The Sex Life of Harbor Porpoises (*Phocoena phocoena*): Lateralized and Aerial Behavior

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Abstract

The Golden Gate Bridge in San Francisco Bay provides a non-invasive aerial platform where harbor porpoises (*Phocoena phocoena*) can be observed mating. We photographed 144 mating events over an eight-year period (2010 to 2018) occurring in all seasons. The mating habits of free-ranging male harbor porpoises are systematically described, a first for any member of the family Phocoenidae. The males' rapid sexual approaches toward females were characterized by high energy and precision timing as males rushed to contact females surfacing to breathe. Males always attempted to copulate by positioning their ventral sides on the females' left side. This extreme laterality in sexual approach has not been reported for any cetacean. Males approached females with force and speed that often resulted in male aerial behaviors (69% of mating attempts). These behaviors, observed exclusively in mating contexts, included leaps and splashes that counter the species' reputation for inconspicuous behavior. Males also displayed their ventrum or penis toward females without attempting to copulate. The penis was visible in 60% of the 96 mating events for which the ventrum could be observed, with intromission confirmed in one event. Males always initiated mating and approached lone females in 62.5% of mating events. Calves accompanied females during 25% of mating events. Calves were temporarily separated from their mothers by the approaching males in approximately half of these events. Additional adults were observed in 12.5% of groups, although no male–male interactions were observed. Our findings on the unique mating pattern exhibited by male harbor porpoises validate some predictions made about their behavior based on their reproductive biology and anatomy. The data support the hypothesis that males compete primarily by sperm competition and not contest competition.

Key Words: mating behavior, sexual interactions, breaching, laterality, sperm competition, San Francisco Bay

Introduction

Little is known about the mating behaviors of free-ranging cetaceans due to logistical challenges, and systematic study has been limited to a few populations (Schaeff, 2007; Lanyon & Burgess, 2014; Orbach et al., 2015). In California, harbor porpoises (*Phocoena phocoena*) recently returned to San Francisco Bay after a 65-year absence, providing an opportunity to observe their behavior from the Golden Gate Bridge, a unique non-invasive aerial platform. A 2011 to 2014 census confirmed the harbor porpoises' daily occurrence year-round (Stern et al., 2017). They are part of the non-migratory San Francisco-Russian River stock (a subpopulation of *P. p. vomerina)*, which has a stable estimated abundance of nearly 10,000 porpoises (Forney et al., 2014). During the high-tide period, approximately 20 harbor porpoises per hour (of which 10% were calves) were observed from the Golden Gate Bridge during visual surveys (Stern et al., 2017).

The average group sizes of harbor porpoises in California waters range from 1.75 (Forney et al., 2014) to 2.15 (Stern et al., 2017) animals per group. Harbor porpoises evade boats and maintain a low profile, with their dorsal fins visible above water only during brief surfacings that last 1 to 2 s (Jefferson et al., 2015). Aerial behaviors have been infrequently reported for this species (Bel'kovich et al., 1991; Sekiguchi, 1995). However, initial observations of harbor porpoises from the Golden Gate Bridge in 2010 demonstrated that their recurrent sexual approaches and brief but conspicuous aerial behavior could be captured in photographs and videos.

Sexually mature harbor porpoises reach 1.5 to 2.0 m in length, weigh 50 to 70 kg (Gaskin et al.,

1974; Jefferson et al., 2015), and display reverse sexual size dimorphism, with males averaging approximately 9% less than female lengths and 21% less than female weights (Gaskin et al., 1984; Hohn & Brownell, 1990; Read & Tolley, 1997; Galatius, 2005b). Harbor porpoises have one of the shortest life spans of any cetacean species (~10 y; Hohn & Brownell, 1990) and the shortest calving intervals (interbirth intervals of 1 to 2 y, possibly varying with resource availability; Hohn & Brownell, 1990; Read & Hohn, 1995). Like other cetaceans, harbor porpoises give birth to single calves (Whitehead & Mann, 2000), and there is no evidence of paternal care (Connor et al., 2000). Harbor porpoises have polygynandrous mating systems (multiple males mate with multiple females; Bjørge & Tolley, 2018), with seasonal reproductive peaks (Lockyer, 1995; Read & Hohn, 1995). Males undergo striking seasonal changes in testes size (Kesselring et al., 2017), with maximum testes masses achieved in June and July when females enter a synchronized estrous phase (Read & Hohn, 1995; Neimanis et al., 2000). The peak calving period for harbor porpoises in California waters is May and June, followed by ovulation in June and July (Simons, 1984; Hohn & Brownell, 1990). Similarly, harbor porpoises in the Gulf of Maine conceive up to the second week in July (Read & Hohn, 1995). There is some evidence for seasonal polyestry in a captive harbor porpoise from Japan based on serum progesterone levels (Arai et al., 2017). Gestation takes 10 to 11 mo, and lactation and calf dependency last for 8 to 12 mo (Mohl-Hansen, 1954; Read, 1990; Teilmann et al., 2007). The average age of sexual maturity is 4.6 y for females and 4 y for males (Hohn & Brownell, 1990).

