

## Yawn-Like Behavior in a Beluga Whale (*Delphinapterus leucas*)

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The yawn is a ubiquitous behavior marked by involuntary mouth opening with elongated inspiration, a peak in mouth gape, followed by a slow expiration with simultaneous mouth closure (Baenninger, 1997; Walusinski & Deputte, 2004; Guggisberg et al., 2010; Palagi et al., 2020). This basic yawning pattern is phylogenetically widespread as it has been reported for primate species (e.g., chimpanzees [*Pan troglodytes*]: Vick & Paukner, 2010; geladas [*Theropithecus gelada*]: Palagi et al., 2009; Tonkean macaques [*Macaca tonkeana*]: Zannella et al., 2017; and humans [*Homo sapiens*]: Provine & Hamernik, 1986; Provine, 2012) and other mammals (e.g., rats: Anias et al., 1984; African lions [*Panthera leo*]: Baenninger, 1987; African elephants [*Loxodonta africana*]: Rossman et al., 2020; wolves [*Canis lupus lupus*]: Romero et al., 2014; and domestic dogs [*Canis lupus familiaris*]: Silva et al., 2012; Romero et al., 2013), amphibians (Bakkegard, 2017; Hartzell et al., 2017), reptiles (Luttenberger, 1975), and some species of birds (Sauer & Sauer, 1967) and fish (Baenninger, 1987). Open mouth behavior similar to this sequence has also been noted for humans (Van Woerden et al., 1988; Sherer et al., 1990; Sepulveda & Mangiamarchi, 1995; Petrikovsky et al., 1999) and rats (Smotherman & Robinson, 1987) *in utero* but has been classified as “yawning without breathing” (Enokizu et al., 2021, p. 2; Enokizu et al., 2022, p. 106) given that fetuses do not breathe through the adult respiratory mechanism. As a result of removing breath from defining the typical yawn sequence, yawn-like behavior may also be classified in aquatic species. Fully aquatic mammals, for example, are voluntary breathers with an anatomically separate trachea and esophagus and, thus, do not breathe through the mouth (e.g., Enokizu et al., 2021, 2022). However, some open mouth behaviors observed in the common bottlenose dolphin (*Tursiops truncatus*; Enokizu et al., 2021) and dugong (*Dugong dugon*; Enokizu et al., 2022) have been described as “yawn-like” as mouth opening and closing behavior during these open mouth

events resembles that of humans and other terrestrial mammals.

In humans, the function of yawning is unclear. Hypotheses regarding yawn behavior range from sleepiness, respiration and/or circulatory needs, boredom and arousal, empathy, and thermoregulation among others (for a review, see Guggisberg et al., 2010). In animals, yawning or yawn-like behavior may occur as a reaction to encountering a conspecific (Siamese fighting fish [*Betta splendens*]: Baenninger, 1987), as an indicator of stress (bugerigars [*Melopsittacus undulatus*]: Miller et al., 2010), related to feeding (Herman’s tortoises [*Testudo hermanni*] and European pond turtles [*Emys orbicularis*]: Luttenberger, 1975; lions and mandrills [*Papio sphinx*]: Baenninger, 1987; Red Hills salamanders [*Phaeognathus hubrichti*]: Bakkegard, 2017; and eastern hellbender salamanders [*Cryptobranchus alleganiensis alleganiensis*]: Hartzell et al., 2017), or during rest (e.g., ostrich [*Struthio camelus australis*]: Sauer & Sauer, 1967; and elephants: Rossman et al., 2020). In aquatic mammals (South American sea lions [*Otaria fave-scens*]: Palagi et al., 2019; dolphins: Enokizu et al., 2021; and dugongs: Enokizu et al., 2022), yawning or yawn-like behavior may be associated with drowsiness and arousal as it occurs during resting states.

