

Short Note

Variation of Male–Male Aggression Patterns in Harbor Seals (*Phoca vitulina*)

Anders Galatius, Jonas Teilmann, Jakob Tougaard, and Rune Dietz

*Marine Mammal Research, Department of Bioscience, Aarhus University,
Frederiksborgvej 399, DK-4000 Roskilde, Denmark
E-mail: agj@bios.au.dk*

The harbor seal (*Phoca vitulina*) is a relatively small phocid seal occurring in coastal waters of the temperate and arctic Northern Hemisphere (Teilmann & Galatius, 2018). Adult females give birth once a year in late spring to early summer, followed by a suckling period of 3 to 4 wks. Mating occurs immediately after the end of suckling and takes place in the water (Sullivan, 1981; Thompson et al., 1994). The exact circumstances surrounding mating are not well understood. Studies from California and northern Europe have shown that males perform underwater displays, which include vocalizations (Hanggi & Schusterman, 1994; Van Parijs et al., 1997; Bjørgesæter et al., 2004; Sabinsky et al., 2017). This has led to the suggestion that mating occurs in a lek-type mating system (Boness et al., 2006) without significant male–male interactions. Here, the male display may serve as some sort of honest signal of male fitness to the females. In particular, the powerful underwater roar may serve as an honest indicator of low infection with lung nematodes (Sabinsky et al., 2017). In addition to the lek hypothesis, there are some reports of male–male aggression during the mating season, resulting in lacerations to the flippers and head/neck (Davis & Renouf, 1987; Thompson, 1988; Perry, 1993; Walker & Bowen, 1993).

Several authors have proposed a number of criteria for a mating system to be called a true lek system (Emlen & Oring, 1977; Bradbury, 1981; Bradbury & Gibson, 1983):

1. Extended breeding season
2. More males than receptive females at mating sites
3. Inability of males to monopolize females (no harems or territories)
4. Mobile females, allowing them to visit different lek sites
5. No male parental care
6. No resources, except males, available to females on the lek site
7. Lek site not used outside breeding season
8. Synchronization of oestrus in females
9. Opportunity for female choice
10. High paternity level for a few, successful males

Some of these conditions are clearly met in harbor seals: Conditions 3 (males are unable to monopolize females as mating occurs in water), 4 (mobile females), 5 (lack of male parental care), 8 (synchronized oestrus in females), and 9 (opportunity for female choice). Other conditions are less certain. Regarding Condition 1 (extended breeding season), male harbor seals vocalize for about 40 d in the Moray Firth, Scotland (Van Parijs et al., 1999), and females come into oestrous about the time of weaning their pups; females without pups enter oestrus about 14 d earlier (Reijnders, 1990; Atkinson, 1997). With some individual variation with regard to pupping date, a 40-d mating period is thus realistic. Regarding Condition 2 (more displaying males than receptive females), the number of active males at any time during the breeding period is unknown, and so is the duration of female receptivity. It is also uncertain whether Condition 6 (no resources on lek site) applies to harbor seals as females may also forage in areas occupied by vocalizing males. Condition 7 (lek area not used outside breeding season) is probably less relevant for aquatic species. Condition 10 is not met for harbor seals as

a high level of paternity rate for a few males has not been detected; available data suggest a modest level of paternity for most males (Coltman et al., 1998; Boness et al., 2006; Hayes et al., 2006).

Harbor seals could also use mating tactics other than lekking. It has been observed that males in some areas patrol the coastline where females have their pups instead of defending underwater territories (Van Parijs et al., 1997; Hayes et al., 2004a; Boness et al., 2006). This is suggestive of some form of mate guarding and/or scramble competition among males. In such contexts, male vocal displays could serve as *ritualized aggression*, helping males establish hierarchies to reduce physical confrontations (Hanggi & Schusterman, 1994). In this case, direct physical confrontation may be seen as an escalation from displays. Such aggressions could either aid in establishing and maintaining a hierarchy within the lek or indicate a density dependent shift between breeding strategies as has been seen in other lekking species (Bradbury & Gibson, 1983).

Male harbor seals in the wild have been observed slapping their flippers at the surface in response to playbacks of vocalizations of displaying males. Rarely is direct aggression towards the speaker observed (Hayes et al., 2004b). During the mating season, males have also been observed to have lacerations to the neck or head (Thompson, 1988) or to the hind flippers (Perry, 1993). Aggression between harbor seals on land is well documented, and it rarely escalates to violent confrontations resulting in serious injury (Sullivan, 1982; Davis & Renouf, 1987). However, such behavior is unlikely to be directly related to mating, which occurs in the water.

