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Defying Evolution: Observations of a Mouth-Breathing Bottlenose Dolphin (*Tursiops truncatus*)

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Abstract

In the Adriatic Sea, a female common bottlenose dolphin named "Boa" was observed on 19 occasions between 2009 and 2019, inhaling via her mouth for every observed respiration. We provide some explanations for the potential cause of this behaviour using existing evidence. Boa appeared to be in good physical shape and displayed behaviour similar to other individuals. She mothered three calves, raising at least one to independence successfully. Because she lived a normal life, we believe she could vocalise and echolocate. Boa may have been forced to breathe through her mouth to deal with internal injuries, occlusion, or disease. Of the potential causes, an occlusion of the upper respiratory tract seems more likely than a perforation or permanent dislocation of the larynx. An occlusion could result from disease, a congenital disorder, and/or wrongly ingested or inhaled food items or foreign materials. To breathe via the mouth, Boa must have been able to circumvent the separation of the respiratory tract from the oral cavity. By relaxing the respiratory muscles, particularly the palatopharyngeus, she could have used the negative pressure of the lungs to pull in air from the oropharynx into the upper respiratory tract. The true cause of Boa's condition will probably never be discovered.

Key Words: anatomy, anatomical anomaly, hyoid, larynx, respiration, cetaceans, unusual behaviour

Introduction

The evolutionary changes of the cetacean respiratory system took millions of years (Berta et al., 2014). Normally, common bottlenose dolphins (*Tursiops truncatus*; Montagu, 1821) and other cetaceans breathe through the blowhole on the top of the head. The blowhole is the external opening of the nasal passageways (upper respiratory tract) that is connected in the pharyngeal region to the trachea and lungs (lower respiratory tract) by a cartilaginous larynx (Cozzi et al., 2016; Figure 1). The epiglottic and corniculate cartilages form the "goose beak" of the larynx that protrudes through the oropharynx into the nasopharynx, which is held in place by the palatopharyngeus. The cuff-like palatopharyngeus is a strong sphincter muscle, able to close the goose beak in a watertight seal (Reidenberg & Laitman, 1987; Brzica et al., 2015; Cozzi et al., 2016). When delphinids inhale, the palatopharyngeus cannot fully contract as it would close off the airway (Huggenberger et al., 2008; Cozzi et al., 2016). This gives the potential for water to be pulled from the oral cavity into the lower respiratory tract by means of the negative pressure in the latter. To circumvent this from happening, delphinids may squeeze their pharynx against the skull base, causing it to collapse and close off from the oesophagus and the respiratory tract (Huggenberger et al., 2008; Cozzi et al., 2016). Alternatively, laryngeal muscles may pull the goose beak cartilages open against the pressure of the encircling palatopharyngeus, thus causing two simultaneous actions: opening the airway while sealing the sphincter against the sides of the goose beak to prevent water leakage (Reidenberg & Laitman, 1987).

Contractions of the muscles surrounding the lower respiratory tract (e.g., intercostals) may push air from the lungs to the upper respiratory tract, over the nasal plugs and phonic lips, which causes vibrations and produces whistles and echolocation clicks (Madsen et al., 2013; Berta et al., 2014; Figure 1). Muscular contractions on the hyoid apparatus can contribute to sound production by elevating or depressing the larynx. These gross movements enable a closed larynx to serve like a piston: moving it up to build pressure in the nasal passageways for click generation, and

