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Mating Behaviors Exhibited by a Captive Male Pacific Walrus (*Odobenus rosmarus divergens*)

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The population of the Pacific walrus (*Odobenus rosmarus divergens*) is currently a topic of conservation efforts. Understanding the mating behaviors of a species can be utilized in conservation efforts to preserve the species. Little is known about the behavioral repertoire of Pacific walruses, due to their isolated Arctic habitats, with limited studies previously describing observations of walrus mating behaviors. The aim of the present case study was to observe the mating behaviors of a single captive male Pacific walrus to examine overall frequency of specific mating behaviors in both social and solitary contexts. The subjects, one male and two females, were recorded at Six Flags Discovery Kingdom from November 2013 through January 2014. Only behaviors exhibited by the male walrus directly associated with mating were noted. Grabs were the most frequently observed behavior, and holds were not significantly observed which could contribute to the infrequent successful copulation attempts. Pharyngeal sac inflation, a vocal and visual behavior, was not frequently observed in a sexual context but has been observed in mating contexts in the wild. The male walrus used other sexual outlets such as self-gratification and toy use; however, these behaviors occurred significantly less than sexual encounters with females. There appeared to be a mate preference for the female with tusks, as the male interacted significantly more with the tusked female compared to the non-tusked female who was in estrus. Studying mating behavior in controlled settings such as this can be revealing of the capabilities of the species as a whole. Understanding more about how walruses interact in their environment can be used for future management and breeding strategies.

Sexual behaviors and reproductive abilities are a subject of interest in multiple species ranging from flies (*Drosophila paulistorum*; Ehrman, 1960) to rhesus monkeys (*Macaca mulatta*; Kaufmann, 1965). Successful breeding (i.e., the production of viable offspring) is essential for a species' survival as the inability to reproduce successfully can result with population decline. In Arctic species, changes in the environment can affect opportunities for reproduction and subsequently population decline. For example, the marked loss of sea ice in the Arctic corresponds with the population decline of the polar bear (*Ursus maritimus*; Post & Brodie, 2012; Post et al., 2009). Other native Arctic species unable to adjust to deviations from their normal habitat conditions may similarly be at risk for population decline and possible extinction (Plesnar-Bielak, Skryznecka, Prokop, & Radwan, 2012; Post & Brodie, 2012). In particular, there is increased concern for conservation efforts for the Pacific walrus, as the species is hypothesized to suffer population loss through the end of the century due to the continued and increased loss of sea ice in the Arctic Ocean (Jay, Marcot, & Douglas, 2011).

The Pacific walrus habitat range includes the continental shelf of Arctic and subarctic waters in the Bering and Chukchi seas (Fay, 1982; Jay et al., 2011). Pacific walrus population trends have fluctuated markedly in the 19th-20th centuries. Prior to commercial hunting, population numbers were estimated to be minimally 200,000 walruses (Fay, 1982). Continued human exploitation caused population levels to drop to approximately 50,000 prior to 1950 (Fay, Eberhardt, Kelly, Burns, & Quakenbush, 1997; Fedoseev, 1962). Between 1950 and 1970, commercial hunting decreased while population growth steadily increased until reaching what researchers believe to be carrying capacity, evidenced by an expansion of habitat range (Estes & Gol'tsev, 1984; Fedoseev, 1982; Gol'tsev, 1972; Pinigin & Prianishnikov, 1975) and physical changes (Fay &

Kelly, 1980; Fay, Kelly, & Sease, 1989; Sease, 1986). Researchers predicted populations of Pacific walrus to decline in the 1980s onward due to reaching carrying capacity, yet there had not been any time-series assessments to determine such population affects during that time period (Speckman et al., 2011).

In 2006, an aerial survey model incorporated thermal imaging and increased spatial resolution to detect group (Burn, Webber, & Udevitz, 2006; Udevitz, Burn, & Webber, 2008) and individual (Jay et al., 2006) haul-out sites as well as walrus in the water. The survey estimated the number of Pacific walrus to be 130,000 walrus, a considerably lower estimate compared to prior surveys in the 1970s (Speckman et al., 2009, 2011). However, haul-out site dependent surveys are limited to walrus that are hauled out at the time and are affected by continued sea ice loss due to climate change (Post & Brodie, 2012). Speckman et al. (2011) state that there is likely a high degree of variability as to the exact number of walrus present during the survey period. Recently, Jay and colleagues (2011) utilized a Bayesian network model to integrate how the changing environmental and anthropogenic factors will affect Pacific walrus population trends throughout the remainder of the century. Their results indicated a steady trend of worsening walrus outcome probabilities, increasing from a current 10% probability to approximately 40% by 2095. While this estimated model determines the environmental stressors that largely contribute to this projected trend, the authors conclude that the influence of other stressors is not well-understood due to how little we currently know about the walrus behavioral repertoire, such as their reproductive behaviors. Examining factors that contribute to breeding in walrus, such as genetics and behavioral functions, may assist with sustaining populations (Lacy, 2013).