Despite their common occurrence nearshore across a wide range in northern temperate waters, the social structure of harbor porpoises remains poorly understood. Unlike delphinids, such as bottlenose dolphins (*Tursiops truncatus*) or killer whales (*Orcinus orca*), harbor porpoises do not appear to live in complex societies (Whitehead & Rendell, 2015). They have been described as asocial due to their small group size, possibly a predator avoidance strategy (Gowans et al., 2007). However, they occasionally form larger groups (Hoek, 1992) and exhibit non-parental care-giving behavior in captivity (Andersen, 1969).

Relative testes size is used to predict mating systems in mammals (Kenagy & Trombulak, 1986), including cetaceans (Brownell & Ralls, 1986). The very large testes-to-body size ratio (with combined testes weights up to 2.7 kg), lack of secondary sexual characteristics, and reverse sexual size dimorphism in harbor porpoises suggest that the primary male mating tactic is sperm competition via large volumes of ejaculate (Fontaine & Barrette, 1997). MacLeod (2010) ranked harbor porpoises highest of 30 cetacean species in terms of inferred level of sperm competition. Noting the "megatestes" found in harbor porpoises, Fontaine & Barrette (1997) predicted males would not fight each other for access to females, would mate with multiple females, and would mate many times with the same female. For a small toothed whale, the harbor porpoise has a long (~50 cm) penis that extends as far as its mandible when erect (Orbach, 2018). The penis consists of a fibro-elastic shaft with vascular tissue (corpus cavernosum) for engorgement in the proximal part and a filiform distal tip (Meek, 1918; Slijper, 1966).

The only published description of mating behavior in the free-ranging harbor porpoise comes from a multi-year expedition in the Black Sea during which harbor porpoises of the subspecies *P. p. relicta* engaged in what ship-board observers assumed was sexual behavior. In this single instance lasting approximately 5 min, an adult male and an adult female, accompanied by a calf, leaped repeatedly and swam "belly-to-belly" (Bel'kovich et al., 1991). The socio-sexual behavior of captive harbor porpoises in mixed-sex groups has been the focus of studies at three facilities. At the Anton Bruun Oceanographic Station in Strib, Denmark, courtship behaviors between males and females included chasing, posturing, tactile rubbing, and "belly-exposure" (in which the male speeds up and swims past the female while rolling his body on his long axis to display his belly to her), but no mating attempts were observed (Andersen & Dziedzic, 1964). At Fjord & Bælt in Kerteminde, Denmark, numerous mating attempts were recorded over the course of multiple projects (Desportes et al., 2003). Males were considered the initiators of sexual activities, and females could accept or reject males, thereby affecting the outcome of the mating attempts (Benham et al., 2001). A short follow-up effort at the Dolfinarium in Harderwijk, Netherlands, concluded that males attempted to mate promiscuously with females, did not form male alliances, and exerted no absolute dominance over other males (Delgado-García, 2009).

This study focuses on male mating behaviors as female mating behaviors have been described for this population (Orbach et al., in press). Our goal was to observe, describe, and quantify the mating behavioral patterns of male harbor porpoises observed in San Francisco Bay. Specifically, the objectives were to (1) describe the sexual approaches of males to females, (2) determine the size and composition of mating groups, and (3) ascertain if there was a seasonal mating pattern.

Methods

Study Area
San Francisco Bay is a large estuary on the west coast of the United States, connected to the ocean via a strait known as the Golden Gate (*U.S. Coast Pilot*, 2016). The bay is a turbid ecosystem, with a mixed semi-diurnal tidal regime and peak currents exceeding 2.5 m/s (Conomos et al., 1985; Barnard et al., 2006). The 113-m-deep strait narrows to 1.5 km where it is spanned by the Golden Gate Bridge (37° 48' 59" N, 122° 28' 39" W). Observations were made from the bridge's eastern public sidewalk, ~70 m above sea level, which afforded unique overhead views of the harbor porpoises. The platform's chief limitation was that focal follows of socially active harbor porpoises could not be continued once they swam west beneath the deck of the bridge. Water visibility ranged from approximately 1 to 2 m below the surface. Sea state was routinely good (≤ Beaufort 2); however, summer fog occasionally reduced visibility.