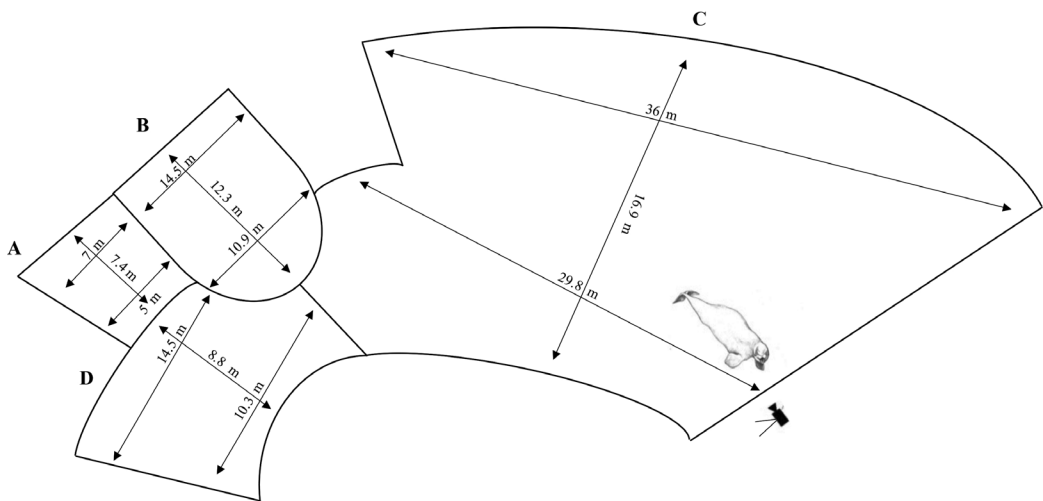
Some aspects of yawn behavior may be socially modulated. Yawn contagion, for example, is a physiological response found in several species of social animals, including humans, that occurs when individuals yawn after perceiving a yawn in another individual (for a review, see Palagi et al., 2020). Contagious yawning has been found in all hominine species (chimpanzees: Anderson et al., 2004; Campbell & de Waal, 2011, 2014; Campbell & Cox, 2019; bonobos [*Pan paniscus*]: Demuru & Palagi, 2012; Tan et al., 2017; and humans: Provine & Hamernik, 1986; Provine, 1989), as well as in orangutans (*Pongo pygmaeus*: van Berlo et al., 2020), cercopithecoid monkeys (geladas: Palagi et al., 2009; Gallo et al., 2021;

and Tonkean macaques: Palagi & Norscia, 2019), elephants (Rossman et al., 2020), lions (Casetta et al., 2021), wolves (Romero et al., 2014), dogs (Joly-Mascheroni et al., 2008; Silva et al., 2012; Romero et al., 2013), and rats (Moyaho et al., 2015). Yawn contagion also occurs interspecifically between humans and other mammal taxa. For example, chimpanzees show higher yawn contagion to humans (both unfamiliar and familiar) than to unfamiliar chimpanzees (Campbell & de Waal, 2014). Similarly, elephants (Rossman et al., 2020) and dogs (Joly-Mascheroni et al., 2008; Silva et al., 2012; Romero et al., 2013) yawn in response to yawning from familiar human caretakers. Herein is provided what is, to the author's knowledge, the first documentation of possible yawn-like behavior in a beluga whale (*Delphinapterus leucas*) while exploring yawn contagion as a possible explanation for this behavior.

During a behavioral observation session for a larger study on beluga vocal development (Ames & Vergara, 2020), a ~20-year-old female beluga ("Yulka"; Oceanogràfic, Valencia, Spain) displayed what appeared to be a yawn-like open mouth behavior (see supplementary video; the supplementary video for this paper is 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](https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147)) in response to a yawn by her human observer (the author, AEA). AEA observed and recorded (using a Canon Vixia HF R700; Canon,

Tokyo, Japan) Yulka's behavior twice daily for 1 h each observation session during the pre-partum period of the larger study (see Ames & Vergara, 2020, for detailed methodology). During a morning observation session, Yulka was drifting at the top of the water column in Oceanogràfic's beluga habitat, oriented towards AEA, when the author spontaneously yawned. During the final phase of the author's yawn (expiration and mouth closure), Yulka tilted her head down and displayed an open mouth behavior for a similar duration to that of the author's yawn (~2 s). There was an obvious climax to Yulka's open mouth behavior, and Yulka was quicker to close than to open her mouth, similar to a typical yawn sequence (e.g., Palagi et al., 2020). Curiously, Yulka emitted a bubble stream immediately following the closure of her mouth, almost as if some exhalation was present at the end of the behavior.

