

Research Article

Cite this article: Pierry JC, Novelli MBS, Louzada CN, Monteiro-Filho ELA (2024). Rings of Power: evidence of mud ring feeding performed by Guiana dolphins. *Journal of the Marine Biological Association of the United Kingdom* **104**, e69, 1–6. <https://doi.org/10.1017/S002531542400078X>

Received: 4 January 2024

Revised: 18 May 2024

Accepted: 18 July 2024

Keywords:


barrier feeding; behavioural plasticity; bottlenose dolphin; cetaceans; estuarine dolphin; foraging tactics

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Rings of Power: evidence of mud ring feeding performed by Guiana dolphins

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Abstract

To capture prey more efficiently, cetaceans can display a wide range of foraging tactics to separate individual prey. Barrier feeding tactics are performed to restrict prey movements, using natural and non-natural barriers and some species can even create barriers with their own bodies. Mud ring feeding has been observed in bottlenose dolphins in Florida Bay and in Chetumal-Corozal Bay, where ring-maker dolphins create ring-shaped mud plumes to encircle fish schools. Here, we document for the first time Guiana dolphins performing the mud ring feeding behaviour in the Cananéia estuarine system, in the southern portion of the state of São Paulo, Brazil. A total of 11 dolphins were recorded in four expeditions through aerial footage engaging in the behaviour. These findings expand our knowledge about the behavioural plasticity of the species and builds upon existing records of mud ring feeding behaviour in cetaceans.

Introduction

To capture prey more efficiently, cetaceans display a wide range of foraging tactics that seek to separate individual prey (Shane, 1990; Nowacek, 1999; Gubbins, 2000; Monteiro-Filho, 2008). Some species perform behaviours associated with habitat features, using them to restrict prey movement and block escape routes, such as bottlenose dolphins (*Tursiops truncatus*) that use estuarine mudflats to perform strand feeding behaviour (Hoese, 1971; Petricig, 1995; Silber and Fertl, 1995), or use shallow sand banks for crater feeding behaviour (Rossbach and Herzing, 1997).

Barrier feeding tactics can be performed using natural and non-natural barriers and some species may create the barriers themselves. Humpback whales (*Megaptera novaeangliae*) are well known for creating bubble barriers to corral or herd fish (Jurasz and Jurasz, 1979; Hain *et al.*, 1982; Acevedo *et al.*, 2011). In some cases, individuals use their pectoral fins as a secondary barrier in combination with bubble barriers to prevent evasion by prey (Kosma *et al.*, 2019). Even in greater depths where barriers are absent, spinner dolphins (*Stenella longirostris*) and bottlenose dolphins can line up or swim in a circle using their bodies as physical barriers (Gazda *et al.*, 2005; Benoit-Bird and Au, 2009).

In the Florida Keys, bottlenose dolphins have been observed creating linear or curvilinear mud plume barriers by moving their flukes in a downwards motion near the substrate, then lunging quickly into it to catch fish prey (Lewis and Schroeder, 2003). The same species has been observed performing mud ring feeding in Florida Bay and in Chetumal-Corozal Bay, where a ring-maker dolphin creates a circular ring-shaped mud plume, used to corral fish schools and capture them when they leap out of the mud ring and into the air (Torres and Read, 2009; Engleby and Powell, 2019; Ramos *et al.*, 2021).

The Cananéia estuary in southeastern Brazil holds a resident population of approximately 400 Guiana dolphins (*Sotalia guianensis*) (Mello *et al.*, 2019), – a small delphinid species that occurs from Honduras (Edwards and Schnell, 2001) to southern Brazil (Simões-Lopes, 1988), mostly inhabiting estuaries, bays, and inlets. This resident population from Cananéia is known for performing a wide array of foraging behaviours, such as using fixed manmade traditional fishing traps (i.e., *cerco-fixa*) to direct their prey (Monteiro-Filho, 1995; Louzada, 2013), using the shoreline along sloping beaches to facilitate prey capture by herding (Monteiro-Filho, 1995) and even using mangrove areas as a barrier-foraging tactic (Pierry *et al.*, 2023).

Here, we document mud ring feeding by Guiana dolphins, a behaviour previously described only in bottlenose dolphins (Torres and Read, 2009; Engleby and Powell, 2019; Ramos *et al.*, 2021). We describe this behaviour for the first time, performed by Guiana dolphins in the Cananéia estuary, using unmanned aerial vehicle (UAV) imagery that allowed us to observe the behaviour in this species and compare it with that already described in bottlenose dolphins. We hypothesize that the habitats' similarities and both species behavioural plasticity drove them to separately evolve the same behaviour, which optimized foraging efforts to capture prey more efficiently.



