

Observations of Courtship in Belugas (*Delphinapterus leucas*)

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Successful copulation is necessary for the continuation of many species, but the courtship behavior (i.e., vocal and behavioral displays) leading to a successful copulation can vary greatly, even among cetaceans. The variation in pre-copulation behavior seems related to the mating system of a particular species. For example, the songs of humpback whales (*Megaptera novaeangliae*) are thought to attract females (see Herman, 2017), and males are often seen escorting females, sometimes while physically competing with each other, in a system of male dominance polygyny (Mobley & Herman, 1985; Clapham, 1996; Pack et al., 2002; Cerchio et al., 2005). North Atlantic right whales (*Eubalaena glacialis*) likely engage in a mating system that includes sperm competition based on genetic analyses and observations of an adult female simultaneously copulating with several adult males (Mate et al., 2005; Frasier et al., 2007). Mate et al. (2005) noted that a female North Atlantic right whale did not attempt to evade the males and remained passively at the surface. Although harbor porpoises (*Phocoena phocoena*) also experience sperm competition, reproductive behavior includes males pursuing and copulating with females at high speeds while the females surface to breathe (Keener et al., 2018; Orbach et al., 2020). Bottlenose dolphins (*Tursiops* spp.) have also been observed in mating contexts where males pursue females prior to copulation (Connor et al., 1992). For some bottlenose dolphin populations, members of male alliances coordinate to herd a female who is ovulating, which increases opportunities for successful copulation (Wiszniewski et al., 2012; Connor & Kritzen, 2015). Cues that a female bottlenose dolphin is receptive to copulation may include chemical signals and behavioral changes such as immobilization (described by Muraco & Kuczaj, 2015).

Cetacean courtship can involve visual or acoustic displays as a means of encouraging other individuals to participate in actual copulation (or intromission), which is necessary for fertilization.

In some cases, courtship does not lead to copulation if the intended audience is not receptive to the display. Copulation and courtship are distinct from socio-sexual behavior, which is not reproductive in nature. Socio-sexual behavior in belugas (*Delphinapterus leucas*) is observed throughout the year, although there is some seasonal variation (Glabicky et al., 2010; Ham et al., 2021b). Sexually immature females and males of all ages engage in socio-sexual behavior, but adult (i.e., 11+ y) females rarely participate (Hill et al., 2015). The socio-sexual repertoire begins to develop in calves during the first 3 y of life (Ham et al., 2022) but is not complete until belugas are closer to sexual maturity (i.e., approximately 6 y for females and 8 y for males; Lilley et al., 2020). The presence of adult males appears to influence the development of socio-sexual behavior (Ham et al., 2022), but it remains to be seen if these opportunities for observation and practice translate into successful reproduction.

In some cetacean species, females may be selective in their mate choice either through physiological or behavioral resistance (see Orbach, 2019). One example of this is the observations of dusky dolphin (*Lagenorhynchus obscurus*) females avoiding copulation attempts with direction changes and accelerated swims (Orbach et al., 2019). Less well-documented is how female cetaceans might be selective in mating by seeking out and actively engaging in copulation with specific males. Both Muraco & Kuczaj (2015) and Orbach et al. (2019) reported female bottlenose dolphins displaying passive behaviors described as listless, floating, and immobile to indicate receptiveness to copulation. However, information regarding specific courtship and copulation behavior for most cetacean species has not been well-described. Belugas, or white whales, live in Arctic and subarctic waters and are categorized into numerous stocks (i.e., populations). Although recent research has described their social structure to vary seasonally, with large summer congregations nearshore and smaller groups dispersed

the remainder of the year (O’Corry-Crowe et al., 2018), their courtship and copulation behavior has not been well-documented in the published literature (Kelley et al., 2015).