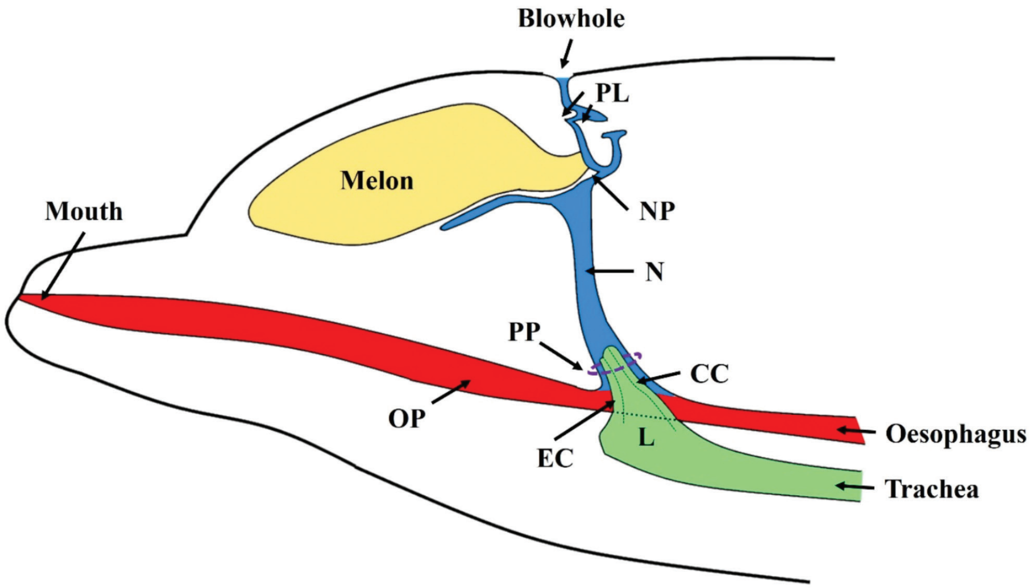

Figure 1. Schematic drawing of a bottlenose dolphin's (*Tursiops truncatus*) head, showing the digestive tract (red) and respiratory tract with the upper respiratory tract (blue) and the lower respiratory tract consisting of the larynx and trachea (green). CC = corniculate cartilage, EC = epiglottic cartilage, L = larynx, N = nasopharynx, NP = nasal plugs, PP (purple) = palatopharyngeus, OP = oropharynx, and PL = phonic lips. Based on Berta et al. (2014), Mead (1975), and Reidenberg & Laitman (1987).

down to relieve pressure between click trains (Huggenberger et al., 2008; Cranford et al., 2011; Cozzi et al., 2016).

When feeding, the interlocking of the larynx and palatopharyngeus separate the respiratory tract from the digestive pathway, preventing water or food from entering the lungs. Prey is ingested through the oral cavity and passes (due to left side placement of the larynx) primarily on the right side of it (Reidenberg & Laitman, 1994; MacLeod et al., 2007; Figure 1). During swallowing, the hyoid apparatus is lowered to enlarge the swallowing passageway, but this also depresses the larynx and risks drowning (Reidenberg & Laitman, 1994). This is mitigated by the elongated goose beak, which allows the larynx to slide inferiorly, while the arrow-head shaped tip keeps the larynx from being completely disconnected from the nasopharynx during this excursion (Reidenberg & Laitman, 1987). When the larynx is positioned normally (interlocked above the palatopharyngeus), separation of the respiratory tract from the oral cavity appears to make it difficult, if not impossible, for a delphinid to breathe through the mouth. However, delphinids appear to be able to withdraw and dislocate the larynx from its usual position when ingesting large prey items (Reidenberg & Laitman, 1987; Stolen et al., 2013; Dold & Ridgway, 2014; Dawson et al., 2017). This is potentially dangerous behaviour; necropsies of stranded delphinids have provided several accounts of asphyxiation through choking where the animals had a dislocated larynx and prey items blocked their respiratory tract (Watson & Gee, 2005; Mignucci-Giannoni et al., 2009; Byard et al., 2010; Stolen et al., 2013; Stephens et al., 2017; Mariani et al., 2020). In rare cases, flexible fish, including eels (*Anguilla* spp.) and sole (*Solea* spp.), got stuck in the upper respiratory tract or escaped through the blowhole when a delphinid tried to ingest them (IJsseldijk et al., 2015; Perkins et al., 2015; Greenfield et al., 2021). In an unusual case, an entire squid was fed to a pilot whale (*Globicephala* sp.; Cuvier, 1812), which blew the squid out through its blowhole (Cozzi et al., 2016).