Materials and methods

The observations took place in the Cananéia estuarine system, located in the southern portion of the state of São Paulo, in southeastern Brazil (Figure 1). All observations occurred at the same place within the Cananéia estuary – in the north portion of Cardoso Island State Park. This specific area is characterized by shallow waters (approximately one metre deep) during low tide, partially protected due to the topography of the Cardoso Island with a large mangrove area, and for presenting a sequence of twelve fixed traditional fishing traps, spaced approximately 100 metres apart (i.e., *cercos-fixos*; Radasewsky, 1976). These traditional fishing traps are characterized by a long sequence of wooden sticks that form a longitudinal barrier from the coast towards the estuary, which direct the fish to the structure's circular edge, where the fish will be trapped in a net that covers the entire structure from the inside.

Half of our expeditions were vessel-based, and the other half land-based, totalling four expeditions. The first two observations were recorded in February 2023 as opportunistic events, during two vessel-based expeditions that were made to record Guiana dolphins in the region for a documentary television programme, which was achieved with the support of our research team. Subsequently we undertook two scientific expeditions in August 2023, both land-based, to document this novel behaviour. In these expeditions, two observers scanned the area from land for four-hour observation periods in each expedition, both with the naked eye and using binoculars to identify the presence of dolphins and assess group size and composition. When dolphins were located, we collected aerial imagery using a UAV (models DJI Mavic Pro and DJI Mavic Air 2) at a pre-established height

range of 20 to 30 metres, under local and national licenses (CadGP n°: 057479/2023; SISBIO n°: 88901-1) following established flight protocols to record small cetaceans (Fettermann *et al.*, 2022; Aubin *et al.*, 2023).

Results

In each of the four field expeditions we observed one group of dolphins performing mud ring feeding to trap and catch fish prey, in each case during mid to low tides. In total, 11 dolphins were observed exhibiting this behaviour, distributed in four small, cohesive groups, each recorded in a separate field expedition: one group was composed of two adults and the other three groups were each comprised of two adults and one calf. Almost seven minutes of aerial video data were recorded of mud ring feeding behaviour being performed by Guiana dolphins. Photo-identification images were not taken of the 11 dolphins, so it was not established whether these were 11 unique individuals or included repeat encounters of some of the same individuals.

The first observation consisted of a group of two adults that performed three mud ring behaviour sequences – two performed by both individuals and one performed by a single animal (Supplementary Movies S1; S2; S3). When in pairs, both dolphins acted as ring-makers, actively moving their flukes towards the substrate while swimming in a circular movement until the dolphin that initiated the behaviour closed the mud ring inside the mud trail created by the second dolphin, turning the final shape into a mud spiral (Figure 2A). Small fish were observed jumping out of the water to flee above the mud plume on one occasion

