Nicklin, NOAA Permit #753-1599)

"Supplementary Video Descriptions" in the supplemental materials).

Female Condition and Behavior

The female was noticeably large in girth and appeared to have a swollen genital area (Figure 1C). She was generally stationary both at depth (~15 to 20 m) and just beneath the sea surface. When not stationary, she was nearly so, only moving forward slowly. Importantly, there was no obvious indication of the female avoiding the males as is often seen on breeding grounds (Glockner-Ferrari & Ferrari, 1985; Jones, 2010). Indeed, on five separate occasions, the female appeared to position the ventral posterior portion of her body in the direction and/or vicinity of the bubbles.

Male Behavior

Three adult males (referred to as M1, M2, and M3) are repeatedly seen throughout the supplemental video. The one male (M1) that was consistently nearest to the female did most, if not all, of the bubble production. A second male with white pectoral fins (M2; see supplemental materials) was usually distant in the video frame and/or at the front periphery of the female. The third male (M3) can be seen four times in the video and may have been responsible for one of the bubble emissions. On two occasions, the female can be seen in the center of two males. There was no obvious coercion of the female or male–male agonistic displays typical of male interactions around a female on the breeding ground (Darling et al., 2006).

Bubble Use and Production

In the supplemental video, 12 discrete instances of underwater bubble streams and/or bubble clouds are produced by a male while moving toward and underneath the posterior one-third of the female's body. These bubbles rise upward, breaking on her underside in the genital-mammary region (see Figure 1). In addition to the underwater expulsion of bubbles from the blowholes toward the female, M1 also releases large bubble clouds from its mouth upon each surfacing.

Female Orientation to the Bubbles

The supplemental video shows that the female does not attempt to evade or avoid the males or the bubbles. On five separate occasions, she can be seen rolling toward, arching, or slightly lifting and/or moving her tail above the bubble releases. On at least two occasions, the female rolls and appears to orient her body toward the bubble releases such that they strike her in the genital-mammary region. In these cases, the bubbles rise toward the surface on either side of her tail stock (Figure 1D).

While this male production, and apparent female acceptance, of bubbles is intriguing and appears to reveal a new dimension to male–female interactions on breeding grounds, any interpretation of the behavior is clearly speculative. Unlike bubble-netting or agonistic behavioral displays, the function of these bubbles directed at the female is neither obvious nor intuitive based on current understanding of reproductive behaviors. While speculative, there are two primary contexts within which to consider this behavior (i.e., adult female humpbacks migrating to breeding grounds with different reproductive objectives): (1) to maximize mating opportunities (mature females without calves) and (2) to ensure successful birth and calf development (Gabriele, 1992; Jones, 2010).

Scenario 1: Mating/Estrus Female—A female present to mate and in estrus could explain (1) the female's receptiveness of the males (compared to fleeing from or leading competitive males in some form of female choice) and (2) male attention toward the female. The supplemental video shows a male producing and directing bubble exhalations toward the female's genital-mammary area and the female responding by orienting her underside toward the bubbles. In this scenario, it seems reasonable to speculate that this interaction may serve a sexual purpose, including some form of pre-copulatory stimulation or assisting in the release of chemical cues as to the female's reproductive status or readiness to mate. Conceivably, it may even play a role in inducing estrus, which has been shown to occur in anestrous ewes in the presence of multiple males (Miquel-Cruz et al., 2019).

Scenario 2: Late Pregnant Female—Another possibility is that the female is late pregnant and about to give birth. This could explain her extended/notable girth, swollen genitals (as described in Patton & Lawless, 2021), and even the presence of multiple males around a birthing female (see review in Ransome et al., 2021). If this is pre-birth behavior, we speculate that the bubbles could stimulate the release of hormones such as oxytocin known to be vital in the birthing process (Fuchs et al., 2001). Oxytocin is released with activation of somatosensory nerves, "induced by touch, stroking, warmth and light pressure on the skin" (Uvnäs-Moberg et al., 2015, p. 6). In this case, mammary glands—especially sensitive—are located on either side of the genital slit where the bubbles appear to be directed and received. It seems possible then that the clouds of bubbles from male humpbacks may also serve this purpose. But the pressing question is, if this is the case, why are males involved? What is in it for them?

In their review on bubble use and production in cetaceans, Moreno & Macgregor (2019) indicate that humpback whales and some species of odontocetes produce bubbles in a sexual context. However, details are limited, and what is described seems to be different than the behaviors described here. Their reference to humpback whales (Baker & Herman, 1984), for example, refers to the use of bubbles in male–male competitive behavior around females. The interpretations of odontocetes using bubbles in sexual contexts is also complicated by associated aggressive behaviors and unsuccessful mating attempts by immature males (e.g., Herzing, 1996), and similar bubble use in social contexts outside of sexual behavior (Moreno, 2017). While interesting, it is not readily apparent that these reports of cetacean bubble use in a sexual context provide any additional insights or contexts for the interpretation of the male–female interactions described here.

Bubble use in humpback whales, as with other cetaceans, is complex; and as this observation indicates, it can occur in a variety of different situations on both feeding and breeding grounds. The male production and female reception of bubbles strongly suggest that they may also play a role in courtship, mating, and/or in the birthing process. Whatever function the bubbles serve, this is a different context for their use than the bubble streams typically associated with male–male agonistic displays on humpback whale breeding grounds. Future research aimed at understanding the hormonal state of male and female humpbacks within different social groups and situations on breeding grounds should provide the insight needed to determine the correct context for the behavior patterns described.

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