Walrus are one of the largest species of pinnipeds, distinguishable by their enlarged canines, or tusks (Fay, 1982; Muraco, Coombs, Procter, Turek, & Muraco, 2012; Riedman, 1990). Male tusks are short and thick, whereas female tusks are long and slender (Fay, 1982; Riedman, 1990). Pacific male walrus can be twice the body size of female Pacific walrus, with males typically weighing around 1,200 kg and females 830 kg (Fay, 1982; Riedman, 1990). Walrus become sexually mature at approximately 10 years of age for females and 15 years for males in wild populations. In captivity, walrus have been noted to reach sexual maturity sooner, with females capable of reproducing around 5-6 years of age and males around 8-10 years of age (Fay, 1982). Mating season for the Pacific walrus is directly associated with the maximum testes size reached by the male due to spermatogenesis, typically during the first few months of the year (i.e., January through March) in wild populations (Fay, 1982; Fay, Ray, & Kibal'chich, 1984) with calving occurring from April-June (15-16 months of gestation; Fay, 1985). However, breeding season has been observed at various times of year for captive populations (Fay, 1982).

Pinniped species exhibit a variety of mating behaviors with shared similarities and individual differences present. For example, Antarctic fur seals (*Arctocephalus gazella*) appear to show mating preferences for mothering Antarctic fur seals as opposed to females without pups (Hoffman, Boyd, & Amos, 2003). In addition, a single male southern elephant seal (*Mirounga leonina*) may defend hundreds of females to prevent other males from having mating opportunities (de Bruyn et al., 2011; Carrick, Csordas, & Ingham, 1962). Most pinniped species including the walrus are polygynous, meaning individuals mate with multiple partners throughout their lifespan (Fay, 1982, 1985; Fay et al., 1984; Kastelein, 2009; Riedman, 1990). A lek is a polygynous mating arrangement that has been observed with Pacific walrus and other pinniped species. Leks consist of dominant males having primary access to surrounding females while subordinate males lie outside of the group. In the Pacific walrus, breeding males in a lek migrate to groups of females hauled out on ice floes (Fay et al., 1984) with copulation occurring in the water as opposed to on land/ice floes (Fay et al., 1984; Jay et al., 2011; Sjare & Stirling, 1996).

While little is known about underwater mating behaviors, several sexual behaviors visible from the surface have been noted in walrus subspecies. For example, Sjare and Stirling (1996) suggest that if a male

Atlantic walrus (*Odobenus rosmarus rosmarus*) appears with its back bent and visible above water accompanied by foreflippers gripping a female, this may visually indicate a copulation attempt. In Pacific walruses, mating displays previously noted in the literature include males producing vocalizations above and below the water, hypothesized to attract females (Fay, 1982; Fay et al., 1984; Riedman, 1990). Fay (1982) described these vocalizations as successions of differing thumps, whistles, and pulses, neglecting to report specific frequency parameters. In addition, Pacific male walruses have displayed inflated pharyngeal sacs around the same time some of these vocalizations were produced. However, there has yet to be conclusive evidence as to whether pharyngeal sac inflation is linked to any vocalizations that occur during mating displays (Fay et al., 1984).

The literature regarding mating behaviors in the Pacific walrus is currently limited to only descriptions of acoustic behaviors and a few surface observations. More detailed observations of visual (i.e., non-acoustic) walrus mating behaviors in the wild have been difficult to record due to the remoteness of the walrus habitat and difficulty to record underwater behaviors (Fay, 1982; Muraco et al., 2012). Observing mating behavior in a captive walrus population can provide an opportunity to fill the gap in knowledge about the walrus mating behavior repertoire. While walruses have been housed in captivity for several decades, there have been less than 15 recorded births in North America (Muraco et al., 2012). Muraco et al. (2012) attempted to artificially inseminate a single ovulating captive female Pacific walrus with sperm from a captive male Pacific walrus that was treated with hormones to prompt spermatogenesis, but no further study of walrus mating in captivity has been reported.

Utilizing only one male and one female captive walrus pair housed at Six Flags Discovery Kingdom in Vallejo, California, Muraco et al. (2012) illuminated valuable information on walrus reproduction which could be used for conservation and managerial strategies. For example, the researchers observed the rut period (i.e., mating susceptibility and receptiveness) of the captive male occurred later (February through May) than previously reported for wild male walruses (January-March; Fay 1982, Fay et al., 1984). However, the captive female walrus's cycle was consistent with previously reported literature on wild females (Fay, 1982; Muraco et al., 2012). Muraco and colleagues (2012) were able to use human chorionic gonadotropin to manipulate the male's rut to sync with the female ovulation, leading to pregnancy. One explanation for the delayed rut time observed for the male was the difference in timing of photoperiods in California where the walruses were housed compared to the habitat range in the Arctic (Muraco et al., 2012). This study serves as a valuable example of how examining a sole male subject (i.e., single case design) can provide pertinent information on walrus reproduction and insight for managerial strategies.

The present study sought to record and to define possible mating behaviors exhibited by a single captive male Pacific walrus. As shown by the findings from Muraco et al. (2012), a single case design can provide pertinent information on walrus mating and can be replicated by other facilities to examine similar issues or trends with mating. Frequency of specific behaviors, particularly those associated with copulation, and male sexual outlet choice was important to observe for likelihood of successful copulation with a female. Although never previously assessed in walruses, evidence of male mate preference was examined to determine if mate choice affected successful copulation attempts or mating behavior frequency. Identifying issues with mating in captivity for this species could provide a basis for future studies and aid with managerial decisions (e.g., recognizing trends or absences of behavior, selecting individuals for breeding loans or artificial insemination, creating and/or conserving environments ideal for mating) that could have implications for both captive and wild walruses.