An early account of beluga mating describes males pursuing females with such aggression that the females died (reviewed by Kleinenberg et al., 1964). Although this early description was anecdotal, a recent report from a managed care setting (Richard et al., 2021) contradicts these observations of such violent behavior and suggests that female belugas may even choose with whom to mate. Richard et al. (2021) systematically observed one female beluga housed with two male belugas and described the female as choosing to engage with one male preferentially over the other by either rolling her ventral region toward or away from each male as they presented their genital region toward her. As erections were only present during a small number of interactions observed, Richard et al. suggest that the courtship behavior of male belugas is mostly displays and that attempted copulation is less frequent.

Purpose and Method

Despite births of beluga calves in managed care occurring in the absence of artificial insemination, few instances of courtship and copulation have ever been reported for belugas. The purpose of this paper is to describe a small number of observations where adult females were observed engaging in courtship interactions with an adult male (see Table 1 for subject demographics). These anecdotal observations are a result of a longitudinal study which has documented a group of 20 individual belugas (12 females and 8 males, ages ranging between birth and 35+ y), multiple times a week, since 2007. The group composition has varied across the study, but, at any given time, has typically included several mature females, one mature male, and several immature belugas born at the facility. Since 2007, on average, 10 belugas were present at any given time. Because they are housed in seven interconnected pools, there are times when all of the belugas are in the same social group; at other times, the belugas are separated into smaller groups of two or

more individuals. The number and size of the social groups are often changed several times within a single day. The overall social behavior of this beluga group reflects the behavior observed in wild beluga populations (see Manitzas Hill et al., 2021).

Observation One: Male Display and Female Participation

In April 2021, an adult female beluga (F1) was observed actively swimming down the water column to join the adult male beluga (M1) on the bottom of the habitat after he presented his ventral side to her (Hill et al., 2015). They swam together for several minutes, but direct copulation was not observed. On a different day in April, F1 and M1 engaged in several interactions over the course of a 30-min observation period. M1 presented his ventrum (i.e., chest, belly, ventral peduncle) to F1 in an S-posture (i.e., body in an S-shape with genitals positioned toward the conspecific as described by Hill et al., 2015) as he swam along the bottom of the environment, and the female swam to join him and positioned herself ventral side up next to his side. As they turned slightly, she turned her ventral side to him. He thrust his genital region to contact her side, but no penile erection was observed. They separated and swam independently for a few minutes before joining again at the bottom of the habitat, where the female once again positioned herself alongside the male, at which point he thrust again. Following his second thrust, F1 stopped swimming until M1 was close in proximity and aligned her body to be parallel to M1. M1 thrust, contacting the female’s side (i.e., lateral part of anterior and posterior peduncle as described in Ham et al., 2021a) in numerous locations with his genital region. This sequence was repeated. On the fourth thrust, the female lifted her flukes and peduncle slightly as the male thrust, which gave him access to her genitals, but still no erection was observed (see Supplemental Video A for an excerpt of this sequence; the Supplemental Videos for this paper are 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). Following this, the two separated and

Table 1. Belugas (*Delphinapterus leucas*) who are the focal subjects for the reported observations

Subject	Sex	Age at observations	Previously produced offspring?
M1	Male	Est. 27-29 y	Yes
F1	Female	11 y	Yes
F2	Female	11 y	Yes
F3	Female	Est. 31 y	Yes

swam independently. After several minutes, M1 began swimming back and forth at the bottom of the habitat with his ventrum presented, exhibiting an S-posture toward F1 who was near the surface and unresponsive to him. The male continued these presentations for about 5 min, at which point the female suddenly swam to the bottom and lined up again with her ventrum up and her side along his ventrum (similar to the copulatory position of wild belugas described by Kleinenberg et al., 1964). M1 thrust his genital region again and released a small stream of bubbles, then a bubble burst (Hill et al., 2011), and immediately formed another S-posture with an erection visible before thrusting once more (see Supplemental Video B for an excerpt of this sequence). The female actively remained near the male's side, and they slowly swam forward through the water. After this sequence, both belugas surfaced to breathe simultaneously, with the male returning to swim underwater while the adult female remained at the surface, which resulted in termination of the male–female interaction for that observation. Although several other individual belugas were present in the social group at the time, only one other female beluga (F2, described below) briefly followed the pair and observed their behavior. In May 2021, F1 was observed engaging with an environmental enrichment device (EED), which she left to join the adult male. M1 thrust his genital region toward her shortly after she joined him. The adult female reciprocated this thrust by slightly turning her body so her ventrum was closer to the male's ventrum. This sequence was the only interaction during the observation period.