The flexibility of the delphinid larynx was further demonstrated during certain veterinary procedures. A veterinarian might dislocate the larynx to the left side (due to asymmetrical laryngeal placement; Reidenberg & Laitman, 1994; MacLeod et al., 2007) to remove harmful material from a delphinid stomach (Dawson et al., 2017). As the veterinarian pushes their arm past the larynx, respiratory muscles try to put the larynx back to its usual position, only succeeding when the arm is removed. The larynx will also be dislocated when a delphinid is intubated through the larynx under anaesthesia for surgery (Dawson et al., 2017). After the operation, the anaesthetic might wear off more quickly for the respiratory muscles than for the nasal muscles, and delphinids have been observed opening the mouth and dislocating the larynx to inhale through the mouth (Dawson et al., 2017). Although flexible, the larynx's central position in the oral cavity makes it vulnerable to larynx strangulation by ingestion of foreign materials, especially abandoned, lost, or otherwise discarded fishing gear. Ingested fishing lines or nets can get wrapped around the laryngeal goose beak, and the subsequent injuries can prove fatal (Ahn, 2017; Đuras et al., 2021; Jerbi et al., 2021).

Dawson et al. (2017) describe a case of a delphinid habitually breathing through its mouth. The Hector's dolphin (*Cephalorhynchus hectori*; Van Beneden, 1881) was found at the entrance of Lyttelton Harbour, New Zealand, and appeared to be unable to widely open its blowhole. While the animal appeared to be in good physical condition, it would surface with its head out of the water, open its mouth, and inhale audibly. Small puffs of spray were visible from both the mouth and blowhole, suggesting that some air from the lungs also expelled through the blowhole.

In September 2009, near the Croatian island of Lastovo in the Adriatic Sea (Figure 2), a bottlenose dolphin was encountered displaying a similar breathing behaviour. The female, later named "Boa," was resighted 19 times in the following decade. On each observed surfacing, she lifted her head above the water surface and opened her mouth to inhale. We use the information collected during these observations to hypothesise on the potential cause of this unique behaviour.

Methods

Since 2007, the Blue World Institute of Marine Research and Conservation has carried out photo-identification surveys of bottlenose dolphins in the central Adriatic Sea from the island of Vis (Holcer, 2012; Pleslić et al., 2019, 2021; Figure 2). Despite the presence of a multitude of islands, mainly to the north and east, the central Adriatic is oceanographically much more of an open sea habitat than the northern Adriatic: water depths exceed 100 m (Pleslić et al., 2019; Vrdoljak, 2021). The seabed consists of sand and mud, but the shores are rocky, and the slopes are steep (Pleslić et al., 2019; Vrdoljak et al., 2021). This area is heavily influenced by fisheries, including purse seiners, gill netters, long liners, and bottom trawlers. In addition, the area is used by recreational boats during the summer.

Boa was sighted on 19 occasions between September 2009 and August 2019. Although photo-identification surveys continued, she was not observed afterwards (Figure 2; see also Table S1; supplemental materials for this article are available on the *Aquatic Mammals* website). Over 1,500 photographs of Boa were obtained during these observations. Multiple videos of Boa and her group members were recorded on 26 August 2016 and