As previously mentioned, it is difficult to classify typical yawning in aquatic mammals given that yawning in the aquatic environment would occur separately from breathing, and open mouth behaviors can also be indicative of alternative behavioral states. Belugas, for example, typically display open mouth behaviors in agonistic and socio-sexual interactions with conspecifics (e.g., Hill et al., 2015), so it is possible that Yulka's open mouth behavior was due to some environmental input related to these contexts. However, Yulka's only other social group member during this period within the larger study ("Kairo," a male beluga estimated to be in his mid-50s) was in a different



**Figure 1.** The pool layout of Oceanogràfic's beluga (*Delphinapterus leucas*) habitat adapted from Ames & Vergara (2020, Figure 1): (A) medical pool, (B) reproduction pool, (C) main public viewing pool, and (D) smaller public viewing pool. The "beluga" (sketch adapted from Hill et al., 2015, with permission from the original artist, Roni Dietrich) marks Yulka's location, and the "camera" marks AEA's location. Kairo was not visible on camera in pool C, which suggested he was in pool B or D at the time of the event.

habitat pool at the time of the event (Figure 1). It is possible that Yulka was directing agonistic or other behavior towards AEA, but Yulka's open mouth behavior was not accompanied by additional agonistic (e.g., bites, head jerks, melon thrusts, jaw claps; Hill et al., 2015; Lilley et al., 2020) or socio-sexual (e.g., S-postures, lateral swims, body/genital rubbing, pelvic thrusts; Hill et al., 2015) behavioral indicators. During the open mouth event, Yulka was slowly drifting at the surface of her habitat, reminiscent of the resting states for which yawning has been described to occur in dolphins and dugongs (Enokizu et al., 2021, 2022). Moreover, agonistic open mouth events are generally  $< 1$  s in duration (Hill et al., 2015), while Yulka's open mouth behavior was  $\sim 2$  s in duration, similar to the duration of yawn-like behavior in dolphins (Enokizu et al., 2021). Finally, the time elapsed from the beginning of Yulka's open mouth behavior to her maximum mouth gape was  $\sim 1$  s in duration, with mouth closure occurring in  $< 1$  s. An open-close duration ratio (i.e., the duration of mouth closure divided by the duration of mouth opening to maximum gape) of  $\leq 1$  is a characteristic of yawning in humans (Barbizet, 1958) and of reported yawn-like behavior in dolphins (Enokizu et al., 2021) and dugongs (Enokizu et al., 2022). Consequently, Yulka's open mouth behavior could be classified as yawn-like, though this raises additional questions as to whether this event was in response to AEA's initiating yawn and whether this exchange was due to yawn contagion.

Yulka was facing AEA at the time of the event, and the author was the only human in the observation area. As stated, it was unlikely Yulka was responding to another social group member, so if Yulka's behavior was a response, it was likely elicited via observation of her human observer. The slight overlap between the end of AEA's yawn and Yulka's open mouth behavior was inconsistent with what has been observed for the timing of yawn contagion in other species, however. Responses to contagious yawns commonly occur several minutes after the initiating yawn (Palagi et al., 2020). In elephants (Rossman et al., 2020) and dogs (Joly-Mascheroni et al., 2008), for example, yawn contagion occurred at least 1 min after repeated yawning by familiar handlers.

In elephants, it is unknown whether familiarity between allospecifics is influential to contagious yawning (Rossman et al., 2020), but familiarity seems to be key in dictating yawn contagion between humans and dogs, and may be related to bond maintenance (Joly-Mascheroni et al., 2008; Silva et al., 2012; Romero et al., 2013). Yulka has been a subject of AEA's ongoing research regarding beluga whales since the beginning of the larger

study (Ames & Vergara, 2020) in September 2016. However, the current case occurred early within data collection for the larger study, so it was unlikely that Yulka was familiar with AEA at the time of the event (or possibly ever throughout the course of the study), although yawn contagion can occur between humans and animals with no degree of familiarity between allospecifics (Campbell & de Waal, 2014).

Alternatively, Yulka's open mouth behavior may have been an imitation of AEA's yawn. Imitation occurs when an individual learns about a behavior by observing another perform it (e.g., Whiten & Ham, 1992; Heyes, 1993). Like yawn contagion, imitation is driven socially (e.g., as a form of social learning; Whiten & Ham, 1992; Heyes, 1993; Kuczaj & Yeater, 2006), but imitation and yawn contagion appear to be mutually exclusive explanations for this open mouth behavior in non-human animals. Imitation, for example, was ruled out as a likely source of open mouth behavior in yawn contagion studies of dogs (Romero et al., 2013) and elephants (Rossman et al., 2020) as responses of animals in mouth movement control trials (i.e., trials in which humans performed mouth-opening or gaping movements without other yawning indicators) were significantly lower than responses during trials in which a familiar human yawned. Yawning may be contagious, then, due to perceived bonds between individuals that are not necessary for successful imitation to occur.