Observation Two: Multiple Female Solicitation and Object Use

In May 2021, a different adult female (F2) was observed engaging in courtship behavior with the adult male (M1). M1 presented his ventrum to F2 a few times before the female swam over to the male and turned her ventrum slightly toward him. Later in the observation, M1 presented his ventrum toward the female in “Observation One,” F1, but that female swam away, and F2 swam over and positioned herself alongside M1 (see Supplemental Video C for an excerpt of this sequence). Although no instances of copulation occurred, the courtship display of the male resulted in the female actively choosing to engage in a sexual interaction with the male by altering her swim direction and speed, similar to “Observation One.”

During another observation day in May 2021, M1 was seen carrying an EED on his head and dorsal ridge before displaying courtship behavior with both F1 and F2 (see Supplemental Video D

for an excerpt of this sequence). Both F1 and F2 had been interacting with the same object earlier that day. Although all other belugas in this managed care population interact with EEDs, M1 had not been observed interacting with an EED spontaneously before this observation.

Observation Three: Synchronized Swimming During Courtship

A third adult female (F3) was observed swimming with M1 on two separate days in April 2019. They swam together for several minutes, both synchronized in their swim direction and swim speed, while M1 presented his genital region toward F3's side. M1 was not observed to have an erection, but F3 maintained her proximity to him and was observed lining up alongside his ventrum. In some instances, F3 rolled so that her ventrum was close to M1's ventrum; and in other instances, she rolled her ventrum away from M1's ventrum. Additionally, the adult female appeared to lift her flukes and peduncle upwards as the male thrust his genital region toward her and made contact in some instances (see Supplemental Video E for an excerpt of this sequence). This interaction took place near the bottom of the habitat and not at the surface, although after several minutes of interacting at the bottom, the pair came to the surface a few times to breathe, after which they floated motionlessly apart from one another. After floating at the surface for a few minutes, both dove back down to the bottom, in synchrony, and resumed swimming together. Although several other belugas were part of this social group, two juvenile males are visible in the video engaging in socio-sexual behavior with each other while potentially observing the above interaction.

While the observations described above are anecdotal, they appear to elucidate the roles of male and female belugas in courtship and mate choice. From these observations, several patterns emerged and appear to partially reflect the limited reports from wild belugas (Kleinenberg et al., 1964; Lomac-MacNair et al., 2016). Unlike some cetacean species, such as harbor porpoises and finless porpoises, where the males pursue the females at high speeds (Keener et al., 2018; Serres et al., 2021), the behavior of the male beluga in these observations was display-based, similar to those reported in wild belugas (Lomac-MacNair et al., 2016) and the findings of Richard et al. (2021). In the present study, the male did have several females he could court at any given time, but, for the most part, he directed his displays at just one female for a given observation period. For each observation period, the female at whom the displays were directed was almost

always the female who later interacted with the male. Because the male was typically some distance away and usually at the bottom of the habitat when he displayed his body in an S-posture presentation with his genital region presented to the female, the three adult females described in this paper were active participants in the interaction. The females changed their swim trajectory to swim over to the male and actively adjusted their body positions to be aligned with the male. In some instances, the females rolled so that their ventrums were closer to the male's ventrum, like descriptions of bottlenose dolphin copulation (Tavolga & Essapian, 1957); and in a few cases, the females were observed to lift their flukes and peduncle up, which seemed to allow the male to gain better access to the female's genitals. Two of the females also displayed a behavior that resembled the immobility described for female bottlenose dolphins and harbor porpoises (Muraco & Kuczaj, 2015; Orbach et al., 2019). Similar to Richard et al. (2021), both the females and male involved in these observations allowed conspecifics in the same habitat to swim close by. As the observing belugas were mostly calves and juveniles, their intent observation of the copulation may provide an opportunity for social learning (Ham et al., 2022).