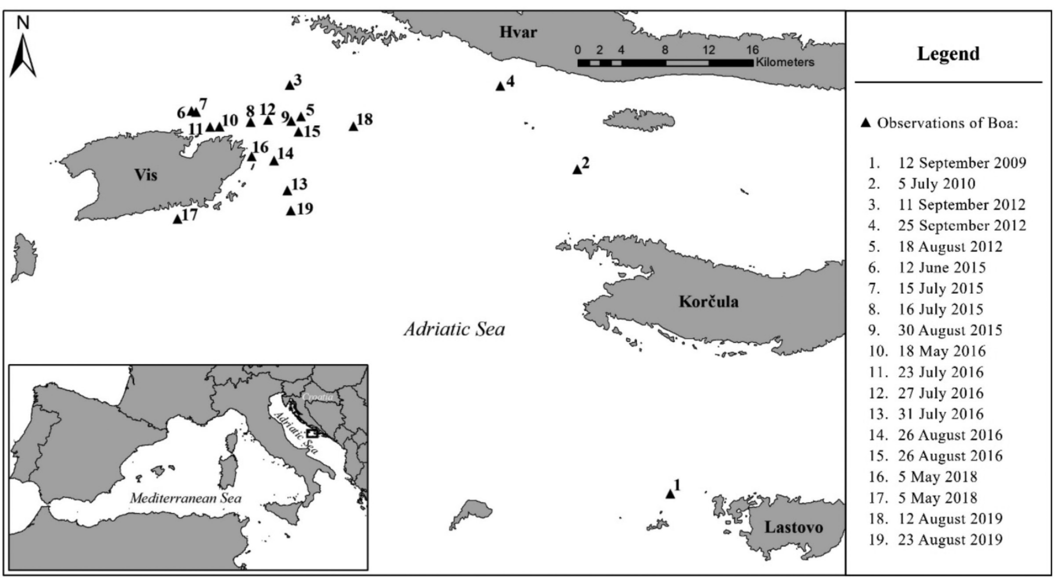

Figure 2. Map with locations and dates of observations of Boa from 2009 until 2019

5 May 2018 (see Supplemental Video link). The groups' behavioural state and the age class of each group member were determined during each "sighting" following the methodology of Fortuna (2006). Group members were identified afterwards using an already established photo-identification catalogue (Pleslić et al., 2019, 2021). The observations, life history, and photographs and videos that were recorded were used to investigate Boa's general health status and identify any peculiarities about her behaviour, besides her breathing.

Results

Throughout a decade of observations, Boa appeared to be in good physical condition. There were no signs of emaciation or abnormal behaviour. Boa was observed with three different calves: one juvenile in 2009 ("Boas09"), one juvenile from 2012 until 2016 ("Boas12"), and one newborn calf in 2019 ("Boas19") (see Figure S1). Boa's calves were never observed displaying her unique breathing behaviour. Boas09 was not observed again after its first observation on 12 September 2009; and Boas12 was raised to adulthood successfully as it was observed without its mother in 2018, 2019, 2021, 2022, and 2023, for a total of 12 occasions. Like its mother, Boas19 was not observed again after 23 August 2019. In this area, it is not unusual to have a multiple year gap between resighting of individuals, especially if they have been observed outside of the main research area. Therefore, it is plausible that Boa and Boas19 are still alive. Boa was observed in groups of different sizes and with different individuals displaying multiple behavioural states: travelling, dive travelling, social travelling, and milling (Pleslić et al., 2015; see Table S1). On 18 August 2012, Boa was observed actively following a bottom trawler, together with her juvenile calf (Boas12) and one adult conspecific, between the islands of Vis and Hvar, where water depth is 80 to 90 m (Figure 2). On 26 August 2016, immediately after surfacing to breathe with her mouth, Boa was observed and recorded logging at the water surface, with the blowhole, but not the mouth, above the surface.