Belugas are known imitators. Individuals have been shown to replicate play behaviors (Jones & Kuczaj, 2014), trained behaviors (Abramson et al., 2017), and vocalizations of conspecifics (e.g., Vergara & Barrett-Lennard, 2008; Murayama et al., 2014) and allospecifics (e.g., Panova & Agafonov, 2017). Some anecdotal (Eaton, 1979; Ridgway et al., 2012) and empirical (Murayama et al., 2014) evidence indicates that belugas imitate human speech. One whale appeared to repeat his own name (Eaton, 1979), while another spontaneously emitted human speech-like sounds (Ridgway et al., 2012). However, there are no reports to the author's knowledge of instances during which belugas matched the motor movements of humans like what has been described herein. Known as kinesthetic imitation (Kuczaj & Yeater, 2006), matching motor movements with other individuals is common in mammals. Examples of kinesthetic imitation in humans include the imitation of facial behaviors (Meltzoff & Moore, 1977; Meltzoff & Prinz, 2002); and in marine mammals, kinesthetic imitation is exemplified in the synchronous behavior of bottlenose dolphins (e.g., Connor et al., 2000; Bauer & Harley, 2001; Herman, 2002; Kuczaj et al., 2012). Bottlenose dolphins have been shown to kinesthetically imitate human behaviors as well. For

example, a dolphin that watched a human push a kickboard with his head on the surface of the water then pushed the kickboard with its rostrum (Kuczaj & Yeater, 2006), and dolphins use echolocation to aid in imitating human-modeled behavior underwater (Jaakkola et al., 2013). Given the beluga's propensity for imitation and social learning, belugas may also have the ability to imitate human motor movements.

In summary, Yulka's open mouth behavior was yawn-like as characteristics of the behavior were similar to what has been described for yawning in other mammal taxa, including a fellow delphinoid species. Further, behavioral indicators corresponding with other beluga open mouth behaviors were not present. More rigorous empirical study is required to elucidate this behavior further in the beluga whale. Future directions of research regarding yawn-like behavior in fully aquatic mammals may illuminate more on yawning as a "breathless" behavior which, in turn, may have implications for the function of this behavior in humans. It was difficult to attribute Yulka's yawn-like behavior to either yawn contagion or imitation, though, as it could not be determined if Yulka's behavioral display was a response to AEA's spontaneous yawn. However, if this were the case, the timing of the event (i.e., the overlap between the spontaneous yawn and the yawn-like behavior) was inconsistent with interspecies yawn contagion in other mammals. This does not eliminate yawn contagion as an explanation for Yulka's open mouth display, but imitation seems more likely given that belugas are demonstrated social learners. Ultimately, empirical study on interspecific kinesthetic imitation in belugas and humans would be necessary to confirm this ability in the beluga. Yawning in interspecies exchanges may occur independent of an animal's familiarity with its human caretakers, and, thus, the social processes underlying these exchanges should be further explored, especially regarding relationships between animals and their human caretakers in managed care settings.