The use of objects in courtship behavior has been suggested for other cetacean species, including river dolphins (*Inia geoffrensis*; Martin et al., 2008) and Australian humpback dolphins (*Sousa sahulensis*; Allen et al., 2017) for which the males of both species have been observed carrying and displaying objects (e.g., sticks, sponges, etc.) in what are hypothesized to be attempts at attracting females. Although this is the first description of a courtship display potentially involving object carrying for belugas, belugas have been previously observed interacting with objects while engaging in both socio-sexual behavior and non-social sexual behavior (Hill et al., 2015; Lilley et al., 2020; Ham, 2021; Ham et al., 2022), and male killer whales (*Orcinus orca*) have been observed carrying objects while courting females in human care (M. Lilley, pers. comm. with animal care staff at SeaWorld of Texas). Wild belugas have also been observed carrying objects, although the context of these instances (e.g., play, socio-sexual, courtship) is unknown (Krasnova et al., 2014).

Unlike socio-sexual interactions that happen above and below the surface, these courtship interactions took place underwater and most frequently at the bottom of the habitat. In addition to the poor visibility that often occurs in wild settings, the depth of courtship behaviors might be why this is not well-documented in wild populations and emphasizes the value of studying belugas

in managed care settings. Similar to Richard et al. (2021), most of the courtship behavior reported herein did not involve the male having an erection. In the few instances where an erection was present, complete intromission was not observed. Based on the observations of beluga behavior thus far, actual copulation is likely a rare event compared to the time spent in courtship displays. It is possible that the belugas engaged in actual copulation outside these observations. Although all three females and the adult male have produced offspring prior to these observations, the events recorded herein did not result in detectable pregnancies.

This paper provides additional information about the active role female belugas play in courtship and copulation behavior and will hopefully spark future research on this topic so that the mating system of belugas can be better understood. Female choice and the quality of the male's display may be important for breeding success and, therefore, a population's survival. Whether males are selected for their behavioral displays, vocal displays, or body condition is not known. Social groups with multiple mature males and multiple mature females are necessary to better understand the complexity of male and female mate choice for belugas. Historically, for many species, there has been a paucity of information on the females' role in courtship and copulation (e.g., female birdsong and ornamentation research; Haines et al., 2020), but the female's role in courtship and mate choice must be remembered when describing mating behaviors. The observations reported herein help to close that gap for belugas, and hopefully future research will continue to do so.

Acknowledgments

The authors thank SeaWorld of Texas (SeaWorld Parks & Entertainment Technical Contribution Number 2022-7) for generously giving us access to observe the animals, the numerous research assistants who have helped with this long-term study, and two anonymous reviewers whose comments have helped to improve the paper.

Literature Cited

- Allen, S. J., King, S. L., Krützen, M., & Brown, A. M. (2017). Multi-modal sexual displays in Australian humpback dolphins. *Scientific Reports*, 7(1), 13644. <https://doi.org/10.1038/s41598-017-13898-9>
- Cerchio, S., Jacobsen, J. K., Cholewiak, D. M., Falcone, E. A., & Merriwether, D. A. (2005). Paternity in humpback whales, *Megaptera novaeangliae*: Assessing polygyny and skew in male reproductive success. *Animal*