Method

Subjects

The single male Pacific walrus focal subject (Sivuqaq) was housed with two additional adult female Pacific walruses (Siku and Uquq). All subjects were rescued after being orphaned as pups in 1994 and were unrelated to one another. The walruses were each estimated to be 19 years of age during the study period and were the only walruses housed at Six Flags Discovery Kingdom located in Vallejo, California, USA. Each walrus was distinguishable from the others (Figure 1). The male, Sivuqaq, has the shortest tusks, weighed approximately 1,400 kg during the study, and has a permanent light circular mark anterior to the right hindflipper. The two females, Uquq and Siku, weighed approximately 816 kg each and are discernable by Uquq having tusks and Siku lacking tusks, which were removed due to infection at an early age. During the time of the study, the animal care staff noted Siku as being in estrus due to behavioral observations. Sivuqaq (male) and Uquq (tusked female) were the single walrus pair subjects in Muraco et al. (2012).



Figure 1. Pacific walruses housed at Six Flags Discovery Kingdom in Vallejo, California. From left to right: Sivuqaq, Siku (no tusks), and Uquq. Photo credit: Nancy Chan, Six Flags Discovery Kingdom

Data Collection

The video footage was collected by staff members of Six Flags Discovery Kingdom daily from November 15, 2013 through January 31, 2014 (e.g., when the male was reported to be most sexually active). Approximately one hour of video footage was recorded per day during the study period (usually between 10:00 a.m. and 3:00 p.m.) and viewed in 20-min segments. All data was collected opportunistically at the discretion of animal care staff. Videos were recorded with surface audio accompanied by simultaneous underwater acoustic recordings from a hydrophone that was placed in the exhibit pool. The video camera (Canon VIXIA HF R400) was stationed outside the public walrus viewing tank area at Six Flags Discovery Kingdom and angled towards the water portion of the tank only, which holds approximately 644,731 L of water. The view from the tank window allowed the researchers to view both underwater surface behaviors. Video recordings often overlapped with park operational hours, so park guests could also be seen around the viewing area at times. All three walruses had access to the front pool recorded in the data. However, all walruses had access to the front land area of the exhibit, the back holding pool, and back land area, where video observation was not available. There were 203 videos collected, totaling 66 hrs, 48 min, and 20 s of data.

Procedure

All video data was coded using all-occurrence sampling for mating behaviors exhibited by the male walrus both with the females and when engaging in self-gratification through another outlet (see Table 1 for ethogram). Only behaviors displayed by the male Pacific walrus were noted, except for when the male was interacting with either female, Uquq or Siku. Sexual encounters were classified by the male walrus initiating a grab, roll, and/or hold with a female, but one encounter could include multiple occurrences of these behaviors (i.e., a grab could be directly followed by a roll then a hold). Sexual encounters could also be accompanied by tusk strikes or nuzzles. These encounters were further categorized by interaction with either female, distinguishable by presence of tusks (Uquq) and the female lacking tusks (Siku), to assess if the male exhibited a sexual mate preference. Sexual behaviors not associated with the females were noted to examine if there was a preference for sexual outlet. Pharyngeal sac inflations (PSI) often accompanied sexual behaviors both with females as well as without. Pharyngeal sac inflations was categorized as sexual when accompanied by sexual behaviors across contexts (i.e., toy use, female encounters, self-gratification) and non-sexual when observed with no sexual behaviors present (i.e., male could be stationary or swimming without interacting with female(s), toy, self, and without exposed penis). The sound mostly occurred in sequence of twos before a break and any following PSI if behavior was repeated; however, an individual PSI could consist of one cycle or more than two cycles before a break of no vocalization.

Video footage was sometimes collected during periods of Six Flags Discovery Kingdom operation hours and thus open to the public. Presence of park guests could potentially influence the behaviors observed, thus it was noted when coding if people were present (e.g., not animal care staff the walruses would potentially see on a routine basis). Presence of park visitors was noted by day and not for specific instances with behavior. Environmental conditions of the enclosure were also noted daily (i.e., if a toy was present in the pool). All behavioral occurrences were categorical data; thus, non-parametric chi-square omnibus tests were used to compare (1) the frequencies of each behavior, (2) male mate choice selection, and (3) sexual outlet utilized (Sharpe, 2015). Residual post hoc tests were completed to further examine each behavior and determine individual significance of occurrence (Sharpe, 2015). Permission for this methodology was approved by the Institutional Animal Care and Use Committee at the University of Southern Mississippi in Hattiesburg, Mississippi, USA.

