

## Young Belugas (*Delphinapterus leucas*) Exhibit Sex-Specific Social Affiliations

Lauren Mazikowski,<sup>1</sup> Heather M. Hill,<sup>2</sup> and Michael Noonan<sup>1,3</sup>

<sup>1</sup>Canisius College, 2001 Main Street, Buffalo, NY 14208, USA

<sup>2</sup>St. Mary's University, 1 Camino Santa Maria, San Antonio, TX 78228, USA

<sup>3</sup>Animal Behavior, Ecology, and Conservation, Canisius College, Buffalo, NY 14208, USA

E-mail: noonan@canisius.edu

### Abstract

The present study investigated the social affiliations of young beluga whales (ages 1 to 5 years). The results indicated that young males were found significantly more often in the proximity of other males (both juvenile and adult) than found in the proximity of females. Young females were found less often with other whales than were males, and they did not show a difference based on sex. These results mimic the male-affiliative patterns found in both wild and captive adult belugas, suggesting that the tendency for males to group together develops at an early age in this species.

**Key Words:** beluga, *Delphinapterus leucas*, sex segregation, social affiliation, juvenile

### Introduction

Maestripieri & Ross (2004) have argued that sex differences in juvenile associations and play behavior can be predicted in diverse species by characteristics of adult behavior and social structure. Specifically, if physical differences (e.g., size or weaponry), behavioral differences (e.g., hunting techniques or timing, predator avoidance, care taking, or tool use), or social preferences (e.g., strong bonds with same sex or opposite sex individuals) exist between the two sexes in adulthood, then sex differences in the behavior of developing offspring could be expected. These predictions have been supported by research with a number of mammals. For example, in a number of non-human primates, juvenile males prefer same sex and age partners more frequently than juvenile females in ways that seem to foreshadow subsequent adult behaviors (*Macaca mulatta*, Ehardt & Bernstein, 1987; *Gorilla gorilla*, Maestripieri & Ross, 2004; *Pan paniscus*, Mendoza-Granados & Sommer, 1995; Palagi, 2006). Similarly, juvenile males of some artiodactyl species have been

observed to display greater levels of aggressive behavior than juvenile females and usually direct it at other juvenile males (*Bison bison*, Rothstein & Griswold, 1991; *Hippotragus niger*, Thompson, 1996; *Capra ibex*, Byers, 1980; *Ovis canadensis*, Hass & Jenni, 1993). By contrast, measures of early sex differences in the social activities of langurs (*Presbytis entellus*), including time in proximity, physical contact, and grooming, all appear to relate to female-based bonds and natal philopatry along with male dispersal (Nikolei & Borries, 1997).

Sex differences in social development that correspond to adult social patterns have also been identified in at least two species of dolphin. Adult male bottlenose dolphins (*Tursiops truncatus* and *Tursiops aduncus*) are known to form long-term, same-sex alliances, while adult females form looser networks with each other (Connor & Krützen, 2015; Ermak et al., 2017), and those sex-differentiated social patterns are reflected in the patterns of reciprocal touching (Dudzinski & Ribic, 2017) and in the spatial associations of immature male and female calves (reviewed by Stanton & Mann, 2014).

Specific knowledge about the behavior of beluga whales (*Delphinapterus leucas*) in their natural habitat is limited compared to what is known about many other cetacean species. Belugas characteristically inhabit Arctic waters where they are often seen near the edge of polar ice (Kleinenberg et al., 1964; Huntington et al., 1999). Belugas are considered a highly gregarious species that are found in large, mixed sex aggregations during their springtime breeding season and during part of the subsequent summer (Kleinenberg et al., 1964; Brodie, 1971; Sergeant, 1973; Heide-Jørgensen & Teilmann, 1994; O'Corry-Crowe et al., 1997; Brown-Gladden et al., 1999; Huntington et al., 1999; Mymrin et al., 1999; Boltunov & Belikov, 2002; Michaud, 2005; Loseto et al., 2006; Chernetsky et al., 2011; Krasnova et al., 2012;

Colbeck et al., 2013; Citta et al., 2017; Smith et al., 2017). However, those same animals appear to divide into sex-segregated groups during winter months and during their migrations between wintering and summering areas (Boltunov & Belikov, 2002; Michaud, 2005; Krasnova et al., 2006, 2009; Chernetsky et al., 2011; Karenina et al., 2013). Evidence for similar sex segregation in captive belugas was obtained when the social affiliations of two mixed-sex social groupings were examined (Hill et al., 2018). Outside of their breeding season, adult males swam in proximity of other adult males at seven times the rate in which they were in the proximity of adult females. By contrast, females were much less often in the presence of other whales and did not show a sex difference in their associations. These results indicated that non-breeding adult male belugas showed a clear preference for associating with other adult males over adult females.