Data Collection
Year-round naked eye searches to count harbor porpoises were conducted from January 2010 through January 2018 while crossing the Golden Gate Bridge on foot, extending the Stern et al. (2017) dataset. Tidal features in the Golden Gate influence spatial and temporal variations in harbor porpoise presence (Duffy, 2015). Harbor porpoises were most often observed along tidal fronts generated by flood currents at high tide, and at the beginning of ebb tides when harbor porpoises consistently transited west under the Golden Gate Bridge and out of the bay in a predictable pattern (Keener et al., 2011; Stern et al., 2017). Photographs and videos were collected opportunistically of mating harbor porpoises; we recorded the time, date, group size, and group composition. Canon EOS 7D Mark I/II digital SLR cameras with 300 mm fixed or 100-400 mm telephoto lenses were primarily used for still photography. A Sony Handycam HDR-XR550V fitted with a 1.7x teleconversion lens (Sony VCL HG1737C) was used to record continuous video footage of behavior at 30 frames/s.

Data Analysis
Photographs were analyzed in the *Photos* application (Apple Inc.), while video analysis was performed in *iMovie* (Apple Inc.). The videos were trimmed to relevant mating events, zoomed in, and slowed to a 50% rate. For both still photographs and video clips, we assessed behavioral patterns frame-by-frame. Durations of mating events and intra-event behaviors were calculated by scrolling video clips in *iMovie* to measure elapsed times with the on-screen playhead chronometer (minimum interval displayed per 30 frames = 1 s). We analyzed these data for date, group size, and composition, including the sex of the adults involved in the mating events. Harbor porpoises were considered in the same group if they were observed within 10 m of each other (10 m chain rule; Smolker et al., 1992). The < 10% difference in size between an adult male and female harbor porpoise was not useful in determining an individual's sex from photographs. Therefore, confirmation of the male's sex was by observation of the penis and the female's sex by close association with a calf. Sex was also presumed based on our observations of typical harbor porpoise behavior: a male initiated a sexual approach to a target female harbor porpoise, and the female responded to the approach. We examined each male's initial orientation to the female at the start of his sexual approach (using videos only), the male's orientation to the female during his sexual approach (when < 1 m away from her), the male's position relative to the female and to the surface during sexual approach, the visibility of the penis, and interactions with calves and other adults.

Proportions of mating events were analyzed by season, group composition, female and male position, and aerial behavior using chi-square and Fisher's exact tests in *VassarStats* (www.vassarstats.net), and charts were produced in Microsoft *Excel*. Proportions of mating events were compared to all data collected from the Golden Gate Bridge between 2010 and 2018 (expanding the dataset used in Stern et al., 2017). Specifically, we compared the total number of sightings in mating and non-mating groups by season and group composition for lone females, lone females with calves, females accompanied by other adults, and females with calves accompanied by other adults, with the assumption of a non-biased sex ratio in sightings for which sex could be neither determined nor inferred.

We defined sexual approach events as social interactions in which males approached females and exhibited either of two basic behavioral types: (1) copulatory attempts (where the male was sufficiently proximate to the female to copulate) and (2) displays (where he was not sufficiently proximate to copulate). Copulatory attempts were of two types: (1) a contact attempt occurred when the male came into physical contact with the female during his sexual approach; and (2) a non-contact attempt occurred when the male approached closely (< 1 m from female) but did not physically touch the female either because of the manner in which he executed his approach maneuver or because of the female's evasive actions. Displays never involved contact as the males did not approach the females closely

but did involve executing a body roll to present the ventrum to the females (belly-exposure) or extruding the penis, with or without the body roll. We subcategorized copulatory attempts and displays based on whether or not the penis was extruded. A schematic chart of these behavioral components of sexual approaches is presented in Figure 1. If we could not determine whether physical contact occurred or whether the penis was visible based on our digital images, those data were excluded from the analysis of sexual approach events. All copulatory attempts or displays were counted as separate events, even when made by a male in succession as he pursued the same female.

The male's initial orientation to the female was defined as the position of the male when he was first observed, immediately prior to making his approach to the female. These initial orientations were categorized as one of six relative spatial positions: (1) her left flank, (2) her right flank, (3) under her, (4) behind her, (5) above her, or (6) ahead of her. The male's orientation to the female during sexual approach was defined as the position of the male relative to the female at his point of closest approach (from < 1 m away to physical contact). As with the initial orientation positions, these possible proximate positions included her left flank, her right flank, under her, behind her, above her, or ahead of her. The male's aerial behavior was categorized by his approximate position relative to the surface when he was closest to the female: aerial (> 1/3 of the male's body above the surface), at surface (≤ 1/3 above the surface), or under water (the male was completely submerged).