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### Literature Cited

- Abramson, J. Z., Hernández-Lloreda, M. V., Esteban, J. A., Colmenares, F., Aboitiz, F., & Call, J. (2017). Contextual imitation of intransitive body actions in a beluga whale (*Delphinapterus leucas*): A "do as other does" study. *PLOS ONE*, *12*(6), e0178906. <https://doi.org/10.1371/journal.pone.0178906>
- Ames, A. E., & Vergara, V. (2020). Trajectories of vocal repertoire development in beluga (*Delphinapterus leucas*) calves: Insights from studies a decade apart. *Aquatic Mammals*, *46*(4), 344-366. <https://doi.org/10.1578/AM.46.4.2020.344>
- Anderson, J. R., Myowa-Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *271*(Supp. 6), S468S470. <https://doi.org/10.1098/rsbl.2004.0224>
- Anias, J., Holmgren, B., Urba-Holmgren, R., & Eguibar, J. R. (1984). Circadian variation of yawning behavior. *Acta Neurobiologiae Experimentalis*, *44*, 179-186.
- Baenninger, R. (1987). Some comparative aspects of yawning in *Betta splendens*, *Homo sapiens*, *Panthera leo*, and *Papio sphinx*. *Journal of Comparative Psychology*, *101*(4), 349-354. <https://doi.org/10.1037/0735-7036.101.4.349>
- Baenninger, R. (1997). On yawning and its functions. *Psychonomic Bulletin & Review*, *4*(2), 198-207. <https://doi.org/10.3758/BF03209394>
- Bakkegard, K. (2017). Yawning by Red Hills salamanders (*Phaeognathus hubrichti*) at their burrow entrance. *Herpetological Review*, *48*, 32-36.
- Barbizet, J. (1958). Yawning. *Journal of Neurology, Neurosurgery, and Psychiatry*, *21*, 203-209. <https://doi.org/10.1136/jnnp.21.3.203>
- Bauer, G. B., & Harley, H. E. (2001). The mimetic dolphin. *Behavioral and Brain Sciences*, *24*, 326-327. <https://doi.org/10.1017/S0140525X01243969>
- Campbell, M. W., & Cox, C. R. (2019). Observational data reveal evidence and parameters of contagious yawning in the behavioral repertoire of captive-reared chimpanzees (*Pan troglodytes*). *Scientific Reports*, *9*, 13271. <https://doi.org/10.1038/s41598-019-49698-6>
- Campbell, M. W., & de Waal, F. B. M. (2011). Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLOS ONE*, *6*, e18283. <https://doi.org/10.1371/journal.pone.0018283>
- Campbell, M. W., & de Waal, F. B. M. (2014). Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20140013. <https://doi.org/10.1098/rspb.2014.0013>
- Casetta, G., Nolfo, A. P., & Palagi, E. (2021). Yawn contagion promotes motor synchrony in wild lions, *Panthera leo*.