Like other bottlenose dolphins, Boa started exhaling when the rostrum tip reached the water surface. She exhaled with what appeared to be a closed mouth: air bubbles appeared around the mouth edges (Figure 3a) instead of around the blowhole (Figure 3d). As the main part of the head breached the surface, a small flow of water was observed leaving Boa's blowhole, rolling from the head along the back (Figure 3b). However, unlike other bottlenose dolphins (Figure 3e), Boa produced no, or very minor, "sprays" from her blowhole (Figure 3b; see Supplemental Video link & Figure S2). After exhaling, Boa lifted most of her head and rostrum above the water, opened her mouth, and inhaled audibly (Figure 3c). Other bottlenose dolphins do not normally lift their mouths above the water when breathing; they exhale and inhale via the blowhole (Figure 3f). Though she seems not to use it, our observations suggested Boa was able to open the blowhole to some extent (see Figure S3).

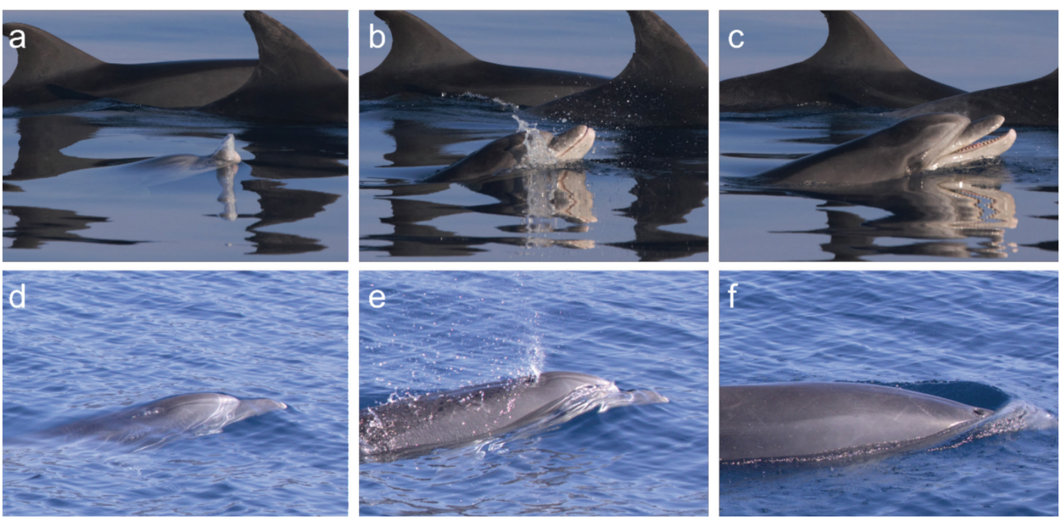

Figure 3. Side-by-side photographs taken on 26 August 2016 and 31 March 2021 by Blue World Institute of Boa's typical surfacing sequence (a, b & c) along with a "regular" bottlenose dolphin surfacing: "V_1060" (d, e & f)

Discussion

Apart from her peculiar breathing behaviour, Boa lived (or has been living) a normal life. She socialised and successfully raised at least one calf, which was likely only possible if she was able to vocalise. Like other bottlenose dolphins, Boa exploited various situations to feed, including actively following a bottom trawler. It would have been impossible to live such a normal life without the ability to echolocate. Similar to the mouth-breathing Hector's dolphin described by Dawson et al. (2017), small, aerosolised water drops were observed around her blowhole when Boa surfaced. Together with her assumed ability to vocalise, this indicated a potential to build up air pressure in the upper respiratory tract. The appearance of air bubbles around Boa's mouth just before surfacing (Figure 3a) showed that most of her exhalation was completed via the mouth.

Internal injuries to the respiratory tract could have forced Boa to breathe via her mouth. However, known injuries, like perforation or permanent dislocation of the larynx, often have dramatic consequences, including mortality (Watson & Gee, 2005; Gomerčić et al., 2009; Levy et al., 2009; Mignucci-Giannoni et al., 2009; Stolen et al., 2013; Stephens et al., 2017; Mariani et al., 2020). A perforation or permanent dislocation can also impair the ability of the larynx to function in sound production (Huggenberger et al., 2008; Cozzi et al., 2016), subsequently preventing or limiting echolocation and vocalisation. Boa was able to vocalise, seemingly to communicate, and to feed. Hence, consequences of such injuries do not seem to be the most likely causes for Boa's observed breathing behaviour.