In free-ranging beluga populations, immature animals of both sexes appear to remain in the same groups as their mothers until around 4 to 5 y of age, after which time males emigrate into seasonal, male social groupings (Krasnova et al., 2006, 2009; Karenina et al., 2013). Anecdotal reports from field researchers have suggested that immature belugas are highly social and often engage in playful chases with each other (Krasnova et al., 2009, 2014), behaviors that have also been documented for immature belugas in managed care (Hill, 2009; Hill et al., 2013, 2015a). Despite these observations, however, research on the development of any sex-based social segregation in this species does not yet exist. The objective of the present investigation therefore was to ascertain whether sex differences in social affiliations occur in young beluga whales as it does in other mammals with similar social structures.

**Methods**

*Subjects*

For the purposes of this study, an animal was considered to be juvenile if it was less than 6 y old. It was considered adult if it was 6 y of age or more. Nineteen juvenile belugas housed at two independent facilities served as the subjects of this investigation. Fifteen subjects (5 males, 10 females) between 1 and 5 y of age were housed at Marineland of Canada (ML), and four subjects (1 male, 3 females) between 1 and 4 y of age were housed at SeaWorld San Antonio (SW). During the periods of observation, the subjects were housed in stable, mixed sex, mixed age social groups that ranged in size between five and 17 whales. The groupings from year to year are summarized in Table 1.

*Data Collection*

A scan sampling protocol was used to document the social state of each juvenile whale on a repeated basis. During each scan, each subject successively became the focal individual, and the identity of any whales within one body length of the focal whale was recorded. At both facilities, observations took place opportunistically between the years 2013 and 2017. Subjects were observed during those years as their housing and availability allowed. At ML, observations were made via underwater viewing windows in real time at intervals of approximately 10 min between successive scan samples of the same subject. At SW, observations were made from video recordings looking down through the water surface at intervals of 1 min between successive scan samples of the same subject. At ML, the number of scans per subject per day ranged between three and 10, and the number of days of observation per subject ranged between eight and 18. At SW, the number of scans per subject per day ranged between 10 and 20, and the number of days of observation per subject ranged between two and 40.

**Table 1.** Beluga whale (*Delphinapterus leucas*) groupings by location and observation year

Year	Location	# adult males	# adult females	# juvenile males	# juvenile females
2013	ML Pool 1	1	7	3	2
2013	ML Pool 2	2	9	3	3
2013	SW	1	2	0	2
2014	ML Pool 2	2	8	3	3
2014	SW	1	4	1	1
2015	ML Pool 2	2	7	2	5
2015	SW	1	4	1	1
2017	ML Pool 1	2	7	2	3

For each subject, on each observation day, four separate adjusted proportions were computed, representing the four possible sex-age categories:

1. *With Adult Male* – The number of scans for that subject in which it was within one body length of an adult male, divided by the number of adult males in the pool, divided by the number of scans on that day.
2. *With Juvenile Male* – The number of scans for that subject in which it was within one body length of a juvenile male, divided by the number of juvenile males in the pool other than itself, divided by the number of scans on that day.
3. *With Adult Female* – The number of scans for that subject in which it was within one body length of an adult female other than its mother, divided by the number of adult females in the pool other than its mother, divided by the number of scans on that day.
4. *With Juvenile Female* – The number of scans for that subject in which it was within one body length of a juvenile female, divided by the number of juvenile females in the pool other than itself, divided by the number of scans on that day.

These data were then averaged across days, thereby creating four values per subject representing its mean for each of the partner sex-age categories. Since the number of scans varied over days, this procedure was used to ensure that the scan days were weighted evenly.

