

RESEARCH NOTE

Bowhead whales (*Balaena mysticetus*) are copycats, imitating sounds heard in their environment

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Abstract

In this study, we provide evidence that bowhead whales (*Balaena mysticetus*) imitate bearded seal (*Erignathus barbatus*) calls, integrating them into their own elaborate songs, demonstrating this cetacean species' capacity for complex vocal learning. Bowhead whales also appear to imitate additional species—narwhal (*Monodon monoceros*)—and even environmental noise (ice sounds) in the Svalbard area. This behaviour likely reflects evolutionary pressure related to song diversity, mating success and ecological adaptation.

Keywords

Arctic marine mammal; complex vocal learning; song evolution; Svalbard; vocal imitation; mimicry

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Abbreviations

EGSB: East Greenland–Svalbard–Barents Sea
NPI: Norwegian Polar Institute

To access the supplementary material, please visit the article landing page

Introduction

Vocal imitation has received considerable research attention in recent decades, partly because our own species is so deeply dependent on acoustic communication (Vernes et al. 2021). Discussions related to this theme have revolved around, among other things, the cognitive skills associated with vocal production and learning and the definitions of imitation or mimicry from a psychological or biological perspective (Mercado et al. 2014). Herein, we use “the capacity to reproduce novel sounds, new to a species' repertoire, based on an auditory input previously experienced” as the definition for vocal mimicry (Nowicki & Searcy 2014; Tyack 2019). This definition differentiates clearly between true vocal learning and other forms of contextual reproduction or spontaneous emission of a sound (Janik 2014; Mercado et al. 2014).

From an evolutionary perspective, vocal imitation is a relevant feature in the emergence of animal vocal cultures and song dialects, but it has an erratically scattered phylogenetic distribution and is a relatively rare trait (Verpooten 2021). Vocal imitation has been reported in avian taxa (songbirds, parrots and hummingbirds) and in mammals (bats, cetaceans, elephants, pinnipeds and humans), suggesting independent evolution of the trait in different clades (Petkov & Jarvis 2012; Tyack 2019).

There is ongoing discussion in the scientific community as to why complex vocal learning is so rare (especially among non-human primates), but it is likely linked to requirements for having specialized neural pathways (Janik & Slater 1997; Nowicki & Searcy 2014; Tyack 2019), general cognitive flexibility (Mercado et al. 2014) and perhaps also a particular suite of socio-ecological traits (Carouso-Peck et al. 2021; Verpooten 2021). Numerous hypotheses have been postulated for the evolutionary origin of vocal imitation, including the mate choice hypothesis (Nottebohm 1972), according to which song learning is driven by sexual selection favouring diverse or specific types of songs; the social cohesion hypothesis (Janik & Slater 1997) that suggests that vocal learning helps maintain individual or group identity; the cooperation and coordination hypothesis (Tomasello 2008) that promotes the idea that vocal learning facilitates group-level coordination; and the dimensionality hypothesis (Puts 2010), which postulates that mechanisms involved in sexual selection drive the development of complex vocal learning in ways that are linked to the dimensionality of the physical environment (Verpooten 2021). These hypotheses and the scattered taxonomic distribution of the trait highlight that a multi-function origin cannot be ruled out. There is, however, some commonality in the non-primate animals that are capable of

complex vocal learning and perform imitation: most of these species inhabit complex three-dimensional environments and have courtship songs that are used to attract partners that cannot be physically monopolized because of a lack of spatial constraints. This theory is consistent with recent theoretical advances—i.e., the coercion and dimensionality hypotheses—along with the long-standing hypothesis that mate choice is a major driver of the origin and evolution of complex vocal learning (Verpoeten 2021).

Complex vocal learning in whales

The only non-primate mammalian group that includes several species capable of complex vocal learning is cetaceans (Mercado et al. 2014). Vocal imitation in whales has been studied in different contexts, supporting the use of complex vocal learning in identity signals, social cohesion and the emergence of culture. Bottlenose dolphins (*Tursiops truncatus*) copy distinctive signature whistles, using them in close interactions among mother–calf pairs and male alliances (King et al. 2013). Killer whales (*Orcinus orca*) can learn novel sounds quickly from conspecifics and humans (Abramson et al. 2018). Members of different killer whale pods have progressively changed shared call types over multiyear periods while leaving other call types unchanged (Deecke et al. 2000), supporting the idea that dialects observed in natural populations can be socially learned by imitation. Sound imitation of other species by white whales (*Delphinapterus leucas*) has repeatedly been reported (Vergara & Barrett-Lennard 2008; Ridgway et al. 2012; Panova & Agafonov 2017).