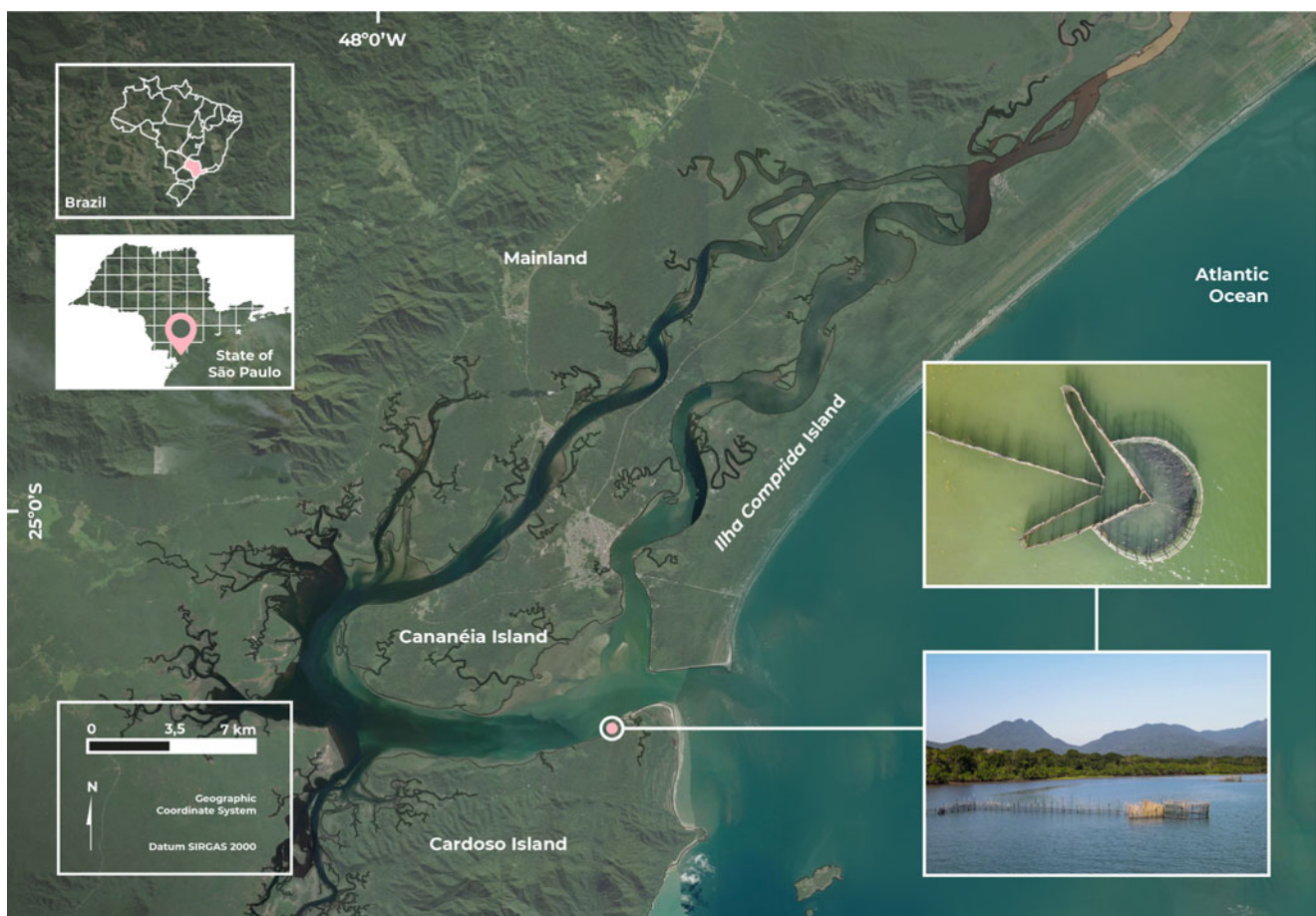


Figure 1. Study area in Cananéia estuary, southeastern Brazil. Detail shows the exact place where the mud ring feeding behaviour was recorded for Guiana dolphins (*Sotalia guianensis*), with an aerial view of the area and of the *cercos-fixos* – a traditional fishing trap.