- Animal Behaviour*, 174, 149-159. <https://doi.org/10.1016/j.anbehav.2021.02.010>
- Connor, R. C., Heithaus, M., Berggren, P., & Miksis, J. L. (2000). "Kerplunking": Surface fluke splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science*, 16(3), 646-653. <https://doi.org/10.1111/j.1748-7692.2000.tb00959.x>
- Demuru, E., & Palagi, E. (2012). In bonobos yawn contagion is higher among kin and friends. *PLOS ONE*, 7, e49613. <https://doi.org/10.1371/journal.pone.0049613>
- Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore*, 2, 22-23.
- Enokizu, A., Morisaka, T., Handa, Y., & Yoshioka, M. (2022). Observation of yawn-like behavior in a dugong (*Dugong dugon*). *Journal of Ethology*, 40(1), 103-108. <https://doi.org/10.1007/s10164-021-00732-z>
- Enokizu, A., Morisaka, T., Murakami, K., Sakurai, N., Ueda, N., & Yoshioka, M. (2021). Yawn-like behavior in captive common bottlenose dolphins (*Tursiops truncatus*). *Behavioural Processes*, 189, 104444. <https://doi.org/10.1016/j.beproc.2021.104444>
- Gallo, A., Zanolli, A., Caselli, M., Palagi, E., & Norscia, I. (2021). First evidence of yawn contagion in a wild monkey species. *Scientific Reports*, 11(1), 1-8. <https://doi.org/10.1038/s41598-021-96423-3>
- Guggisberg, A. G., Mathis, J., Schnider, A., & Hess, C. W. (2010). Why do we yawn? *Neuroscience and Biobehavioral Reviews*, 34(8), 1267-1276. <https://doi.org/10.1016/j.neubiorev.2010.03.008>
- Hartzell, S. M., Pitt, A. L., & Davis, S. (2017). Observations of yawning behaviour in the eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*). *Herpetological Bulletin*, 142, 46-47.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In K. Dautenhahn & C. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 63-108). MIT Press.
- Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour*, 46, 999-1010. <https://doi.org/10.1006/anbe.1993.1281>
- 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>
- Jaakkola, K., Guarino, E., Rodriguez, M., & Hecksher, J. (2013). Switching strategies: A dolphin's use of passive and active acoustics to imitate motor actions. *Animal Cognition*, 16(5), 701-709. <https://doi.org/10.1007/s10071-013-0605-3>
- Joly-Mascheroni, R. M., Senju, A., & Shepherd, A. J. (2008). Dogs catch human yawns. *Biology Letters*, 4(5), 446-448. <https://doi.org/10.1098/rsbl.2008.0333>
- Jones, B. L., & Kuczaj II, S. A. (2014). Beluga (*Delphinapterus leucas*) novel bubble helix play behavior. *Animal Behavior and Cognition*, 1(2), 206-214. <https://doi.org/10.12966/abc.05.10.2014>
- Kuczaj II, S. A., & Yeater, D. B. (2006). Dolphin imitation: Who, what, when, and why? *Aquatic Mammals*, 32(4), 413-422. <https://doi.org/10.1578/AM.32.4.2006.413>
- Kuczaj II, S. A., Yeater, D., & Highfill, L. (2012). How selective is social learning in dolphins? *International Journal of Comparative Psychology*, 25(3), 221-236.
- 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>
- Luttenberger, F. (1975). The problem of yawning in reptiles. *Zeitschrift für Tierpsychologie*, 37, 113-137. <https://doi.org/10.1111/j.1439-0310.1975.tb01131.x>
- Meltzoff, A. N., & Moore, K. (1977). Imitation of facial and manual gestures by newborn infants. *Science*, 198, 75-78. <https://doi.org/10.1126/science.198.4312.75>
- Meltzoff, A. N., & Prinz, W. (Eds.). (2002). *The imitative mind: Development, evolution, and brain bases*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511489969>
- Miller, M. L., Gallup, A. C., Vogel, A. R., & Clark, A. B. (2010). Handling stress initially inhibits, but then potentiates yawning in budgerigars (*Melopsittacus undulatus*). *Animal Behaviour*, 80, 615-619. <https://doi.org/10.1016/j.anbehav.2010.05.018>
- Moyaho, A., Rivas-Zamudio, X., Ugarte, A., Eguibar, J. R., & Valencia, J. (2015). Smell facilitates auditory contagious yawning in stranger rats. *Animal Cognition*, 18(1), 279-290. <https://doi.org/10.1007/s10071-014-0798-0>
- Murayama, T., Iijima, S., Katsumata, H., & Arai, K. (2014). Vocal imitation of human speech, synthetic sounds and beluga sounds, by a beluga (*Delphinapterus leucas*). *International Journal of Comparative Psychology*, 27(3), 369-384. <https://doi.org/10.46867/ijcp.2014.27.03.10>
- Palagi, E., & Norscia, I. (2019). Etologia dell'emozione animale: Studio e interpretazione [Ethology of animal emotion: Study and interpretation]. *Sistemi Intelligenti*, 31(1), 11-31.
- Palagi, E., Guillén-Salazar, F., & Llamazares-Martín, C. (2019). Spontaneous yawning and its potential functions in South American sea lions (*Otaria flavescens*). *Scientific Reports*, 9, 17226. <https://doi.org/10.1038/s41598-019-53613-4>
- Palagi, E., Leone, A., Mancini, G., & Ferrari, P. F. (2009). Contagious yawning in gelada baboons as a possible expression of empathy. *Proceedings of the National Academy of Sciences*, 106(46), 19262-19267. <https://doi.org/10.1073/pnas.0910891106>
- Palagi, E., Celeghin, A., Tamietto, M., Winkielman, P., & Norscia, I. (2020). The neuroethology of spontaneous mimicry and emotional contagion in human and non-human animals. *Neuroscience & Biobehavioral Reviews*, 111, 149-165. <https://doi.org/10.1016/j.neubiorev.2020.01.020>
- Panova, E. M., & Agafonov, A. V. (2017). A beluga whale socialized with bottlenose dolphins imitates their whistles. *Animal Cognition*, 20(6), 1153-1160. <https://doi.org/10.1007/s10071-017-1132-4>