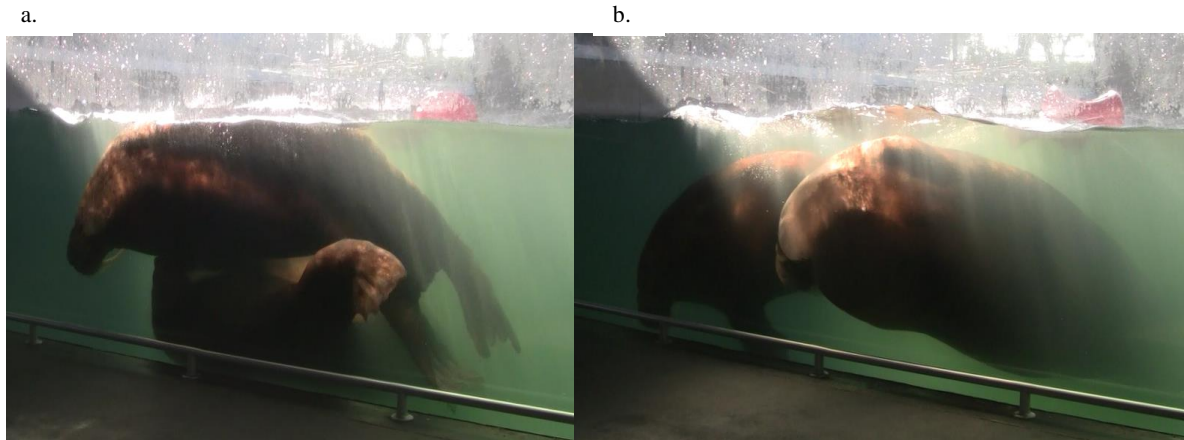


Figure 2. (a) Male Pacific walrus initiating a roll behavior starting from underneath and (b) sliding around the side of a female Pacific walrus.



Figure 3. Male Pacific walrus maintaining a hold behavior with both foreflippers around sides of female Pacific walrus.

Table 1
Operational Definitions of Coded Mating Behaviors

| Behavior | Operational Definition |
|------------------------------------|--|
| Sexual Encounters | |
| Grab | Male actively attempting to place foreflippers on sides of female; could be initiated from (1) above, posterior to female (2) below with female in neutral dorsal position and male ventral side up (3) from either side of the female |
| Roll | Male takes a female walrus from underneath and slides along the side of the female until the male is positioned upright posterior to the dorsal side of female (Figure 2) |
| Hold | Male maintains position posterior to female with both foreflippers secured around the sides of the female; state at which copulation most likely to occur (Figure 3) |
| Tusk strike | Jabbing the tusks downward upon or towards a female; denoted as (1) sexual – occurring during a sexual encounter (2) nonsexual – no apparent relation to a sexual encounter |
| Nuzzle | Male snout pressed against and moving around female during a hold |
| Sexual Outlet | |
| Toy use | Male placing enrichment item over or directly in front of genitals (Figure 4) |
| Self-gratification | Male placing both foreflippers around genital area or holding erected penis; could be accompanied by notably shaking while floating at water level (Figure 5) |
| Standalone Sexual Behaviors | |
| Penal exposure | Male walrus noticeably had an erect penis; could be observed during sexual encounters, while engaging with other sexual outlets, paired with pharyngeal sac inflation, or by itself (Figure 6) |
| Pharyngeal sac inflation (PSI) | Visual and audible behavior consisting of neck area of male expanding, release of bubbles from mouth, and concurrent with vocal resembling scraping of washboard followed by hitting a gong |

Note. Adapted from Fay, 1982; Fay et al., 1984; Sjare & Stirling, 1996.



Figure 4. Male Pacific walrus with blue ring enrichment item over genitals engaging in sexual toy use.



Figure 5. Male Pacific walrus exhibiting self-gratification by grabbing erect penis.



Figure 6. Male Pacific walrus floating in pool with exposed penis.

Results

The male exhibited a preference in mate selection, $\chi^2(1, N = 68) = 39.77, p < 0.001$ being significantly more likely to interact with the female with tusks, Uquq (*std residual* = 4.459), and less likely to interact with non-tusked female, Siku (*std residual* = -4.459; Figure 7). There was an overall significant difference in the frequencies of specific behaviors grab ($n = 58$), roll ($n = 21$), hold ($n = 34$), nuzzle ($n = 21$), and tusk strike, ($n = 37$), $\chi^2(4, N = 171) = 26.98, p < 0.001$. The male was significantly more likely to grab (*std residual* = 4.07) and significantly less likely to roll (*std residual* = -2.26) or nuzzle (*std residual* = -2.26) a female (Figure 8). Frequencies of hold (*std residual* = -0.03) and tusk strikes (*std residual* = 0.48) were not found to be significant.

Sexual encounters initiated by the male were combined for both females and compared with male self-gratification and sexual toy use to test for preference of sexual outlet, $\chi^2(2, N = 107) = 48.02, p < 0.001$; Figure 9). The male was more likely to engage in mating behaviors with the females (*std residual* = 5.41) than exhibit self-gratification (*std residual* = -4.13); toy use was not found to be significant as a sexual outlet (*std residual* = -1.28).