Boness et al. (2006) found indications that harbor seals use different strategies in different areas with regard to clear or flexible boundaries of display territories, display territory sizes, and locations relative to pupping grounds. Such differences suggest different male tactics between as well as within colonies. After a dramatic decline in the number of females due to shark predation and/or competition from grey seals, Boness et al. observed an increased number of males with a large near-shore range, indicative of a shift from a lekking-type tactic towards roving (scramble competition) for females during the mating season. Such a shift, with roving males rather than aggregations, would likely reduce the amount of aggressive interactions between males. Thus, the exact nature of the harbor seal mating system remains unclear, with indications of a lek system, some reports of male–male aggression, and evidence for variations according to demographic or other circumstances.

Herein we report lacerations observed on harbor seals caught in southern Kattegat, Denmark, during the mating seasons of 2016 and 2017, and compare our findings to those of other reports of

injuries to infer patterns of male physical confrontations. Harbor seals were caught in connection with satellite tagging operations using seine nets with a lead line to weigh down the bottom of the net and a float line to provide buoyancy to the top of the net. The nets were deployed from two boats to surround a herd of seals on land and subsequently hauled onto the beach. Caught seals were then carefully examined, weighed, measured, and equipped with satellite tags. A total of 13 harbor seals were caught at the end of and immediately after the mating period between 26 July and 12 August of 2016 and 2017 at the haulouts Bosserne, Svanegrunden, and Møllegunden around Samsø in southern Kattegat. Of these seals, four were adult males, six were juvenile males, two were adult females, and one was a juvenile female. All four adult males (100%) had open lacerations on the hind flippers, covering between approximately 25 and 70% of the lateral digit of the flipper (Figure 1). There were no visible injuries to other parts of the body (e.g., neck or face) of any of the adult males. All females and juvenile males were without visible injuries.

Reported observations and evidence of male fighting among harbor seals during the mating season are scarce, probably because they mainly take place in the water (Sullivan, 1981, 1982). Walker & Bowen (1993) saw lacerations on the face, neck, and/or hind flippers of 14 out of 22 (64%) tagged adult males during the breeding season at Sable Island, Nova Scotia, Canada. Perry (1993) observed 12 fights between males at Miquelon, Newfoundland, all described as attempts to bite the hind flipper of the opponent. One of these fights escalated to lunges at the neck, with large wounds being inflicted. Perry also noted that towards the end of the weaning period, almost all males had wounds covering large parts of their hind flippers, making it difficult to draw blood samples. Davis & Renouf (1987) observed 11 fights between adult males for which the nature of the agonistic behavior is not described in exact terms but fights were reported as being more damaging and of longer duration than conflicts between other segments of the population. Hanggi & Schusterman (1994) report aquatic fighting among male harbor seals in California, also without detailed descriptions. Thompson (1988) observed that almost all mature male harbor seals at a haulout in the Orkneys had fresh neck wounds in the latter half of July 1985. These observations were made with a telescope, and, thus, injuries to the hind flippers may have been overlooked. On Sable Island, Godsell (1988) observed 16 fights on land, also involving bites to the head, neck, and flippers, without describing patterns of escalation.



Figure 1. Typical lacerations on the lateral digit of the left hind flipper of an adult male harbor seal (*Phoca vitulina*) caught for tagging in southern Kattegat, Denmark, on 12 August 2016

Given the observations of Perry (1993) and the potential for permanent damage to important tissues in the head and neck area, fights involving lunges at these body parts seem to be an escalation from attacks on the hind flippers, which are less risky for the involved males. In many species, males compete for female reproductive capacity (Andersson, 1994). Ritualized contest behaviors reduce the risk of injury and energy cost. There is evidence that harbor seals use displays to attract females and/or establish hierarchies (Van Parijs et al., 2000). Such hierarchies would reduce the amount of physical confrontations and thus alleviate the related risks and energy expenditure. Under certain circumstances (e.g., evenly matched contestants and valuable contested resources), such confrontations may escalate to physical confrontations, which for harbor seals initially may be limited to attempted bites and grasps at the opponent's hind flippers with minor risk to the contestants. If unresolved, such fights may escalate further to lunges to the neck and head. Such escalation patterns are common in male–male behaviors related to mating privileges among many groups

of animals and serve to minimize cost and injuries for the contestants (Huntingford & Turner, 1987). However, the low sexual dimorphism in size of harbor seals indicates that powerful attacks on opponents are not central to the mating success of individual males as this would otherwise create a strong selection pressure for large size in males such as seen in truly polygynous species.