## Results

The results of a mixed model ANOVA was conducted with subject sex (male vs female) and location (ML vs SW) as between-subject variables, and partner sex-age category (with adult male, with juvenile male, with adult female, and with juvenile female) as a within-subjects variable are presented in Table 2. Although the mean adjusted proportion of scans in which juvenile male belugas ( $M = 0.062$ ,  $SEM = 0.009$ ) were in the proximity of any other beluga was 1.6 times greater than that for juvenile female belugas ( $M = 0.038$ ,  $SEM = 0.006$ ), the main effect for subject sex was not significant,  $F(1, 14) = 2.7$ , ns. The main effect of partner sex-age category reflected significant differences in the adjusted proportions with which all subjects were in the proximity of other whales. Those proportions were highest for With Juvenile Male and lowest for With Adult Male. The significant interaction between partner sex-age category and location was explored using independent  $t$  tests with a Bonferonni correction for each partner sex-age category. The only significant difference found was a significantly higher overall proportion for being with adult females at ML ( $M = 0.069$ ,  $SEM = 0.013$ ) than at SW ( $M = 0.003$ ,  $SEM = 0.002$ ) for both male and female subjects,  $t(14.91) = 5.01$ ,  $p < 0.001$ . Hereafter, the data were pooled across locations.

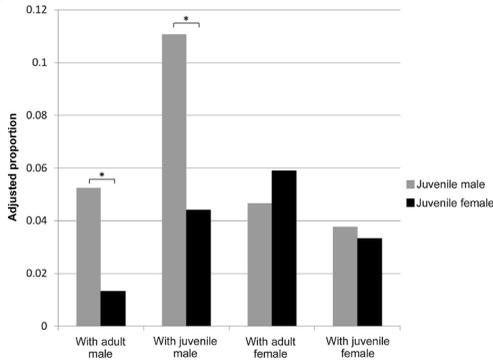
Subsequently, *a priori t* tests were performed comparing the male and female juvenile subjects for each partner sex-age category separately. The results are summarized in Table 3 and Figure 1. Juvenile males were significantly more often in the proximity of adult males and other juvenile males than were juvenile females. Juvenile males did not differ from juvenile females in the proportions with which they were with adult females or juvenile females.

**Table 2.** ANOVA comparing adjusted proportions by subject sex (male vs female) and location (ML vs SW) as between-subject variables, and partner sex-age category (with adult male, with juvenile male, with adult female, and with juvenile female) as a within-subjects variable

Variables	MS	df	F	sig
Subject sex	0.005	1	2.7	ns
Location	0.003	1	1.7	ns
Partner sex-age category	0.016	3	10.9	0.001
Subject sex by location	0.001	1	0.0	ns
Subject sex by partner sex-age category	0.003	3	2.9	ns
Location by partner sex-age category	0.014	3	9.5	0.001
Subject sex by location by partner sex-age category	0.001	3	0.1	ns

**Table 3.** Juvenile beluga sex differences in social affiliation as a function of sex and age of partner

Partner category	Male (n = 6)		Female (n = 13)		t	p
	M	SEM	M	SEM		
With adult male	0.05	0.01	0.01	0.01	3.54	0.015
With juvenile male	0.11	0.03	0.04	0.02	2.00	0.031
With adult female	0.05	0.01	0.06	0.02	< 1.00	ns
With juvenile female	0.04	0.01	0.03	0.01	<1.00	ns



**Figure 1.** Juvenile beluga social proximity as a function of partner sex and age; adjusted proportion is average proportion of scans per day in each category divided by the number of possible partners in that category. \* indicates significant differences at  $p < 0.05$ , 1-tailed.

**Discussion**

The present study provides clear evidence that juvenile male belugas prefer to be in proximity to other males (both juvenile and adult), while juvenile females do not show a preference. These results indicate that the sex segregation that is characteristic of adult beluga society is already emerging in immature belugas ranging between 1 and 5 y of age.

Despite there being some anecdotal reports that adult male belugas become more vocal during their breeding season and that they sometimes chase subadult males from females presumed to be sexually receptive (H. Hill, M. Noonan, and V. Vergara, pers. obs.), the reproductive behavior of belugas is poorly understood. Unlike their closest relatives, the narwhals (*Monodon monoceros*), belugas do not appear to engage in strong physical-based intrasexual competition (Gerson & Hickie, 1985; Michaud, 2005), an observation that appears to argue against a need in juvenile males to engage in motor training as an explanation of the observed sex-based affiliations.