Calves were defined as individuals ≤ 2/3 body length of an adult that maintained a position proximate to a presumed female, usually swimming in echelon formation by the adult's mid-lateral flank (Gubbins et al., 1999). Due to their rapid growth rate, we did not distinguish juveniles/subadults from adults. We documented when a sexual approach temporarily separated a calf from its mother.

Results

We recorded 144 sexual approach events between 1 January 2010 through 15 January 2018 of which 110 were captured exclusively on digital SLR cameras, 23 were captured exclusively on video, and 11 events were captured on both digital SLR cameras and videos. The typical duration of a mating event was 1 to 2 s based on analysis of 34 videos (see example sexual approach videos in the "Supplementary Material" section of the *Aquatic Mammals* website: https://www.aquaticmammals journal.org/index.php?option=com_content& view=article&id=10&Itemid=147).

The sex of one or both of the individuals comprising the mating pairs was confirmed in 55% ($n = 80$) of all events, and both the male and female were known in 13% ($n = 19$). Males extruded their penises (either fully or partially erect) in 60% ($n = 58$) of 96 sexual approaches. Penis extrusions in the remaining 48 of 144 events could not be determined because the view was blocked by the animals' bodies or by splashes. In 14 events, the male's penis was visible as he approached a female with a calf. In an additional five events, we were able to determine the sex of both animals because they were photo-identified as uniquely marked, and their sex was confirmed in other mating events. The results of the 19 events in which the sexes were known and the 58 events involving known males are available in summary form in Supplementary Tables 1 and 2 (tables are available in the "Supplementary Material" section of the *Aquatic Mammals* website: https://www.aquatic mammalsjournal.org/index.php?option=com_ content&view=article&id=10&Itemid=147) and were similar to those of our full dataset. Therefore, the following results are reported for the total 144 mating events, and the terms *male* and *female* include both confirmed and presumed members of the sex.

Sexual Approaches

Males initiated all mating events. Copulatory attempts consisted of rapid, high-energy sexual approaches in which males accelerated toward females, usually from 1 to 4 s (maximum 10 s) prior to contact. Males engaged in copulatory attempts in 87% of mating events ($n = 125$), and males contacted the females in 74% of events ($n = 106$). Male displays accounted for the remaining 13% of mating events ($n = 19$). Of these displays, 58% ($n = 11$) consisted of postures in which males
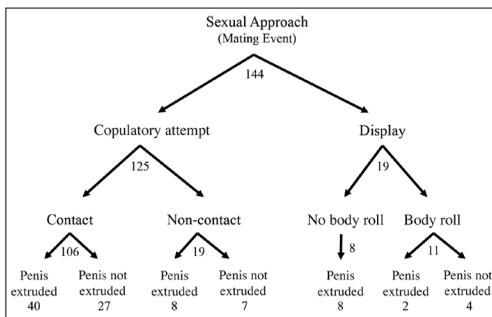

Figure 1. Schematic chart of sexual approach types exhibited by male harbor porpoises (*Phocoena phocoena*); numbers refer to behaviors recorded based on a total of 144 mating events of which 96 events could be assessed for penis extrusions (*bottom row*).

Figure 2. Sexual approach types by male harbor porpoises: (a) Contact attempt with penis extruded, 28 August 2011; (b) display with body roll and penis extruded, 2 July 2010; (c) aerial behavior with penis extruded, 22 April 2010; (d) aerial behavior with tip of penis visible near male's right flipper, 15 May 2011; (e) underwater approach with tip of penis extending to female's right side, 7 October 2011; (f) intromission achieved after male approached female with neonate calf, 2 July 2010; (g) probable copulation, with penis in contact with female's genital area, 4 December 2017; and (h) mating event including extraneous adult and a calf momentarily separated from its mother by a male, 23 February 2016. See enlarged views of each of these approach types in the "Supplemental Material" section on the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.
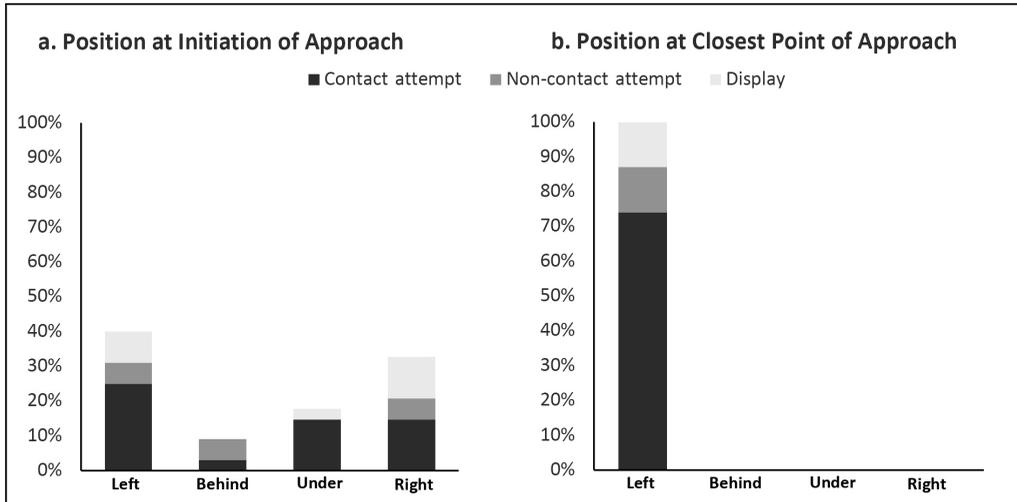
Figure 3. Percent of sexual approach types by harbor porpoises compared for (a) their positions at initiation of approach (n = 34 videos) and (b) their positions when closest to the target harbor porpoise (n = 142 still photos/videos). The four columns correspond to positions (approach vectors) relative to the target harbor porpoise: (1) left side, (2) right side, (3) behind, and (4) under. Positions in front of and above the target porpoise are not displayed because their values are zero in both charts.