Some baleen whales display complex vocal learning with respect to song (Janik 2014). The whale that has been most studied in this regard is the humpback whale (*Megaptera novaeangliae*). In this species males sing, primarily during the breeding season, with a pattern wherein most males within a population produce very similar songs at a given time, but song structure changes within and across years, spreading among populations (Tyack 2018). These patterns suggest that humpback whales might be imitating the songs they hear sung by neighbouring whales (Garland & Rendell 2024). It is difficult to explain the diversity of songs and the rapid evolution of the singing repertoire, synchronized in multiple individuals, without the involvement of complex vocal learning (Janik & Knörnschild 2021; Mercado 2022).

The bowhead whale (*Balaena mysticetus*) also sings complex songs (Tervo et al. 2011; Stafford et al. 2012). Although previously considered to have a simpler song structure than humpback whales, bowhead whales in

the EGSB population have been recently shown to have a remarkably diverse song repertoire (Stafford et al. 2018). Bowhead whale singing behaviour is seasonal, being detected mainly from October to April, peaking in the winter months around the time of peak breeding (Moore et al. 2012). The structure of bowhead whale song consists of a few basic phrases repeated in series (simple song), but these elements can be accompanied by frequency-modulated and amplitude-modulated sounds that can be produced independently or combined simultaneously in song units (biphonism), creating song compositions that differ greatly in structure (Stafford 2022). Unlike humpback whales, bowhead whales change their song structure continuously, generating vast intra- and interannual variability, such that a song first detected in autumn might not be used by the following spring (Stafford et al. 2018). The EGSB bowhead whale population is the most ice-affiliated population across the species' range (Kovacs et al. 2020), and it exhibits the greatest song diversity (Stafford et al. 2018). The purpose of this extreme song diversity is not known, but it is assumed that it plays a role in bowhead whale reproductive tactics (Würsig & Clark 1993).

Bowhead whale vocalizations in the Svalbard area

We recently reported diverse, complex singing by bowhead whales throughout winter in what is likely a newly discovered breeding ground of the EGSB population in north-east Svalbard, Norway (Llobet et al. 2023). During manual inspection of these acoustic data (see the Supplementary material for instrument and methodological details), we found several examples of bowhead whales imitating bearded seals (*Erignathus barbatus*). The most distinctive examples involved bearded seal long trill vocalizations being embedded in the bowhead songs (Fig. 1). The long trill (Fig. 1c) is a highly stereotyped bearded seal vocalization that involves an extended, frequency-descending vocalization and pronounced frequency modulation combined with marked frequency steps (Risch et al. 2007). In eastern Svalbard, these calls are heard starting in late autumn at low rates and increasing until the bearded seal's mating period in spring (April–May; Llobet et al. 2023). The first imitation event was detected in spectrograms from early winter 2020 (22 December 2020). Imitated bearded seal trills were incorporated into bowhead whale songs for several weeks thereafter at this site (Fig. 1a, b). Further inspection of acoustic recordings from this area produced several additional cases of bearded seal imitations by bowhead whales