Despite the lack of data, our observations indicate differences in the nature and level of escalation of male contests as compared to previous observations by Thompson (1988), Perry (1993), and Walker & Bowen (1993) (see Table 1 for a summary of information from previous as well as our recent observations of male–male aggressions or injuries observed on males during or after the mating season). In southern Kattegat and at Miquelon (Perry, 1993), injuries to the hind flippers are common, while injuries to the head and neck seem rare. On the contrary, injuries to the head and neck were observed on almost all males in the Thompson (1988) study in the Orkneys and seemed prevalent at Sable Island based on the observations of Walker & Bowen (1993).

Table 1. Direct or indirect observations of the nature of violent harbor seal (*Phoca vitulina*) male–male interactions during the breeding season from the current and previous studies. All numbers and fractions concern adult male seals.

Area	Year(s)	Fraction with lacerations	Hind flipper bites	Head/neck bites	Method	Reference
Miquelon, off Newfoundland, Canada	1987-1988	Almost all	Almost all	Apparently few, if any	Observations of fights and caught seals	Perry, 1993
Sable Island, Nova Scotia, Canada	1991	64% ($N = 22$)	Not quantified	Not quantified	Caught and investigated	Walker & Bowen, 1993
Orkney, UK	1985	90-100% ($N > 100$)	Not quantified	90-100%	Observations of hauled-out males	Thompson, 1988
Southern Kattegat, Denmark	2016-2017	100% ($N = 4$)	100%	0%	Caught and investigated	Current study

Such differences are likely to be caused by different levels of male success. In colonies with more disparity in male success, escalations would be expected to be more common as the stakes in conflicts are higher. A factor potentially affecting disparity of male success could be fiercer competition for male territories/display grounds when the distribution of receptive females is patchier. Thus, increased violent aggression in male harbor seals may be expected to occur in a lekking-type mating system and to be reduced as the system shifts to scramble competition.

Acknowledgments

The tagging operation was carried out in connection with tagging work sponsored by the Danish Environmental Protection Agency under the “Wildlife Contract.” The Danish Environmental Protection Agency (MST-560-00060) and Animal Experiments Inspectorate (Ministry of Environment and Food of Denmark, 2015-15-0201-00549) provided the necessary permits for the handling and tagging operations of the harbor seals. We acknowledge several colleagues for assistance during the tagging and handling work.

Literature Cited

- Andersson, M. (1994). *Sexual selection*. Princeton University Press.
- Atkinson, S. (1997). Reproductive biology of seals. *Reviews of Reproduction*, 2, 175-194. <https://doi.org/10.1530/ror.0.0020175>
- Bjørøgsæter, A., Ugland, K. I., & Bjørge, A. (2004). Geographic variation and acoustic structure of the underwater vocalization of harbor seal (*Phoca vitulina*) in Norway, Sweden and Scotland. *The Journal of the Acoustical Society of America*, 116, 2459-2468. <https://doi.org/10.1121/1.1782933>
- Boness, D. J., Bowen, W. D., Buhleier, B. M., & Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology*, 61, 119-130. <https://doi.org/10.1007/s00265-006-0242-9>
- Bradbury, J. W. (1981). The evolution of leks. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior* (pp. 138-169). Chiron Press.
- Bradbury, J. W., & Gibson, R. M. (1983). Leks and mate choice. In P. Bateson (Ed.), *Mate choice* (pp. 109-138). Cambridge University Press.
- Coltman, D. W., Bowen, W. D., & Wright, J. M. (1998). Male mating success in an aquatically mating pinniped, the harbour seal (*Phoca vitulina*), assessed by microsatellite DNA markers. *Molecular Ecology*, 7, 627-638. <https://doi.org/10.1046/j.1365-294x.1998.00373.x>
- Davis, M. B., & Renouf, D. (1987). Social behavior of harbor seals, *Phoca vitulina*, on haulout grounds at Miquelon. *Canadian Field-Naturalist*, 101, 1-5.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and evolution of mating systems. *Science*, 197, 215-223. <https://doi.org/10.1126/science.327542>
- Godsell, J. (1988). Herd formation and haul-out behavior in harbor seals (*Phoca vitulina*). *Journal of Zoology*, 215, 83-98. <https://doi.org/10.1111/j.1469-7998.1988.tb04886.x>
- Hanggi, E. B., & Schusterman, R. J. (1994). Underwater acoustic displays and individual variation in male harbor seals, *Phoca vitulina*. *Animal Behaviour*, 48, 1275-1283. <https://doi.org/10.1006/anbe.1994.1363>
- Hayes, S. A., Costa, D. P., Harvey, J. T., & Le Boeuf, B. J. (2004a). Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): Are males defending the hotspot? *Marine Mammal Science*, 20, 639-656. <https://doi.org/10.1111/j.1748-7692.2004.tb01184.x>
- Hayes, S. A., Pearse, D. E., Costa, D. P., Harvey, J. T., Le Boeuf, B. J., & Garza, J. C. (2006). Mating system and reproductive success in eastern Pacific harbour