On the other hand, since adult male–adult male social interactions are commonly seen in socio-sexual interactions by belugas in managed care (Glabicky et al., 2010; Hill et al., 2015b) and possibly in their natural habitat (Lomac-MacNair et al., 2015), the same-sex preference observed in the juvenile males in the current study is compatible with a social bonding explanation. Juvenile male belugas may be developing their social bonds for their future social affiliations through these early sex-based socialization preferences. A similar pattern has been suggested for social development in the bottlenose dolphin (Stanton & Mann, 2014; Connor & Krützen, 2015; Ermak et al., 2017).

Finally, the juvenile females in the present study showed less social affiliations overall compared to the juvenile males. These results similarly appear to foreshadow future social patterns since adult female belugas are also reported to have weaker social bonds than males both in the wild (reviewed in Michaud, 2005) and in managed care (Hill et al., 2016, 2018).

Future research should examine the nature of the social interactions of juvenile belugas to better understand the relationship between this developmental period and future behavior. It will be interesting to learn more about the nature of the calf interactions and whether there is any segregation along familial lines. That latter possibility is suggested by the genetic relatedness of beluga populations displaying fidelity in their migration patterns (O’Corry-Crowe et al., 2018). The more that is learned about these social preferences, the better social groupings of belugas in human care can be managed to enhance beluga welfare. Moreover, such knowledge may inform critical decisions about subsistence harvests, especially for endangered populations. If juvenile animals, especially males who appear to be highly social, demonstrate a preference for same-sex adults and peers, then removing adult males from a population may be particularly harmful to that population’s stability and growth since it is likely that relationships formed as immature animals play critical roles for future fitness.

### Acknowledgments

The authors gratefully acknowledge the contributions of Kristen Whyte and Debora Silva who assisted in data collection. Marineland of Canada and SeaWorld San Antonio generously provided their hospitality for this research. This manuscript was substantially improved by the constructive feedback provided by three reviewers.