rolled their bodies to present the ventrum toward the females (with or without extruding the penis), and 42% (n = 8) were penis extrusions without an accompanying body roll. Penis extrusions did not vary significantly between contact attempts, non-contact attempts, and displays ($\chi^2 = 3.98$, $df = 2$, ns). Photographed examples of sexual approach types appear in Figure 2.

Based on analysis of the 34 videos, male harbor porpoises beginning their sexual approach were initially observed on the female's left in 41% (n = 14) of mating events, on her right in 32% (n = 11) of the events, under her in 18% (n = 6), and behind her in 9% (n = 3) (Figure 3a). No approaching harbor porpoise was initially observed above or in front of a female. Regardless of the location at the initiation of his sexual approach, the male was positioned on the female's left side in 100% of mating events at his closest point to her (n = 142 events in which his position could be assessed by still photos or videos; Figure 3b). Males initially positioned on the female's left side made contact in 45% of events, while males initially positioned on the female's right side made contact in 33% of events.

Males were significantly more likely to time their sexual approaches to contact females at the surface than when females were under water ($p <$ 0.0001, Fisher's exact test; Figure 4). Of the 102 contact attempts that could be assessed for this parameter, 95% (n = 97) occurred as she was at the surface, and 5% (n = 5) occurred when she was

under water. Of 18 displays, 50% (n = 9) took place at the surface, and 50% (n = 9) were under water.

Males frequently exhibited aerial behaviors at the termination of their rapid sexual approaches (Figure 2c & 2d). In some cases, they executed full-body breaches as they leaped clear of the water. The presence or absence of aerial behavior differed significantly by approach type (χ^2 = 34.94, $df = 2$, $p <$ 0.0001). Of the 142 events for which this behavior could be assessed, males were observed to be aerial in 60% (n = 85), at the
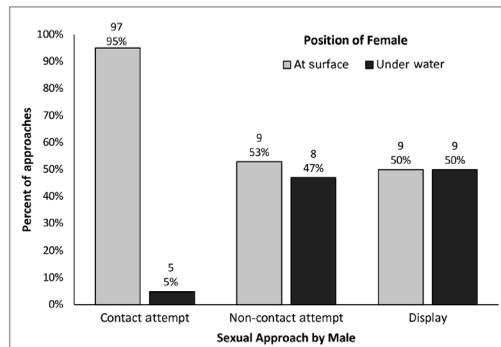

Figure 4. Percent of sexual approach types by male harbor porpoises compared for females at the surface and under water (Fisher's exact test, $p <$ 0.0001); values above percentages are the numbers of mating events that could be assessed by still photos or videos (n = 137).

surface in 25% (*n* = 35), and under water in 15% (*n* = 22). Of the 123 copulatory attempts, 69% involved aerial behavior (*n* = 85). No displays involved aerial behavior (Figure 5).