- Petrikovsky, B., Kaplan, G., & Holsten, N. (1999). Fetal yawning activity in normal and high risk fetuses: A preliminary observation. *Ultrasound in Obstetrics and Gynecology*, *13*(2), 127-130. <https://doi.org/10.1046/j.1469-0705.1999.13020127.x>
- Provine, R. R. (1989). Faces as releasers of contagious yawning: An approach to face detection using normal human subjects. *Bulletin of the Psychonomic Society*, *27*(3), 211-214. <https://doi.org/10.3758/BF03334587>
- Provine, R. R. (Ed.). (2012). *Curious behavior: Yawning, laughing, hiccupping, and beyond*. Harvard University Press. <https://doi.org/10.4159/harvard.9780674067226>
- Provine, R. R., & Hamernik, H. B. (1986). Yawning: Effects of stimulus interest. *Bulletin of the Psychonomic Society*, *24*(6), 437-438. <https://doi.org/10.3758/BF03330574>
- Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860-R861. <https://doi.org/10.1016/j.cub.2012.08.044>
- Romero, T., Konno, A., & Hasegawa, T. (2013). Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. *PLOS ONE*, *8*, e71365. <https://doi.org/10.1371/journal.pone.0071365>
- Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. *PLOS ONE*, *9*(8), e105963. <https://doi.org/10.1371/journal.pone.0105963>
- Rossmann, Z. T., Padfield, C., Young, D., Hart, B. L., & Hart, L. A. (2020). Contagious yawning in African elephants (*Loxodonta africana*): Responses to other elephants and familiar humans. *Frontiers in Veterinary Science*, *7*, 252. <https://doi.org/10.3389/fvets.2020.00252>
- Sauer, E. G. F., & Sauer, E. M. (1967). Yawning and other maintenance activities in the South African ostrich. *Auk*, *84*, 571-587. <https://doi.org/10.2307/4083337>
- Sepulveda, W., & Mangiamarchi, M. (1995). Fetal yawning. *Ultrasound in Obstetrics and Gynecology*, *5*, 57-59. <https://doi.org/10.1046/j.1469-0705.1995.05010057.x>
- Sherer, D. M., Smith, S. A., & Abramowicz, J. S. (1990). Fetal yawning in utero. *Journal of Clinical Investigation*, *68*, 176-177.
- Silva, K., Bessa, J., & de Sousa, L. (2012). Auditory contagious yawning in domestic dogs (*Canis familiaris*): First evidence for social modulation. *Animal Cognition*, *15*, 721-724. <https://doi.org/10.1007/s10071-012-0473-2>
- Smotherman, W. P., & Robinson, S. R. (1987). Prenatal expression of species-typical action patterns in the rat fetus (*Rattus norvegicus*). *Journal of Comparative Psychology*, *101*(2), 190-196. <https://doi.org/10.1037/0735-7036.101.2.190>
- Tan, J., Ariely, D., & Hare, B. (2017). Bonobos respond prosocially toward members of other groups. *Scientific Reports*, *7*, 14733. <https://doi.org/10.1038/s41598-017-15320-w>
- van Berlo, E., Díaz-Loyo, A. P., Juárez-Mora, O. E., Kret, M. E., & Massen, J. J. (2020). Experimental evidence for yawn contagion in orangutans (*Pongo pygmaeus*). *Scientific Reports*, *10*(1), 1-11. <https://doi.org/10.1038/s41598-020-79160-x>
- Van Woerden, E. E., Van Geijn, H. P., Caron, F. J. M., Van der Valk, A. W., Swartjes, J. M., & Arts, N. T. (1988). Fetal mouth movements during behavioural states 1F and 2F. *European Journal of Obstetrics & Gynecology and Reproductive Biology*, *29*(2), 97-105. [https://doi.org/10.1016/0028-2243\(88\)90135-9](https://doi.org/10.1016/0028-2243(88)90135-9)
- Vergara, V., & Barrett-Lennard, L. G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals*, *34*(1), 123-143. <https://doi.org/10.1578/AM.34.1.2008.123>
- Vick, S. J., & Paukner, A. (2010). Variation and context of yawns in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *72*(3), 262-269. <https://doi.org/10.1002/ajp.20781>
- Walusinski, O., & Deputte, B. L. (2004). The phylogeny, ethology and nosology of yawning. *Revue Neurologique*, *160*(11), 1011-1021. [https://doi.org/10.1016/S0035-3787\(04\)71138-8](https://doi.org/10.1016/S0035-3787(04)71138-8)
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Advances in the Study of Behavior*, *21*, 239-283. [https://doi.org/10.1016/S0065-3454\(08\)60146-1](https://doi.org/10.1016/S0065-3454(08)60146-1)
- Zannella, A., Stanyon, R., & Palagi, E. (2017). Yawning and social styles: Different functions in tolerant and despotic macaques (*Macaca tonkeana* and *Macaca fasciata*). *Journal of Comparative Psychology*, *131*(3), 179-188. <https://doi.org/10.1037/com0000062>