### Literature Cited

- Boltunov, A. N., & Belikov, S. E. (2002). Belugas (*Delphinapterus leucas*) of the Barents, Kara and Laptev Seas. *NAMMCO Scientific Publications*, 4, 149-168. <https://doi.org/10.7557/3.2842>
- Brodie, P. F. (1971). A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *Journal of the Fisheries Board of Canada*, 28(9), 1309-1318. <https://doi.org/10.7557/3.2842>
- Brown-Gladden, J. G., Ferguson, M. M., Friesen, M. K., & Clayton, J. W. (1999). Population structure of North American beluga whales (*Delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. *Molecular Ecology*, 8(3), 347-363. <https://doi.org/10.1046/j.1365-294X.1998.00559.x>
- Byers, J. A. (1980). Play partner preferences in Siberian ibex, *Capra ibex sibirica*. *Ethology*, 53, 23-40. <https://doi.org/10.1111/j.1439-0310.1980.tb00731.x>
- Chernetsky, A. D., Krasnova, V. V., & Bel'kovich, V. M. (2011). Studies of the structure of the Solovetsky reproductive gathering of beluga whales (*Delphinapterus leucas*) in the White Sea using the photo identification method. *Oceanology*, 51(2), 275-280. <https://doi.org/10.1134/S0001437011020044>
- Citta, J. J., Richard, P., Lowry, L. F., O'Corry-Crowe, G., Marcoux, M., Suydam, R., & Gray, T. (2017). Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. *Marine Mammal Science*, 33(1), 236-250. <https://doi.org/10.1111/mms.12357>
- Colbeck, G. J., Duchesne, P., Postma, L. D., Lesage, V., Hammill, M. O., & Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B: Biological Sciences*, 280, 2552-2561. <https://doi.org/10.1098/rspb.2012.2552>
- 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>
- Dudzinski, K. M., & Ribic, C. A. (2017). Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal Behavior and Cognition*, 4(1), 30-48. <https://doi.org/10.12966/abc.03.02.2017>
- Ehardt, C. L., & Bernstein, I. S. (1987). Patterns of affiliation among immature rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology*, 13(3), 255-269. <https://doi.org/10.1002/ajp.1350130304>
- Ermak, J., Brightwell, K., & Gibson, Q. (2017). Multi-level dolphin alliances in northeastern Florida offer comparative insight into pressures shaping alliance formation. *Journal of Mammalogy*, 98(4), 1096-1104. <https://doi.org/10.1093/jmammal/gyx053>
- Gerson, H. B., & Hickie, J. P. (1985). Head scarring on male narwhals (*Monodon monoceros*): Evidence for aggressive tusk use. *Canadian Journal of Zoology*, 63(9), 2083-2087. <https://doi.org/10.1139/z85-306>
- Glabicky, N., DuBrava, A., & Noonan, M. (2010). Social-sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). *Polar Biology*, 33, 1145-1147. <https://doi.org/10.1007/s00300-010-0790-3>
- Hass, C. C., & Jenni, D. A. (1993). Social play among juvenile bighorn sheep: Structure, development, and relationship to adult behavior. *Ethology*, 93, 105-116. <https://doi.org/10.1111/j.1439-0310.1993.tb00982.x>
- Heide-Jørgensen, M. P., & Teilmann, J. (1994). Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. *Meddelelser om Grønland Bioscience*, 39, 195-212.
- Hill, H. M. (2009). The behavioral development of two beluga calves during the first year of life. *International Journal of Comparative Psychology*, 22, 234-253.
- Hill, H. M., Garcia de Oliveira Silva-Gruber, D., & Noonan, M. (2018). Sex-specific social affiliation in captive beluga whales (*Delphinapterus leucas*). *Aquatic Mammals*, 44(3), 250-255. <https://doi.org/10.1578/AM.44.3.2018.250>
- Hill, H. M., Alvarez, C., Dietrich, S., & Lacy, K. (2016). Preliminary findings in beluga (*Delphinapterus leucas*) tactile interactions. *Aquatic Mammals*, 42(3), 277-291. <https://doi.org/10.1578/AM.42.3.2016.277>
- Hill, H. M., Campbell, C., Dalton, L., & Osborn, S. (2013). The first year of behavioral development and maternal care of beluga (*Delphinapterus leucas*) calves in human care. *Zoo Biology*, 32, 565-570. <https://doi.org/10.1002/zoo.21093>
- Hill, H. M., Guarino, S., Crandall, S., Lenhart, E., & Dietrich, S. (2015a). Young belugas diversify adult beluga (*Delphinapterus leucas*) behavior. *Animal Behavior and Cognition*, 2(3), 267-284. <https://doi.org/10.12966/abc.08.06.2015>
- Hill, H. M., Dietrich, S., Yeater, D., McKinnon, M., Miller, M., Aibel, S., & Dove, A. (2015b). Developing an ethogram of sexual and socio-sexual behaviors of beluga whales in the care of humans. *Animal Behavior and Cognition*, 2(2), 105-123. <https://doi.org/10.12966/abc.05.01.2015>
- Huntington, H. P., & Communities of Buckland, Elim, Koyuk, Point Lay, and Shaktoolik. (1999). Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the eastern Chukchi and northern Bering Seas, Alaska. *Arctic*, 52(1), 49-61. <https://doi.org/10.14430/arctic909>