We were able to photographically document two copulations. In one mating event, intromission was achieved as the copulating pair was positioned crosswise at the surface, with the male upside-down and his ventrum against the female's left flank as she rolled left. The shaft of the male's penis was angled to his left as the tip of the penis was inserted in her urogenital opening (Figure 2f). The duration of this event, from first contact to
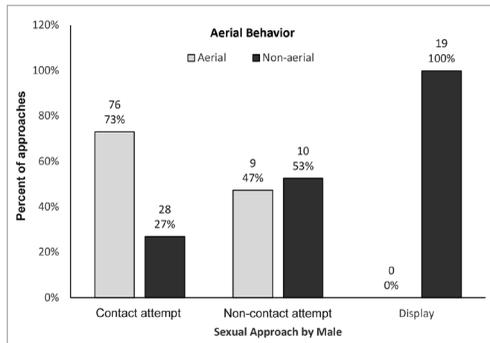

Figure 7. Harbor porpoise sexual events throughout the year, comparing percentages of days in which mating was recorded to all days in which harbor porpoises were sighted (2010 to 2018); mating days were analyzed to eliminate pseudo-replication introduced by multiple mating attempts in succession. Whiskers indicate inter-annual variation SEM.

Figure 5. Percent of sexual approach types by male harbor porpoises compared for their aerial and non-aerial (surface/underwater) behavior (χ^2 = 34.94, *df* = 2, *p* < 0.0001); values above percentages are the numbers of mating events that could be assessed by still photos or videos (*n* = 142).
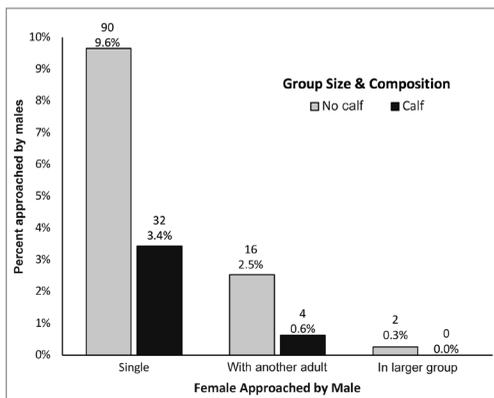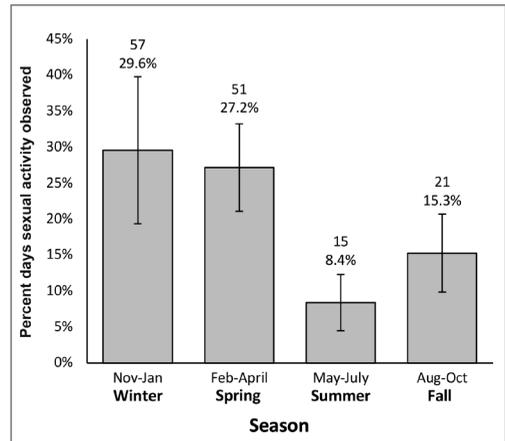

Figure 6. Percent of females sexually approached by males compared for females (with and without calves) that were single, in groups with one other adult, or in larger groups with two or more adults; percentages are based on harbor porpoise sightings from 2010 to 2018 (*n* = 2,328) and assume a 1:1 sex ratio for individuals sighted without calves. Values above percentages are the numbers of mating events (*n* = 144).

separation, was approximately 2 s. A different event involving probable copulation occurred when the male first contacted the female on her left flank with his ventrum, and then maintained contact with his penis while the female reacted by lifting her flukes out of the water. The erect penis was at a right angle to the male's body, and the female's genital area was slightly distended (Figure 2g). For all mating events observed, it was not possible to determine whether males ejaculated.

Group Dynamics
Only lone males approached females. Lone females (62.5%; *n* = 90 of 144 mating events) were approached more often than females with calves (25.0%; *n* = 36). In 18 events (12.5%), one to three extraneous adults of unknown sex were observed in the groups (Figure 2h). Multiple males were never observed attempting to copulate with the same female simultaneously or consecutively. The number of lone females, females with calves, and females near extraneous adults approached by males differed significantly compared with the 2010 to 2018 survey data (χ^2 = 115.45, *df* = 2, *p* < 0.0001; Figure 6).

In some instances, a male was observed making repeated sexual approaches toward a female. In eight occurrences, a male made multiple attempts to mate with the same female in succession, totaling 19 mating events. In one of those occurrences, an individual photo-identified male also approached three different females in succession.

Of the 36 mating events in which a calf was present, only one calf was present per group. In 33 events, calves were in close proximity to their mothers and positioned on their mothers' left (*n* = 16) or right (*n* = 17) sides. Calves positioned on the left side were temporarily separated by the male's approach 88% of the time (14 of 16 events; Figure 2h). In the two events when calves were not separated while on the left, the males' sexual approaches consisted of underwater displays only. Calves positioned on the right side of their mothers were not separated during mating activity. Males made no sexual approaches to calves and usually ignored their presence. In a single instance, a male drove a calf away from its mother before pursuing her.