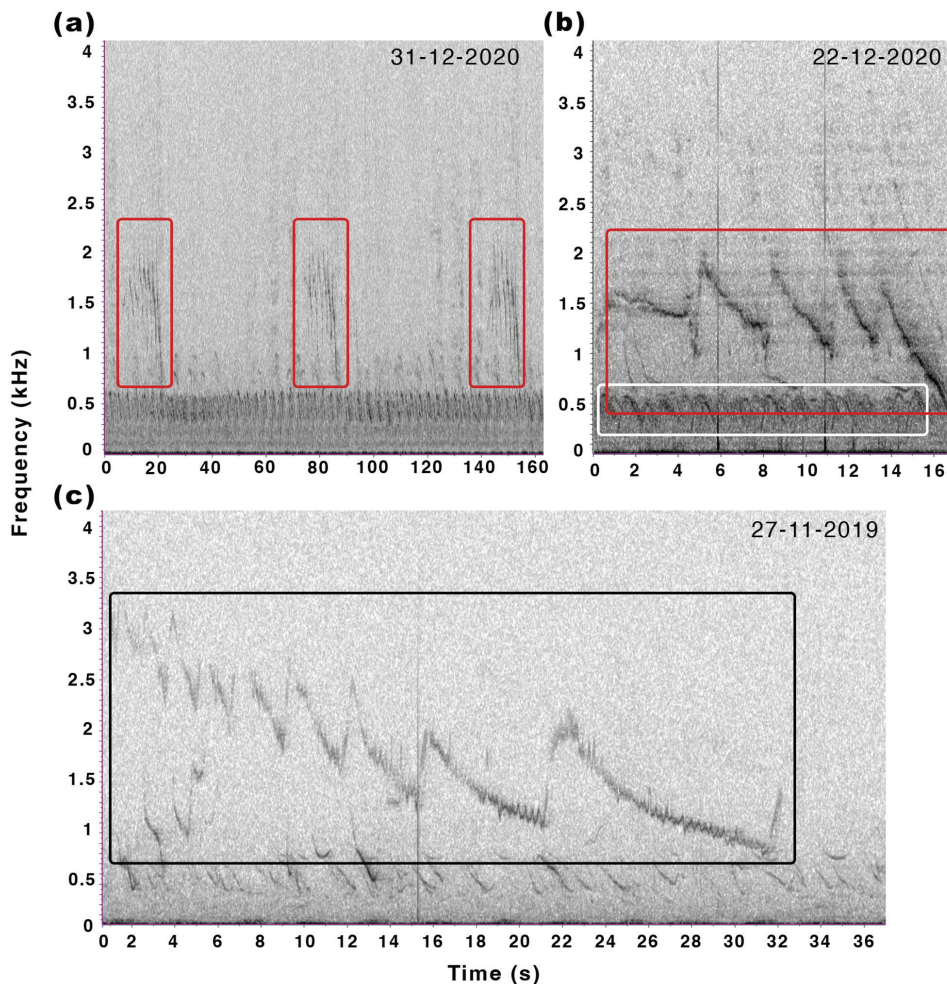


Fig. 1 (a) A section of a bowhead whale vocalization with embedded imitated bearded seal long trill song elements (framed by the red rectangles), recorded on 31 December 2020. (b) Close-up of imitated bearded seal long trill elements in a bowhead whale's song and background bowhead whale chorus (white rectangle), recorded on 22 December 2020 at the same site as the song depicted in (a). (c) Example of bearded seal long trill vocalization (framed by the black rectangle), recorded at the same location as (a) and (b) on 27 November 2019. Note the similar frequency band used by the two species for this song element and the similar duration of the down-sweep elements.

from different years and seasons (Fig. 2). Frequency modulation is characteristic of the bowhead whale's own vocal behaviour; however, the similarities in duration, highest and lowest frequencies and the classical bearded seal down-sweep rates in the trill sounds produced by the bowhead whales were quite clearly imitations of the other species. Examples of bowhead whales imitating bearded seal sounds other than the downward sweeping long trill can be seen in Fig. 2; see also the Supplementary sound files. It is noteworthy that the imitated sounds were incorporated into the song pattern of the bowhead whales in various ways. This was a diagnostic feature identifying the sounds as belonging to bowhead whales, since such structured repeats do not occur in bearded seal singing behaviour.

Spectral correlation analysis conducted on sound pairs (bowhead whale versus bearded seal) produced moderate correlation values (Supplementary Table S1). But this analytical tool does not account for some qualitative elements, such as the fact that the long trill of the bearded seal is a highly stereotyped descending vocalization with very diagnostic frequency steps, limiting the value of this tool in this context.

We also found cases where it appears that bowhead whales were imitating pulsed tones from narwhals (*Monodon monoceros*), but these sounds are not stereotyped in the manner of bearded seal calls, leaving some uncertainty as to whether the bowhead whales are imitating these sounds (Supplementary Fig. S1). Similarly, we found examples of sea-ice-like squeaking together