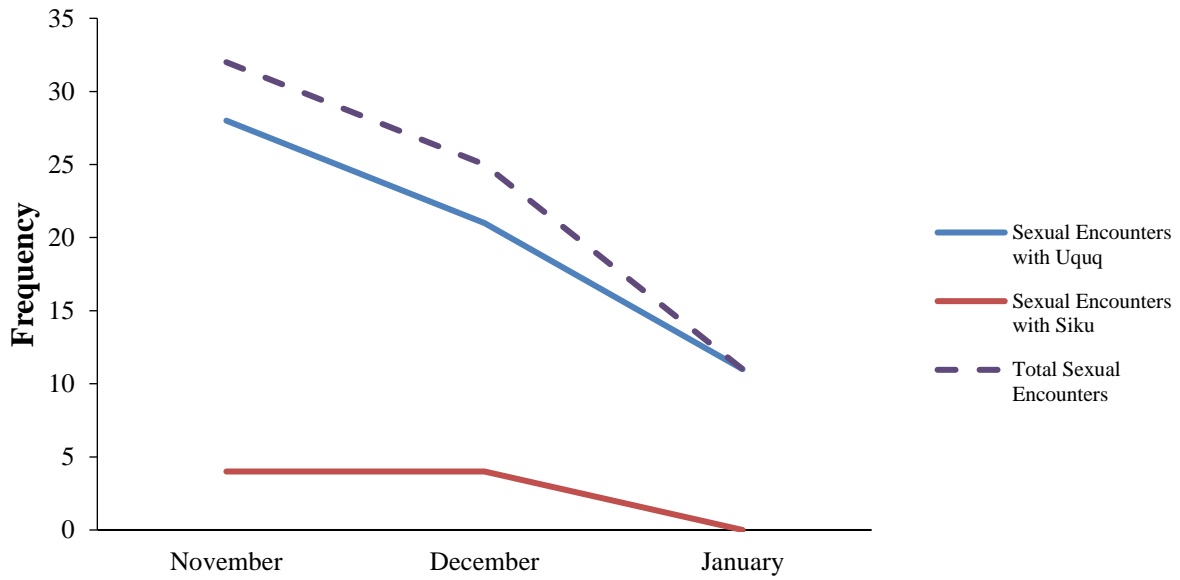


Figure 7. Frequencies of sexual encounters between the male and Uquq (tusked female) or Siku in comparison to the total sexual encounters observed.

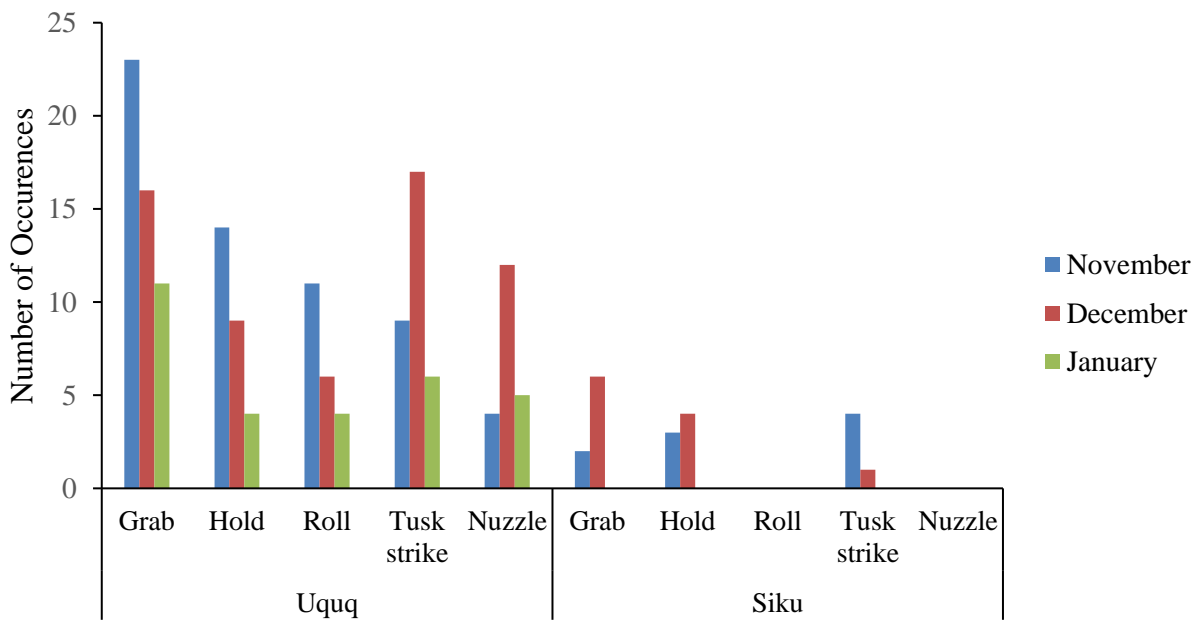


Figure 8. Frequency comparison for the occurrence of each mating-associated behavior performed by the male with females Uquq (tusked female) and Siku, per month of the study.