Seasonality

Mating events were observed in all months except June, when fog was prevalent in the Golden Gate, limiting visibility and research effort. The percentages of days in which mating was recorded were compared to all days in which harbor porpoises were sighted and binned by season (Figure 7). Mating days, rather than mating events, were analyzed to eliminate pseudo-replication introduced by multiple mating attempts by the same male in succession. Variable search effort on the Golden Gate Bridge was mitigated by comparing mating data to harbor porpoise counts collected during an 8-year census (2010 to 2018) with overlapping dates. The frequency of mating events varied significantly between seasons with peaks in spring (April to June) and autumn (October to December; $\chi^2 = 26.01$, *df* = 3, *p* < 0.0001). However, the male's sexual approach (copulatory attempt or display) did not vary significantly by season ($\chi^2 = 24.07$, *df* = 3, ns).

Discussion

We present the first systematic description of male harbor porpoise mating patterns in a free-swimming population. Strikingly, males approached females on the female's left sides in every copulatory attempt. Males engaged in high-energy, rapid, precision-timed sexual approaches that often involved aerial behavior, which has been reported rarely for other harbor porpoise populations. Rather than physically competing with other males, male approaches were performed individually and were energetically demanding.

Sexual Approaches

During their high-speed approaches, males always targeted the female's left side. If a male initiated an approach while on the female's right side, he actively switched sides to attempt contact on her left side or engage in a display on her left side. This unusual and unvarying laterality in sexual approach has not been reported in cetaceans. The left-sided approach by males may be driven by anatomical co-evolution with females (Dixson & Anderson, 2004; Orbach et al., 2017). The large vaginal fold in the spiral-shaped harbor porpoise vagina inhibits penetration of the penis (Orbach et al., 2017). Laterality of penis penetration, as well as speed and force, may enable males to overcome mechanical barriers during copulation. Other types of lateralized behavior are well-known in cetaceans, particularly those associated with feeding (MacNeilage 2014; Friedlaender et al., 2017), swimming (Platto et al., 2017), or visual preference (Karenina et al., 2010). A study of skeletal asymmetry revealed that harbor porpoises of both sexes have more robust right flippers compared to left flippers, which may reflect usage (Galatius, 2005a).

Male sexual contact with a female tended to occur when she surfaced briefly, presumably to limit her maneuverability by trapping her against the surface. Similar behavior has been reported in other species such as dusky dolphins (*Lagenorhynchus obscurus*; Markowitz et al., 2010; Orbach et al., 2015). Male harbor porpoises did not force females to the surface prematurely but contacted the females the moment they surfaced as part of their normal respiratory pattern. Females typically responded to sexual approaches with a suite of behaviors such as body rolls, fluke lifts, peduncle curls, dives, and directional changes (Orbach et al., in press).

The energetic mating performance exhibited by males did not conform to the harbor porpoises' well-known tendencies for inconspicuous behavior. In our study, aerial behavior was observed in 73% of contact attempts and was not observed outside of sexual contexts. Aerial behavior appeared to be the consequence of the forceful approaches to females. Marked splashing was caused by the males falling back to the surface and by high-intensity evasive responses by the females (e.g., rapid aggressive fluke lifts). Males were never seen to execute a smooth head first re-entry and, instead, hit the water hard on their ventrum or flanks. Aerial or lateralized mating behaviors have not been noted in captive harbor porpoises (Andersen & Dziedzic, 1964; Desportes et al., 2003; Delgado-García, 2009), although Desportes et al. (2003) characterized the male's initial sexual approaches to the female as short, "violent" contacts that de-escalated over time into slower approaches with "softer" contacts.

In contrast to the aerial displays associated with copulatory attempts, sexual displays did not result in such conspicuous behavior. Male displays

involved rolling the pale ventrum toward the female, extruding the penis near her, or a combination of both actions. The body roll displays were similar to the "belly-exposures" seen in captive harbor porpoises (Andersen & Dziedzic, 1964). These displays may be executed to test female receptivity or induce positive responses. Other cetaceans are known to extrude their penis prior to copulation, including Atlantic white-sided dolphins (*Lagenorhynchus acutus*; Nelson & Lien, 1994) and sperm whales (*Physeter macrocephalus*; Gordon et al., 1998), perhaps as a sexual display for mate choice. Genital signaling may also be associated with male–male agonism as found in some primates (Henzi, 1985; Miller, 2010).

Copulations were photographed twice. The male's dorsal penis-to-ventral vagina orientation during intromission (Figure 2g) is consistent with a prediction for the best genital fit in this species (Orbach et al., 2017). The low number of copulations observed undoubtedly underreports the actual rate since the bridge platform did not afford lengthy focal follows; and depending on the angle of view and amount of splashing, intromission would not always be visible. Our observations were possible because harbor porpoise mating occurred at or near the surface, but some mating events or other social interactions may occur at depth.