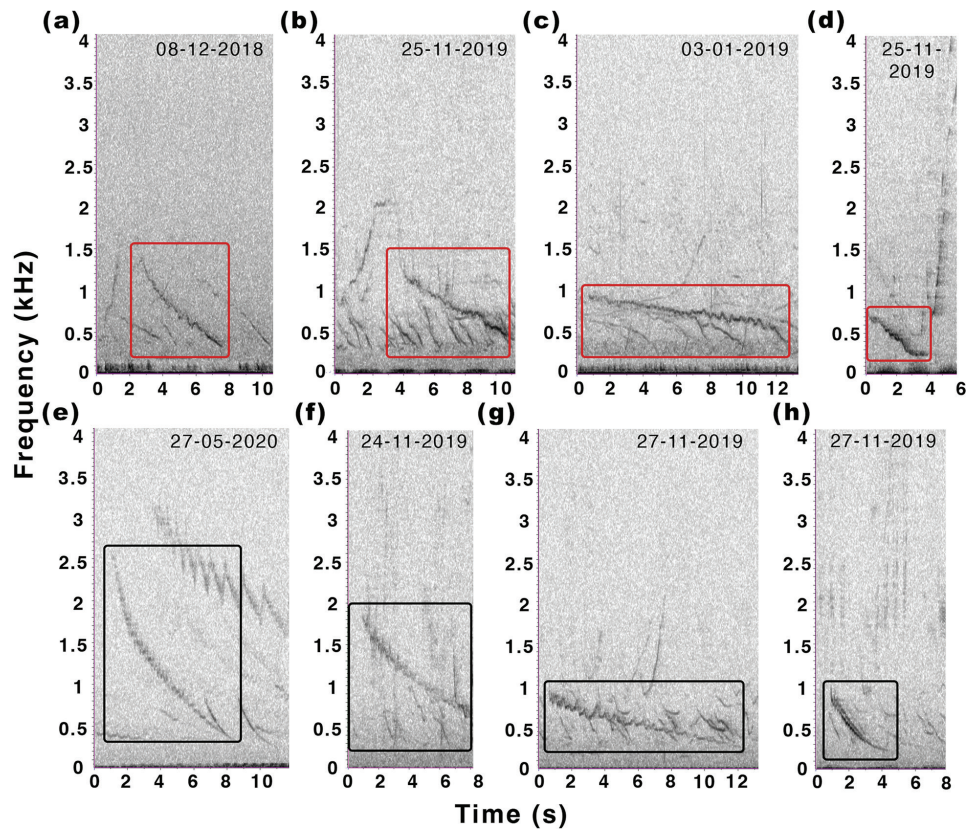


Fig. 2 (a–d) Bowhead whale songs that incorporate imitations of various bearded seal sounds (framed in red), recorded across different seasons in north-eastern Svalbard and the bearded seal equivalents of these sound types (framed in black): (e) boomerang trill; (f) step trill fragment; (g) linear trill and (h) linear sweep.

with amplitude-modulated sounds that end in frequency-modulated sweeps in bowhead whale songs (Supplementary Fig. S2), but again there is uncertainty as to whether bowheads are actually imitating these noises when they produce these sounds.

It is noteworthy that bearded seals were the main target of the bowhead whale imitations. Both species are major contributors to the biotic soundscape in the Svalbard region, and their songs occupy a similar frequency range. Males of both species vocalize virtually continuously during their respective mating seasons to attract potential female partners, using elaborate songs. Their peak vocal periods do not overlap, but both species vocalize at other times of year as well, and they do co-exist in drift-ice areas (and they presumably co-occurred in Svalbard’s ice-covered fjords before whales in these areas were extirpated in the 17th century). The two species are therefore acoustically exposed to one another’s songs.

Some authors have suggested that the dynamic Arctic soundscape might act as a driver of novelty in bowhead whale singing behaviour (Clark et al. 2015; Stafford 2022). Although little is known about the specifics of the

bowhead whale’s mating system, it is presumed to be similar to the other right whale species given the similar morphologies of males (a very long penis compared to other baleen whales and very large testicles) and their general social behaviour; males do not engage in direct combat. The system is thought to be polygynandrous with sperm competition and potentially female choice playing roles (given that females cannot be physically restrained) in determining male mating success (Koski et al. 2023). Bowhead whales live a long life in a three-dimensional habitat with high seasonal variability, where their soundscape can be both cluttered and continuously changing. Their songs, while highly structured, evolve continuously, and their complexity might serve as an indicator of individual fitness and thus be subject to strong selection pressure. The use of long-duration, highly frequency modulated sounds (trills) has been suggested to be an indicator of physical fitness among songbirds and bearded seals (Van Parijs et al. 2003; Ballentine et al. 2004), and incorporating such challenging vocalizations may serve a similar role in bowhead whales (Erbs et al. 2021).

Conclusion

Stafford & Clark (2021) stated that bowhead whales are superb “mimics” of the ice and of other species living in the ice. But documentation of these remarkable skills has not previously been brought into the scientific literature for further scrutiny and reflection. We think that the vocal skills of this species are quite remarkable and warrant more systematic study. Although the bowhead whale’s breeding areas present significant logistical challenges, further, more systematic studies of the role of imitation and complex vocal learning in its mating behaviour will deepen our understanding of the species’ ecology.