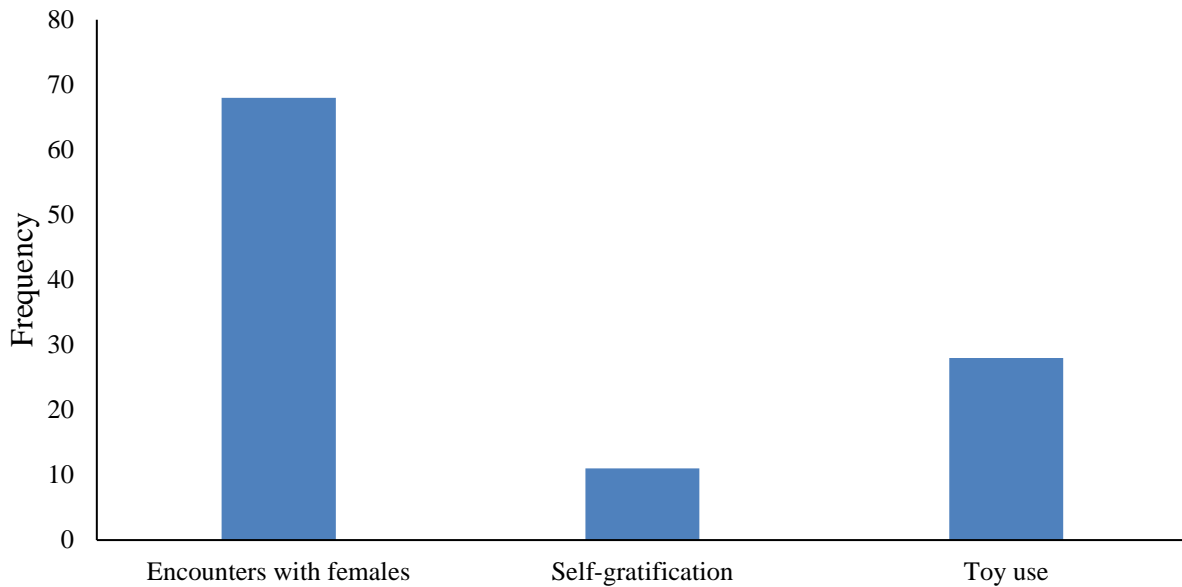


Figure 9. Number of sexual events per sexual outlet utilized by the male walrus.

Overall, there were 1,908 recorded instances of pharyngeal sac inflation (PSI) by the male walrus. This vocal and visual behavior was observed during both sexual and nonsexual instances. The male exhibited PSI in nonsexual context 77.72% of the time compared to the sexual context (22.27%). Pharyngeal sac inflations occurred during sexual encounters with the female walrus ($n = 14$), toy use ($n = 168$), self-gratification ($n = 7$), and exposed penis ($n = 241$; Figure 10). There was an overall significant difference in PSI frequency based on these contexts, $\chi^2(4, N = 430) = 576.40, p < 0.001$. Pharyngeal sac inflations was observed significantly more frequently when the penis was exposed ($std\ residual = 16.71$) and during toy use ($std\ residual = 8.84$) than encounters with either female ($std\ residual = -7.76$ [Uquq], -9.27 [Siku]) or self-gratification ($std\ residual = -8.52$). No instances were recorded of the male performing a PSI during sexual encounters with Siku. Pharyngeal sac inflations was also monitored in relation to presence or absence of park guests, $\chi^2(1, N = 1908) = 20.13, p < 0.001$ (Figure 11). The male was significantly more likely to display PSI when park guests were present ($std\ residual = 3.17$).

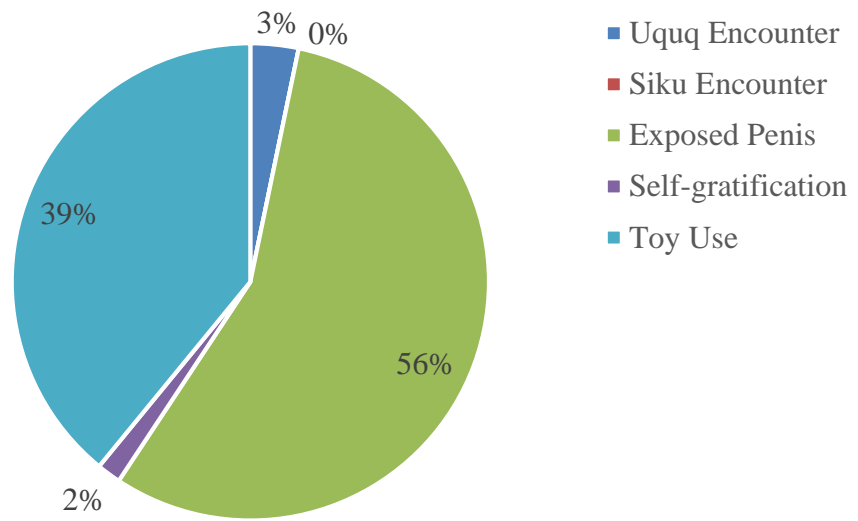


Figure 10. Comparison of pharyngeal sac inflation (PSI) during three sexual contexts (exposed penis, $n = 241$; self-gratification, $n = 7$; toy use, $n = 168$) and female encounters (Uquq, $n = 14$; Siku, $n = 0$).