Group Dynamics
Extraneous adults were seen on the periphery of mating events, but none of them interfered with the mating males, nor did they sexually approach the females. No contest competition was observed, providing some validation of the prediction that harbor porpoise males do not fight each other (Fontaine & Barrette, 1997). Males occasionally approached one or more females repeatedly, consistent with predictions about mating strategies based on sperm competition (Gomendio et al., 1998). Males are smaller than females and presumably more maneuverable. Males did not herd or coerce females, and there was no evidence of mate guarding as exhibited by male Dall's porpoises (*Phocoenoides dalli*; Willis & Dill, 2007).

Males targeted single females primarily, and females with a calf less often. Unlike some other toothed whale species in which calves are segregated from intense mating activity (e.g., dusky dolphins; Weir et al., 2008), harbor porpoise calves remained near the adults. The mother–calf pair was frequently and briefly separated by approaching males when calves were positioned on their mothers' left sides. Calves exhibited limited responses to the male's presence besides moving away from their mothers. Mothers did not protect their calves from approaching males.

Males generally ignored the presence of calves; however, the only aggressive interaction observed in our study was an instance in which a presumed male charged and drove away a calf.

Our presumptions that males initiate sexual approaches and females are the targets of those approaches were supported by behaviors recorded for 19 events in which both sexes were distinguished, as well as for the 58 events involving males with an extruded penis (Supplementary Tables 1 & 2). Given the preference for using a larger sample size, we analyzed the results of our full set of observations. Some statistics presented, such as seasonality, did not depend on assigning sexes to the animals involved. In the majority of the 144 mating events, the sex of the harbor porpoise approached by a male was not confirmed but was presumed female, leaving open the possibility that some of the targeted harbor porpoises were male.

Homosexual behavior is widespread in the animal kingdom (Sommer & Vasey, 2006) and is frequently observed in bottlenose dolphins in captivity (Östman, 1991) and in the wild (Mann, 2006). Both male and female captive harbor porpoises engage in non-reproductive homosexual behavior, although sexual approaches are largely initiated by males (Andersen & Dziedzic, 1964; Amundin & Amundin, 1971 [a study consisting of males only]; Delgado-Garcia, 2009). In our study, no sexual approaches were made toward a harbor porpoise that had an extruded penis, and there were no groups in which two penises were visible. No males displayed agonistic behavior toward another male, underscoring a difference in social structures between the sperm competitor harbor porpoise and the contest competitor bottlenose dolphin, a species featuring complex male–male alliances and rivalries (Connor, 2007). However, some of the sexual approaches we observed may have social dimensions beyond reproductive utility, particularly those that occurred outside the breeding season.

Seasonality
Despite evidence for regression of testes size and a synchronized reproductive cycle in harbor porpoises, we observed mating activity year-round (Figure 7). Mating activity was unexpectedly low for the summer calving/breeding season (May through July). This may reflect a sampling bias attributed to weather and limitations of the Golden Gate Bridge platform. Mating events, including penis extrusions, were commonly observed in the winter when harbor porpoise testes are apparently inactive (Neimanis et al., 2000). Mating activity outside the breeding season may involve young, inexperienced individuals honing the

skills needed to successfully copulate during the breeding season. Gaskin et al. (1984) reported sexual behaviors exhibited by immature Atlantic harbor porpoises from May to September, a period longer than the short summer breeding season. At Fjord & Bælt, one study recorded attempts by an immature male harbor porpoise to mate during the winter and spring when his testosterone levels were low (Desportes et al., 2003), although a later 2-mo study recorded no mating activity among one male and three females during December and January (Delgado-García, 2009). As male mating behavior is a high-intensity performance, year-round practice of approach maneuvers with correct timing could be important even for mature males.

This study yields insights into the sex life of harbor porpoises that may be helpful in designing conservation practices. Harbor porpoise social behavior in the wild is rarely reported, yet mating activity was seen repeatedly from the Golden Gate Bridge. By comparison, observers (including WK, MAW, and IDS) on dedicated boat-based harbor porpoise surveys in the adjacent Gulf of the Farallones visually encountered 639 harbor porpoises over a 3-year period and detected no signs of mating (Calambokidis et al., 1990). The relatively high rate of mating events seen in the Golden Gate may be an indicator of its importance as a social hotspot for the local stock of harbor porpoises. Researchers should be cognizant that aerial behavior may be a sign of mating activity wherever harbor porpoises aggregate.

Acknowledgments

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