- Behaviour*, 70(2), 267-277. <https://doi.org/10.1016/j.anbehav.2004.10.028>
- Clapham, P. J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. *Mammal Review*, 26(1), 27-49. <https://doi.org/10.1111/j.1365-2907.1996.tb00145.x>
- Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Animal Behaviour*, 103, 223-235. <https://doi.org/10.1016/j.anbehav.2015.02.019>
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences*, 89(3), 987-990. <https://doi.org/10.1073/pnas.89.3.987>
- Frasier, T. R., Hamilton, P. K., Brown, M. W., Conger, L. A., Knowlton, A. R., Marx, M. K., Slay, C. K., Kraus, S. D., & White, B. N. (2007). Patterns of male reproductive success in a highly promiscuous whale species: The endangered North Atlantic right whale. *Molecular Ecology*, 16(24), 5277-5293. <https://doi.org/10.1111/j.1365-294X.2007.03570.x>
- Glabicky, N., DuBrava, A., & Noonan, M. (2010). Social-sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). *Polar Biology*, 33(8), 1145-1147. <https://doi.org/10.1007/s00300-010-0790-3>
- Haines, C. D., Rose, E. M., Odom, K. J., & Omland, K. E. (2020). The role of diversity in science: A case study of women advancing female birdsong research. *Animal Behaviour*, 168, 19-24. <https://doi.org/10.1016/j.anbehav.2020.07.021>
- Ham, J. R. (2021). *Social and non-social play in beluga whales* (*Delphinapterus leucas*) (Master's thesis). University of Lethbridge, Lethbridge, Alberta, Canada. <https://hdl.handle.net/10133/6087>
- Ham, J. R., Lilley, M. K., & Manitzas Hill, H. M. (2021a). Conspecific scarring on wild belugas (*Delphinapterus leucas*) in Cunningham Inlet. *Behaviour*, 158(8-9), 663-683. <https://doi.org/10.1163/1568539X-bja10086>
- Ham, J. R., Lilley, M. K., Miller, M. R., & Manitzas Hill, H. M. (2021b). Seasonality of social behaviour among immature belugas (*Delphinapterus leucas*) in managed care. *Polar Research*, 40, 5498. <https://doi.org/10.33265/polar.v40.5498>
- Ham, J. R., Lilley, M. K., Lelekach, J., Miller, M. R., Robeck, T. R., Pellis, S. M., & Manitzas Hill, H. M. (2022). The emergence and early development of socio-sexual behavior in beluga calves (*Delphinapterus leucas*). *Behavioural Processes*, 200, 104695. <https://doi.org/10.1016/j.beproc.2022.104695>
- Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews*, 92(3), 1795-1818. <https://doi.org/10.1111/brv.12309>
- Hill, H. M. M., Kahn, M. S., Brilliot, L. J., Roberts, B. M., Gutierrez, C., & Artz, S. (2011). Beluga (*Delphinapterus leucas*) bubble bursts: Surprise, protection, or play? *International Journal of Comparative Psychology*, 24(2), 235-243.
- Hill, H. M., Dietrich, S., Yeater, D., McKinnon, M., Miller, M., Aibel, S., & Dove, A. (2015). Developing a catalog of socio-sexual behaviors of beluga whales (*Delphinapterus leucas*). *Animal Behavior and Cognition*, 2(2), 105-123. <https://doi.org/10.12966/abc.05.01.2015>
- Keener, W., Webber, M. A., Szczeplaniak, I. D., Markowitz, T. M., & Orbach, D. N. (2018). The sex life of harbor porpoises (*Phocoena phocoena*): Lateralized and aerial behavior. *Aquatic Mammals*, 44(6), 620-632. <https://doi.org/10.1578/AM.44.6.2018.620>
- Kelley, T. C., Stewart, R. E. A., Yurkowski, D. J., Ryan, A., & Ferguson, S. H. (2015). Mating ecology of beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) as estimated by reproductive tract metrics. *Marine Mammal Science*, 31(2), 479-500. <https://doi.org/10.1111/mms.12165>
- Kleinenberg, S. E., Yablokov, A. V., Bel'kovich, B. M., & Tarasevich, M. N. (1964). *Beluga* (*Delphinapterus leucas*): Investigation of the species. Israel Program for Scientific Translations.
- Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., & Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (*Delphinapterus leucas*) in natural environment. *Biology Bulletin*, 41(4), 349-356. <https://doi.org/10.1134/S1062359014040062>
- Lilley, M. K., Ham, J. R., & Hill, H. M. (2020). The development of socio-sexual behavior in belugas (*Delphinapterus leucas*) under human care. *Behavioural Processes*, 171, 104025. <https://doi.org/10.1016/j.beproc.2019.104025>
- Lomac-MacNair, K. S., Smultea, M. A., Cotter, M. P., Thissen, C., & Parker, L. (2016). Socio-sexual and probable mating behavior of Cook Inlet beluga whales, *Delphinapterus leucas*, observed from an aircraft. *Marine Fisheries Review*, 77(2), 32-39. <https://doi.org/10.7755/MFR.77.2.2>
- Manitzas Hill, H. M., Yeater, D. B., & Noonan, M. (2021). Synergy between behavioural research on beluga whales (*Delphinapterus leucas*) conducted in zoological and wild settings. *Polar Research*, 40, 5508. <https://doi.org/10.33265/polar.v40.5508>
- Martin, A. R., da Silva, V. M. F., & Rothery, P. (2008). Object carrying as socio-sexual display in an aquatic mammal. *Biology Letters*, 4(3), 243-245. <https://doi.org/10.1098/rsbl.2008.0067>
- Mate, B., Duley, P., Lagerquist, B., Wenzel, F., Stimpert, A., & Clapham, P. (2005). Observations of a female North Atlantic right whale (*Eubalaena glacialis*) in simultaneous copulation with two males: Supporting evidence for sperm competition. *Aquatic Mammals*, 31(2), 157-160. <https://doi.org/10.1578/AM.31.2.2005.157>
- Mobley, J. R., Jr., & Herman, L. M. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, 63(4), 762-772. <https://doi.org/10.1139/z85-111>