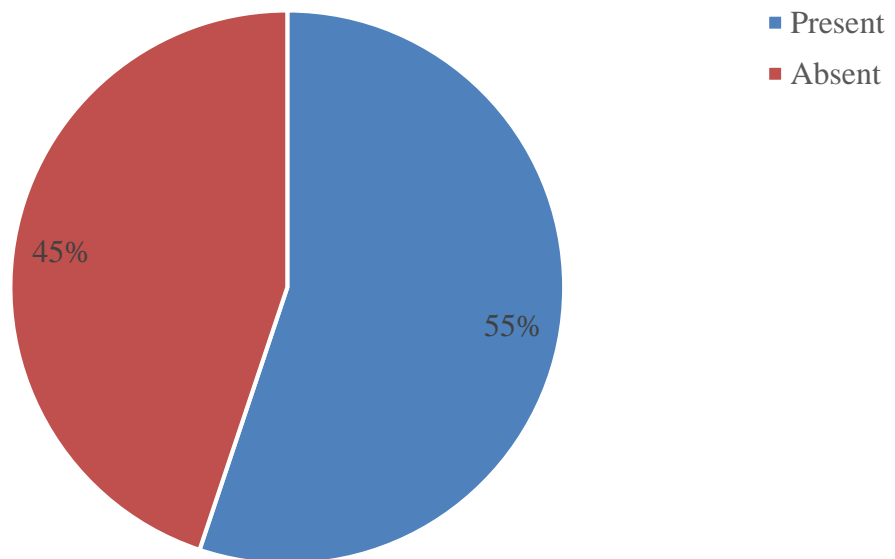


Figure 11. Comparison of number of pharyngeal sac inflation (PSI) when park guests were present ($n = 1052$) or absent ($n = 846$).

Discussion

Mate Preference

Wild walruses are primarily polygynous creatures (Fay, 1982, 1985; Fay et al., 1984; Kastelein, 2009; Riedman, 1990). It is suggested female Pacific walruses have a choice in mating partner, whereas this is not always the case for female Atlantic walruses (Fay et al., 1984; Sjare & Stirling, 1996). However, a male mating preference for a particular female(s) has not been previously reported in the literature. In the current study, the focal male walrus (Sivuqaq) engaged in mating behaviors significantly less often with the female walrus without tusks (Siku). Additionally, there were no recorded instances of the pharyngeal sac inflation, a noted mating display, during the male's interactions with Siku. Moreover, Siku was the only female in estrus during the time of the study, and despite her hormonal state, the male walrus appeared to prefer engaging in mating attempts with Uquq (i.e., the female with tusks). Riedman (1990) notes female walruses may identify tusks as characteristic to identify quality males to mate with. Uquq also had previously been impregnated by Sivuqaq, while no pregnancies have been reported for Siku (Muraco et al., 2012). The preference of Sivuqaq to interact with Uquq could suggest tusks may be a contributing factor for the preference of mate for the male walrus in this study.

Mating Behaviors

Few studies have previously examined underwater mating behaviors of Pacific walruses. Fay (1982) observed male walruses performing mating displays near female walruses on ice floes and females sliding into the water approaching the male to engage in copulation. Fay (1982) and other researchers observing wild walrus populations mating have been limited to surface viewing; this project was able to examine behaviors occurring underwater. A case study, such as this, contributes to what little is already known on mating behaviors for male Pacific walruses by providing underwater observation and identifying that a captive male walrus may exhibit a mate preference. Furthermore, the procedure can be replicated at other facilities to examine differences or similarities between the present study's focal male with other male walruses. Although Muraco et al. (2012) was a single pair case report, the findings were still valuable for discovering more about walrus reproduction and identifying possible limitations to successful captive breeding such as altered photoperiod cues. Any information that was not previously known or recorded can be valuable in expanding our understanding of walrus mating.

For this study, male behaviors when directly interacting with the females were characterized as grabs, rolls, holds, tusk strikes and nuzzles. Other noted behaviors included pharyngeal sac inflation, penis exposure, self-gratification and toy use. Sjare and Stirling (1996) described mating behaviors in Atlantic walrus that were visible from the surface and were similar to the grab (referred to as flipper touch), roll, and hold. Holding behavior frequency in the present study was not found to be significant, suggesting actual occurrences of successful copulation were few. Sjare and Stirling (1996) findings also speculated few occurrences of successful copulation(s) occurred despite the frequency of other mating behaviors exhibited, which parallels the results in the present study. Grabs were the most frequently observed mating behavior observed when interacting with both females. Attempts at copulation—as determined by the male attempting to grab a female—were abundant but actual frequency of successful copulation (which would be completed during a hold behavior) did not occur frequently. Rolls were observed but significantly infrequent, a finding concurrent to Sjare and Stirling's (1996) report of rolls occurring intermittently.

Tusk strikes and nuzzles were not frequently observed. Tusk strikes exhibited in the present study could potentially be signs of aggression rather than mating specific. Walruses have been known to use their tusks as means of defense and establishing territory (Fay, 1982; Riedman, 1990; Sjare & Stirling, 1996). Although tusk strikes did occur during sexual encounters, the striking could have been a sign of irritation towards the female (i.e., if the female was not cooperating with the advances of the male). Additionally, nuzzles could have been modified tusk strikes with the snout of the male already making contact with the female, as it was observed that male at times lacked the flexibility to tilt his head back and strike down.

Vocalizations of the walrus previously described during mating have been described as continuous vocalizations consisting of knocking sounds or bells (Fay, 1982; Fay et al., 1984; Sjare & Stirling, 1996). Charrier, Burlet, and Aubin (2011) reported that during mating displays, captive Pacific walruses only emitted whistles rather than knocks. Such vocalizations are thought to accompany pharyngeal sac inflation (PSI), but the association between this behavior and any vocalization is still contended (Fay et al., 1984). While the vocalizations paired with pharyngeal sac inflation observed from this study are possibly the same vocalizations described previously (Charrier et al., 2011; Fay, 1982; Fay et al., 1984; Sjare & Stirling, 1996) further acoustic analysis would be required to make that determination.