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Disclosure statement

The authors declare no conflict of interest.

Data availability

The data to reproduce the results of this study are available at the NPI’s Norwegian Polar Data Centre (contact via Heidi Ahonen).

References

Abramson J.Z., Hernández-Lloreda M.V., García L., Colmenares F., Aboitiz F. & Call J. 2018. Imitation of novel conspecific and human speech sounds in the killer whale (*Orcinus orca*). *Proceedings of the Royal Society B* 285, article no. 20172171, doi: 10.1098/rspb.2017.2171.

- Ballentine B., Hyman J. & Nowicki S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioural Ecology* 15, 163–168, doi: 10.1093/beheco/arg090.
- Carouso-Peck S., Goldstein M.H. & Fitch W.T. 2021. The many functions of vocal learning. *Philosophical Transactions of the Royal Society B* 376, article no. 20200235, doi: 10.1098/rstb.2020.0235.
- Clark C.W., Berchok L.L., Blackwell S.B., Hannay D.E., Jones J., Ponirakis D. & Stafford K.M. 2015. A year in the acoustic world of bowhead whales in the Bering, Chukchi and Beaufort seas. *Progress in Oceanography* 136, 223–240, doi: 10.1016/j.pocean.2015.05.007.
- Deecke V.B., Ford J.K.B. & Spong P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour* 60, 629–638, doi: 10.1006/anbe.2000.1454.
- Erbs F., van der Schaar M., Weissenberger J., Zaugg S. & André M. 2021. Contribution to unravel variability in bowhead whale songs and better understand its ecological significance. *Scientific Reports* 11, article no. 168, doi: 10.1038/s41598-020-80220-5.
- Garland E.C. & Rendell L. 2024. Culture in cetaceans. In J.J. Tehrani et al. (eds.): *The Oxford handbook of cultural evolution*. Pp. 325–338. Oxford: Oxford University Press.
- Janik V.M. 2014. Cetacean vocal learning and communication. *Current Opinions in Neurobiology* 28, 60–65, doi: 10.1016/j.conb.2014.06.010.
- Janik V.M. & Knörnschild M. 2021. Vocal production learning in mammals revisited. *Philosophical Transactions of the Royal Society B* 376, article no. 20200255, doi: 10.1098/rstb.2020.0244.
- Janik V.M. & Slater P.J.B. 1997. Vocal learning in mammals. *Advances in the Study of Behaviour* 26, 59–100, doi: 10.1016/S0065-3454(08)60377-0.
- King S.L., Sayigh L.S., Wells R.S., Fellner W. & Janik V.M. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proceedings of the Royal Society B* 280, article no. 20130053, doi: 10.1098/rspb.2013.0053.
- Koski W.R., George J.C. & Würsig B. 2023. Bowhead whale reproductive strategy. In B. Würsig & D.N. Orbach (eds.): *Sex in cetaceans. Morphology, behaviour and the evolution of sexual strategies*. Pp. 521–541. Cham: Springer.
- Kovacs K.M., Lydersen C., Vacquière-García J., Shpak O., Glazov D. & Heide-Jørgensen M.P. 2020. The endangered Spitsbergen bowhead whales’ secrets revealed after hundreds of years in hiding. *Biology Letters* 16, article no. 20200148, doi: 10.1098/rsbl.2020.0148.
- Llobet S.M., Ahonen H., Lydersen C. & Kovacs K.M. 2023. The Arctic and the future Arctic? Soundscapes and marine mammal communities on the east and west sides of Svalbard characterized through acoustic data. *Frontiers in Marine Science* 10, article no. 1208049, doi: 10.3389/fmars.2023.1208049.
- Mercado E. III. 2022. Intra-individual variation in the songs of humpback whales suggests they are sonically searching for conspecifics. *Learning & Behavior* 50, 456–481, doi: 10.3758/s13420-021-00495-0.