It is more likely that Boa suffered a partial occlusion of the upper respiratory tract, which forced her to breathe via the mouth. Such an occlusion could be caused by an infection, tumour, inhalation of a foreign object, wrongful ingestion of food items, or due to a congenital disorder causing deformation of the upper respiratory tract (IJsseldijk et al., 2015; Dawson et al., 2017; Greenfield et al., 2021). In case of the latter, Boa may have been breathing through her mouth since birth. The severity of this potential occlusion appears to be mild as, in accordance with our observations of her social behaviour and food procurement, Boa is likely able to vocalise. Furthermore, a partial occlusion of the internal nares could explain why some air made it through the upper respiratory tract, creating small sprays when she exhaled. However, without further visual evidence or a postmortem analysis, these theories can neither be confirmed nor dismissed.

If an occlusion of the internal nares forced Boa to breathe via her mouth, she would have needed to circumvent the physical separation of the respiratory tract from the oral cavity. To achieve that, she may have voluntarily dislocated her larynx at every surfacing to breathe. Bottlenose dolphins have been observed voluntarily dislocating and replacing the larynx incidentally (Reidenberg & Laitman, 1987; Dold & Ridgway, 2014; Dawson et al., 2017). The behaviour might be somewhat common in delphinids, based on multiple cases of larynx dislocation combined with lodging of food items in the oral cavity (Watson & Gee, 2005; Mignucci-Giannoni et al., 2009; Byard et al., 2010; Stolen et al., 2013; IJsseldijk et al., 2015; Stephens et al., 2017; Mariani et al., 2020; Greenfield et al., 2021). However, it seems a physically demanding and risky behaviour to perform before every breath. More elegantly, Boa might have been able to inhale air through her mouth by fully relaxing the palatopharyngeus while not collapsing the pharynx, using the lungs' negative pressure to pull air from the oral cavity dorsally between the sphincter and the larynx into the nasopharyngeal region of the upper respiratory tract (Huggenberger et al., 2008; Cozzi et al., 2016; Figure 1). In this case, the negative pressure of the lungs may have pulled some water into the upper respiratory tract when Boa inhaled via her mouth. Martins et al. (2020) showed how seawater may enter the upper respiratory tract of humpback whales (*Megaptera novaeangliae*; Borowski, 1781) as they submerge with the blowhole still open. Hence, cetaceans like Boa might tolerate limited amounts of seawater inside the respiratory tract. However, while water entering from the humpback's blowholes could be squeezed back out through upward movements of the nasal plugs, it is unclear how water entering the dolphin's nasal passageways from below would be evacuated. Perhaps maintaining an upright position with respect to gravity allows the water to drain inferiorly, flowing passively past the relaxed palatopharyngeal sphincter into the oropharynx. This matter could be investigated further by collecting and analysing drone- and underwater footage of delphinids and by studying the findings of necropsies.

Although Boa showed a remarkable ability to deal with a significant physical impairment, injuries to the respiratory tract often prove fatal to delphinids. In the Croatian part of the Adriatic, between 1990 and 2019, 300 cetaceans were examined postmortem (mostly bottlenose dolphins; Đuras et al., 2021). Of the examined animals, at least 30 exhibited injuries from interactions with fishing gear—through entanglement, ingestion, or larynx strangulations. Considering the potential for negative interactions with abandoned, lost, or otherwise discarded fishing gear or other marine debris in the area, there is a chance that Boa's behaviour was caused by anthropogenic pollution. However, with the evidence available now, no hard conclusions can be drawn. Unfortunately, unless she is recovered and examined either alive (e.g., endoscopy, imaging) or postmortem (i.e., necropsy), the true cause of Boa's mouth-breathing behaviour will never be determined.

Note: The supplemental materials for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.

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