Mating vocalizations are not solely for attracting females but also for alerting other competition (Kastelein, 2009). The focal male in the present study was more likely to perform PSI when park guests were present. In absence of other competing male walruses, the increase in PSI vocalizations when park guests were present could be attributed to the male exhibiting territorial behavioral displays towards possible threats for mating competition (i.e., the figures outside the glass). Pharyngeal sac inflation was much more likely to occur during nonsexual states (i.e., male could be stationary or swimming without interacting with female(s), toy, self, and without exposed penis); however, these instances could be the result of the male possibly signaling to a female and not receiving a response captured on the video and audio data. For sexual events, PSI occurred more frequently in the contexts of toy use and when exposed penis was present. This supports the notion that PSI could serve as a mating display, which refers to a behavior prior to direct interaction, rather than a behavior to occur during a copulation attempt with a female. Over the duration of the study, all observed sexual events associated with PSI were exclusive, excluding five PSI in succession that were performed during toy use and exposed penis.

Sexual Outlet Preference

The male infrequently engaged in sexual behaviors with toys or self-gratification, compared to his frequency of sexual behaviors and interactions with the females, which is conducive to mating and successful copulation. While sexual toy use and self-gratification were intermittently observed, their presence suggests the male walrus would at times utilize other external factors for sexual stimulation than a female conspecific. Evidence of self-gratification has been noted in other animal species such as rhesus macaques (*Macaca mulatta*; Dubuc, Coyne, & Maestripieri, 2013) and Cape ground squirrels (*Xerus inauris*; Waterman, 2010). Additionally, whether the animals studied are housed in captivity or observed in the wild does not have an apparent effect on frequency of self-gratification noted to date (Dixson & Anderson, 2004). Waterman (2010) suggests self-gratification could have evolutionary significance, such as being used to signal virility to other individuals and replenish sperm by excreting old sperm. Self-gratification could also be inversely linked to success of mating in males, with unsuccessful males more likely to engage in self-gratification if there is decreased access to a mate (Dubuc et al., 2013).

Limitations

Sexual encounters in general occurred less frequently over the duration of this study. Start time of video recordings was not always the same for each day but mostly occurred during the mid-morning. Activeness could vary given the time of day which also could account for the behaviors noted. Recordings were made throughout all of December and January; however, video recording did not start in November until halfway through the month. The start and end period of video recording was believed to be when the focal male was most sexually active during the year. Fay (1982) stated that captive walrus mating may occur year round with greater frequency in the earlier months of the year similar to wild populations. The single male observed exhibited mating behaviors more in late fall compared to early winter; however, more observations spanning throughout the year are needed to determine the most sexually active months as this same focal male has exhibited an altered rut period in previous research (Muraco et al., 2012).

Although the literature supports the notion that walruses copulate primarily underwater, there are a few observations of captive walruses mating on land (Kastelein, 2009). The view of video footage was limited to only the pool area, thus presence of sexual interactions on land were not observed, if present. In addition, female access to pool and availability of enrichment items was beyond the control of the researchers. If the female with no tusks (Siku) was observed staying on land rather than entering the water while she was in estrus, this could account for the lack of sexual interactions observed. Incorporating simultaneous underwater and land observations could provide more information on sexual behaviors that occur on land that could precede or follow an underwater copulation attempt.

Visibility was often limited by presence of park guests crowding the walrus tank viewing area. Furthermore, not all instances of pharyngeal sac inflation were directly visually observable, and were only detected audibly. Only PSI behaviors that were observable by the male walrus being oriented at the viewing window were considered for statistical analysis. The nature of behaviors was difficult to determine by the orientation of the male walrus in relation to view of the camera. For instance, it is likely not all instances of exposed penis were recorded due to the limited visibility of the male floating in the water.

As the subjects of the present study were raised under human care from a young age, the male of the study had not had any exposure to other male walruses, which could have implications for the frequencies and types of behaviors observed. Furthermore, only one single male was available for observation for the present study. Although it is difficult to speculate male Pacific walrus mating behaviors from one individual male, this study may be identified as a case study, serve as a launching point for replication and continued research that can compare these results with other breeding males, both captive and wild. In the United States as well as abroad, there are a limited number of male walruses under human care, even less that are sexually mature, available as subjects of behavioral observation and research. Continued examination of both captive and wild populations of walrus mating behavior are necessary to solidify our knowledge on the reproductive behaviors in this species.

Conclusions

Few reports have previously been able to thoroughly examine and define mating behaviors of walruses. The present study provides a detailed descriptive basis for examining mating behaviors of a single captive male Pacific walrus that can be expanded upon in the future. Further research may identify distinctive differences between captive and wild settings that could allude to the limited reproductive success in captivity, such as the possible limitations identified in the Muraco et al. (2012) case report. Although the Pacific walrus

population is not currently listed as endangered, understanding more about walrus reproduction could assist in bettering conservation efforts before the population experiences a decline. It is imperative to examine and determine what behaviors are important to walrus breeding, and subsequently, successful reproduction of a viable offspring. Continuing to define and determine the function of mating behaviors, both acoustic and non-acoustic, is necessary to understand the function of the walrus behavioral repertoire, as well as to inform management strategies to best preserve this species both in the wild and captivity.

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