- Mercado E. III, Mantell J.T. & Pfordresher P.Q. 2014. Imitating sounds: a cognitive approach to understanding vocal imitation. *Comparative Cognition and Behavioural Reviews* 9, 1–57, doi: 10.3819/ccbr.2014.90002.
- Moore S.E., Stafford K.M., Melling H., Berchok C., Wiig Ø., Kovacs K.M., Lydersen C. & Richter-Menge J. 2012. Comparing marine mammal acoustic habitats in Atlantic and Pacific sectors of the High Arctic: year-long records from Fram Strait and the Chukchi Plateau. *Polar Biology* 35, 475–480, doi: 10.1007/s00300-011-1086-y.
- Nottebohm F. 1972. The origins of vocal learning. *The American Naturalist* 106, 116–140, doi: 10.1086/282756.
- Nowicki S. & Searcy W.A. 2014. The evolution of vocal learning. *Current Opinion in Neurobiology* 28, 48–53, doi: 10.1016/j.conb.2014.06.007.
- Panova E.M. & Agafonov A.V. 2017. A beluga whale socialized with bottlenose dolphins imitates their whistles. *Animal Cognition* 20, 1153–1160, doi: 10.1007/s10071-017-1132-4.
- Petkov C.I. & Jarvis E.D. 2012. Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. *Frontiers in Evolution and Neuroscience* 4, article no. 12, doi: 10.3389/fnevo.2012.00012.
- Puts D.A. 2010. Beauty and the beast: mechanisms of sexual selection in humans. *Evolution and Human Behavior* 31, 157–175, doi: 10.1016/j.evolhumbehav.2010.02.005.
- Ridgway S.H., Carder D.A., Jeffries M. & Todd M. 2012. Spontaneous human speech mimicry by a cetacean. *Current Biology* 22, R860–R861, doi: 10.1016/j.cub.2012.08.044.
- Risch D., Clark C.W., Corkeron P.J., Elepfandt A., Kovacs K.M., Lydersen C., Stirling I. & Van Parijs S.M. 2007. Vocalizations of male bearded seals, *Erignathus barbatus*: classification and geographical variation. *Animal Behaviour* 73, 747–762, doi: 10.1016/j.anbehav.2006.06.012.
- Stafford K.M. 2022. Singing behavior in the bowhead whale. In C.W. Clark & E.C. Garland (eds.): *Ethology and behavioral ecology of mysticetes*. Pp. 277–295. Cham: Springer.
- Stafford K.M. & Clark C.W. 2021. Acoustic behavior. In J.C. George & J.G.M. Thewissen (eds.): *The bowhead whale. Balaena mysticetus: biology and human interaction*. Pp. 323–338. London: Academic Press.
- Stafford K.M., Lydersen C., Wiig Ø. & Kovacs K.M. 2018. Extreme diversity in the songs of Spitsbergen's bowhead whales. *Biology Letters* 14, article no. 20180056, doi: 10.1098/rsbl.2018.0056.
- Stafford K.M., Moore S.E., Berchok C.L., Wiig Ø., Lydersen C., Hansen E., Kalmbach D. & Kovacs K.M. 2012. Spitsbergen's endangered bowhead whales sing through the polar night. *Endangered Species Research* 18, 95–103, doi: 10.3354/esr00444.
- Tervo O.M., Parks S.E., Christoffersen M.F., Miller L.A. & Kristensen R.M. 2011. Annual changes in the winter song of bowhead whales (*Balaena mysticetus*) in Disko Bay, eastern Greenland. *Marine Mammal Science* 27, E241, doi: 10.1111/j.1748-7692.2010.00451.x.
- Tomasello M. 2008. *Origins of human communication*. Cambridge, MA: MIT Press.
- Tyack P.L. 2018. Mimicry. In B. Würsig et al. (eds.): *Encyclopedia of marine mammals*. Pp. 606–608. London: Academic Press.
- Tyack P.L. 2019. A taxonomy for vocal learning. *Philosophical Transactions of the Royal Society B* 375, article no. 20180406, doi: 10.1098/rstb.2018.0406.
- Van Parijs S.M., Lydersen C. & Kovacs K.M. 2003. Vocalizations and movements suggest alternative mating tactics in male bearded seals. *Animal Behaviour* 65, 273–283, doi: 10.1006/anbe.2003.2048.
- Vergara V. & Barrett-Lennard L.G. 2008. Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals* 34, 123–143, doi: 10.1578/AM.34.1.2008.123.
- Vernes S.C., Janik V.M., Fitch W.T. & Slater P.J.B. 2021. Vocal learning in animals and humans. *Philosophical Transactions of the Royal Society B* 376, article no. 20200234, doi: 10.1098/rstb.2020.0234.
- Verpooten J. 2021. Complex vocal learning and three-dimensional mating environments. *Biology & Philosophy* 36, article no. 12, doi: 10.1007/s10539-021-09786-2.
- Würsig B. & Clark C.W. 1993. Behavior. In J.J. Burns et al. (eds.): *The bowhead whale*. Pp. 157–199. Lawrence, KS: Allen Press.