- Muraco, H., & Kuczaj II, S. A. (2015). Conceptive estrus behavior in three bottlenose dolphins (*Tursiops truncatus*). *Animal Behavior and Cognition*, 2(1), 30-48. <https://doi.org/10.12966/abc.02.03.2015>
- O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K., & Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLOS ONE*, 13(3), e0194201. <https://doi.org/10.1371/journal.pone.0194201>
- Orbach, D. N. (2019). Sexual strategies: Male and female mating tactics. In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 75-93). Springer International Publishing. https://doi.org/10.1007/978-3-030-16663-2_4
- Orbach, D. N., Packard, J. M., Keener, W., Ziltener, A., & Würsig, B. (2019). Testes size, vaginal complexity, and behavior in toothed whales (odontocetes): Arms race or tradeoff model for dusky dolphins (*Lagenorhynchus obscurus*), harbor porpoises (*Phocoena phocoena*), and bottlenose dolphins (*Tursiops* spp.)? *Journal of Comparative Psychology*, 133(3), 359-372. <https://doi.org/10.1037/com0000162>
- Orbach, D. N., Eaton, J., Fiori, L., Piwetz, S., Weir, J. S., Würsig, M., & Würsig, B. (2020). Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. *Marine Mammal Science*, 36(4), 1097-1110. <https://doi.org/10.1111/mms.12695>
- Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., & Deakos, M. H. (2002). Penis extrusions by humpback whales (*Megaptera novaeangliae*). *Aquatic Mammals*, 28(2), 131-146.
- Richard, J. T., Levine, R., Romano, T. A., & Sartini, B. L. (2021). Minimally invasive physiological correlates of social behaviour in belugas (*Delphinapterus leucas*) under human care. *Polar Research*, 40, 1-16. <https://doi.org/10.33265/polar.v40.5504>
- Serres, A., Hao, Y., & Wang, D. (2021). Socio-sexual interactions in captive finless porpoises and bottlenose dolphins. *Marine Mammal Science*, 38(2), 812-821. <https://doi.org/10.1111/mms.12887>
- Tavolga, M. C., & Essapian, F. S. (1957). The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. *Zoologica*, 42(1), 11-31.
- Wiszniewski, J., Corrigan, S., Beheregaray, L. B., & Möller, L. M. (2012). Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Journal of Animal Ecology*, 81(2), 423-431. <https://doi.org/10.1111/j.1365-2656.2011.01910.x>