- Karenina, K., Giljov, A., Glazov, D., & Malashichev, Y. (2013). Social laterality in wild beluga whale infants: Comparisons between locations, escort conditions, and ages. *Behavioral Ecology and Sociobiology*, 67(7), 1195-1204. <https://doi.org/10.1007/s00265-013-1545-2>
- Kleinenberg, S. E., Yablokov, A. V., Bel'kovich, V. M., & Tarasevich, M. N. (1964). Beluga (*Delphinapterus leucas*): Investigation of the species. *Akademiya Nauk SSSR, Moscow*. (Translated from Russian by Israel Program for Scientific Translation, Jerusalem, 1969)
- Krasnova, V. V., Bel'kovich, V. M., & Chernetsky, A. D. (2006). Mother-infant spatial relations in wild beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. *Biology Bulletin*, 33(1), 53-58. <https://doi.org/10.1134/S1062359006010079>
- Krasnova, V. V., Bel'kovich, V. M., & Chernetsky, A. D. (2009). Formation of behavior in the White Sea beluga calf, *Delphinapterus leucas*, during early postnatal ontogenesis. *Russian Journal of Marine Biology*, 35, 53-59. <https://doi.org/10.1134/S1063074009010088>
- Krasnova, V. V., Chernetsky, A. D., Kirillova, O. I., & Bel'kovich, V. M. (2012). The dynamics of the abundance, age, and sex structure of the Solovetsky reproductive gathering of the beluga whale *Delphinapterus leucas* (Onega Bay, White Sea). *Russian Journal of Marine Biology*, 38(3), 218-225. <https://doi.org/10.1134/S1063074012030078>
- 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>
- Lomac-MacNair, K. S., Smultea, M. A., Cotter, M. P., Thissen, C., & Parker, L. (2015). 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>
- Loseto, L. L., Richard, P., Stern, G. A., Orr, J., & Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology*, 84(12), 1743-1751. <https://doi.org/10.1139/z06-160>
- Maestriperi, D., & Ross, S. R. (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure. *American Journal of Physical Anthropology*, 123(1), 52-61. <https://doi.org/10.1002/ajpa.10295>
- Mendoza-Granados, D., & Sommer, V. (1995). Play in chimpanzees of the Arnhem Zoo: Self-serving compromises. *Primates*, 36(1), 57-68. <https://doi.org/10.1007/BF02381915>
- Michaud, R. (2005). Sociality and ecology of the odontocetes. In K. Ruckstuhl & P. Neuhaus (Eds.), *Sexual segregation in vertebrates: Ecology of the two sexes* (pp. 303-326). Cambridge, UK: Cambridge University.
- Mymrin, N. I., Communities of Novoe Chaplino, Sireniki, Uelen, and Yanrakinnot, & Huntington, H. P. (1999). Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the northern Bering Sea, Chukotka, Russia. *Arctic*, 52(1), 62-70. <https://doi.org/10.14430/arctic910>
- Nikolei, J., & Borries, C. (1997). Sex differential behavior of immature human langurs (*Presbytis entellus*) in Ramnagar, South Nepal. *International Journal of Primatology*, 18(3), 415-437. <https://doi.org/10.1023/A:1026390517948>
- O'Corry-Crowe, G. M., Suydam, R. S., Rosenberg, A., Frost, K. J., & Dizon, A. E. (1997). Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology*, 6, 955-970. <https://doi.org/10.1046/j.1365-294X.1997.00267.x>
- O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., & Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLOS ONE*, 13, e0194201. <https://doi.org/10.1371/journal.pone.0194201>
- Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and inter-individual relationships. *American Journal of Physical Anthropology*, 129(3), 418-426. <https://doi.org/10.1002/ajpa.20289>
- Rothstein, A., & Griswold, J. G. (1991). Age and sex preferences for social partners by juvenile bison bulls, *Bison bison*. *Animal Behaviour*, 41(2), 227-237. [https://doi.org/10.1016/S0003-3472\(05\)80474-9](https://doi.org/10.1016/S0003-3472(05)80474-9)
- Sergeant, D. E. (1973). Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. *Journal of the Fisheries Board of Canada*, 30(8), 1065-1090. <https://doi.org/10.1139/f73-178>
- Smith, A. J., Higdon, J. W., Richard, P., Orr, J., Bernhardt, W., & Ferguson, S. H. (2017). Beluga whale summer habitat associations in the Nelson River estuary, western Hudson Bay, Canada. *PLOS ONE*, 12(8), e0181045. <https://doi.org/10.1371/journal.pone.0181045>
- Stanton, M. A., & Mann, J. (2014). Social network analysis: Applications to primate and cetacean societies. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans* (pp. 345-354). Tokyo, Japan: Springer Japan. [https://doi.org/10.1007/978-4-431-54523-1\\_18](https://doi.org/10.1007/978-4-431-54523-1_18)
- Thompson, K. V. (1996). Play-partner preferences and the function of social play in infant sable antelope, *Hippotragus niger*. *Animal Behaviour*, 52(6), 1143-1155. <https://doi.org/10.1006/anbe.1996.0261>