- seals. *Molecular Ecology*, 15, 3023-3034. <https://doi.org/10.1111/j.1365-294X.2006.02984.x>
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., & Le Boeuf, B. J. (2004b). Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour*, 67, 1133-1139. <https://doi.org/10.1016/j.anbehav.2003.06.019>
- Huntingford, F. A., & Turner, A. K. (1987). *Animal conflict*. Chapman and Hall. 443 pp. <https://doi.org/10.1007/978-94-009-3145-9>
- Perry, A. P. (1993). *Aquatic territory defence by male harbour seals (Phoca vitulina) at Miquelon: Relationship between active defence and male reproductive success* (Doctoral dissertation). Memorial University of Newfoundland, St. John's, Newfoundland. https://research.library.mun.ca/1667/3/Perry_ElizabethAnne2.pdf
- Reijnders, P. J. H. (1990). Progesterone and estradiol-17-beta concentration profiles throughout the reproductive cycle in harbour seals (*Phoca vitulina*). *Journal of Reproduction and Fertility*, 90, 403-409. <https://doi.org/10.1530/jrf.0.0900403>
- Sabinsky, P. F., Larsen, O. N., Wahlberg, M., & Tougaard, J. (2017). Temporal and spatial variation in harbor seal (*Phoca vitulina* L.) roar calls from southern Scandinavia. *The Journal of the Acoustical Society of America*, 141, 1824-1834. <https://doi.org/10.1121/1.4977999>
- Sullivan, R. M. (1981). Aquatic displays and interactions in harbor seals, *Phoca vitulina*, with comments on mating systems. *Journal of Mammalogy*, 62, 825-831. <https://doi.org/10.2307/1380606>
- Sullivan, R. M. (1982). Agonistic behavior and dominance relationships in the harbor seal, *Phoca vitulina*. *Journal of Mammalogy*, 63, 554-569. <https://doi.org/10.2307/1380260>
- Teilmann, J., & Galatius, A. (2018). Harbor seal (*Phoca vitulina*). In B. Würsig, J. G. M. Thewissen, & K. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 451-455). Academic Press. <https://doi.org/10.1016/B978-0-12-804327-1.00145-X>
- Thompson, P. (1988). Timing of mating in the common seal (*Phoca vitulina*). *Mammal Review*, 18, 105-112. <https://doi.org/10.1111/j.1365-2907.1988.tb00080.x>
- Thompson, P. M., Miller, D., Cooper, R., & Hammond, P. S. (1994). Changes in the distribution and activity of female harbor seals during the breeding-season—Implications for their lactation strategy and mating patterns. *Journal of Animal Ecology*, 63, 24-30. <https://doi.org/10.2307/5579>
- Van Parijs, S. M., Hastie, G. D., & Thompson, P. M. (1999). Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season. *Animal Behaviour*, 58, 1231-1239. <https://doi.org/10.1006/anbe.1999.1258>
- Van Parijs, S. M., Janik, V. M., & Thompson, P. M. (2000). Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, 78, 2209-2217. <https://doi.org/10.1139/z00-165>
- Van Parijs, S. M., Thompson, P. M., Tollit, D. J., & Mackay, A. (1997). Distribution and activity of male harbour seals during the mating season. *Animal Behaviour*, 54, 35-43. <https://doi.org/10.1006/anbe.1996.0426>
- Walker, B. G., & Bowen, W. D. (1993). Behavioral differences among adult male harbor seals during the breeding season may provide evidence of reproductive strategies. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, 71, 1585-1591. <https://doi.org/10.1139/z93-224>