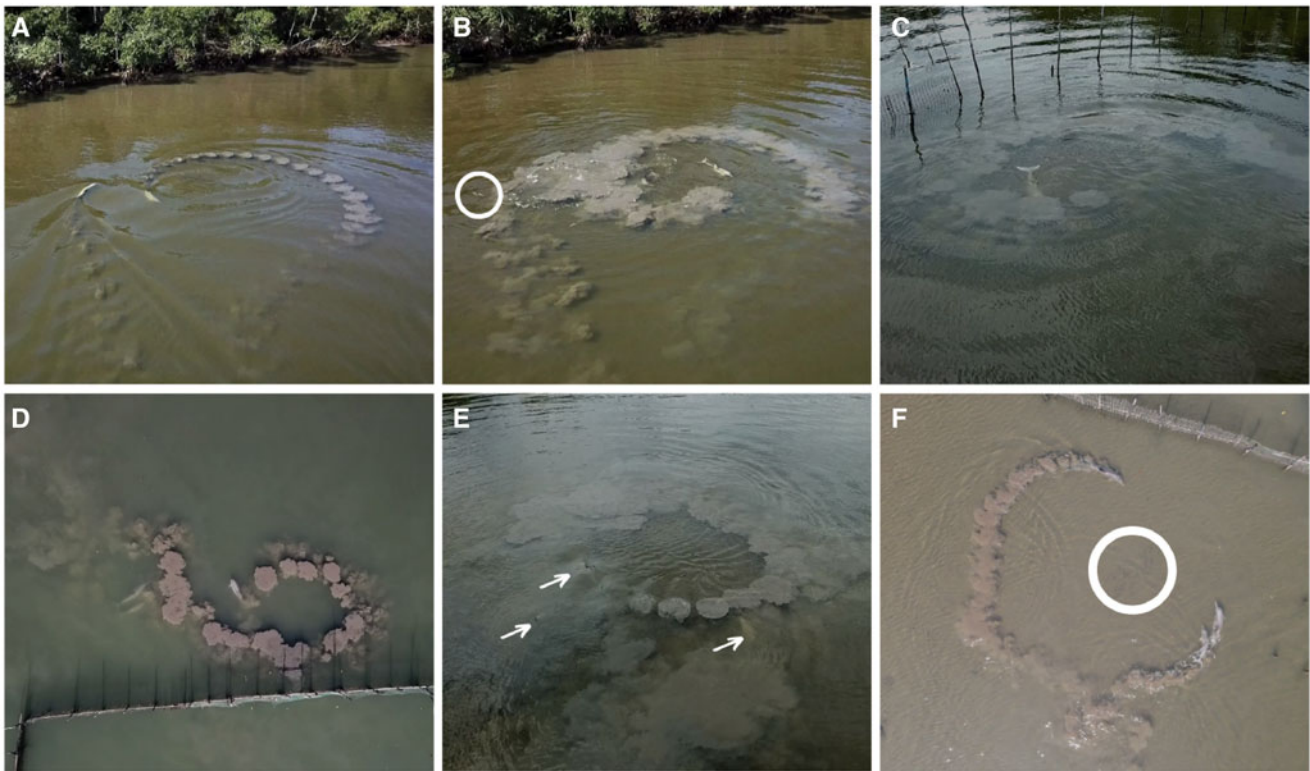


Figure 2. Mud ring feeding behaviour performed by Guiana dolphins (*Sotalia guianensis*) in the Cananéia estuary, southeastern Brazil. In (A) two dolphins acting as the ring-maker with the final mud spiral shape; in (B) it is possible to observe small fish jumping above the mud on the left side of the mud ring (circled); in (C) the spiral-shaped mud created by a single dolphin that swam into the mud plume after creating it; (D) shows a mother-calf pair approaching the mud ring created by the escort adult (arrowed); in (E) the escort adult just remade the mud ring while the mother (closest to the ring-maker) and calf both remain stationary at the mud plume (arrowed); and (F) illustrates both adults performing as ring-makers, with the mother-calf pair swimming in echelon formation and a fish school being encircled (circled). Photos A, B, C, E: Marcelo Ferri; photos D, F: Julia Pierry.

(Figure 2B). The spiral-like mud trail was also observed when the behaviour was performed by a single dolphin (Figure 2C). Both individually and in pairs, after completing the mud ring, the dolphins turned their bodies quickly in a 180° movement, returning their rostrum to the ring centre or to the mud suspended by the ring formation and sometimes swimming thorough the mud, likely to catch fish separated from their school.

The remaining three observations were of groups with three individuals, each being a mother-calf pair accompanied by another adult and each group performed one mud ring behaviour sequence. On these occasions, the ring-maker role was taken by either both adults simultaneously or by the escort dolphin alone. In the latter case, the mother-calf pair quickly moved towards the mud ring to position themselves at the mud plume once the escort dolphin initiated it (Figure 2D; Supplementary Movie S4). In one of the two occasions in which the escort dolphin created the mud ring, it was necessary to remake the ring, as a reinforcement for the barrier created by the mud. Then, instead of searching for fish in the mud, both adults and the calf remained in a stationary position with the rostrum directed to the ring centre for over 15 s after the mud ring was remade (Figure 2E; Supplementary Movie S5).

When performed simultaneously, one adult initiated the mud ring, being immediately followed by the mother-calf pair that swam in the opposite direction with the mother also acting as a ring-maker, until meeting the first adult midway around the formed mud ring. In this case, the calf stayed close to the mother until the ring was closed (i.e., echelon swimming *cf.* Rautenberg and Monteiro-Filho, 2008; Teixeira *et al.*, 2018), then the calf swam alone in the interior of the ring while both adults swam through the mud ring formation chasing fish. A fish school was observed trapped inside the mud ring (Figure 2F; Supplementary Movie

S6). In half of the observed cases, the mud ring behaviour was performed near the fixed traditional fishing traps (less than 1 metre away), which allowed the dolphins to pursue their prey both within the mud ring and between the mud ring and the fixed traps.

We refer to the behaviour described here in Guiana dolphins as mud ring feeding since it shares close similarities with the behaviour described in bottlenose dolphins from Florida Bay and Chetumal-Corozal Bay (Table 1) – mainly due to the circular shape created in the mud, similar substrate and habitat features, occurring in inner-basin mud banks and for being a cooperative foraging tactic, rather than an individual behaviour as described in mud plume behaviour (Torres and Read, 2009; Engleby and Powell, 2019; Ramos *et al.*, 2021). The depths were similar in all sites for both bottlenose and Guiana dolphins. The target prey in each case varied from exclusively mugilid fish in Florida and Chetumal-Corozal Bays to multiple species in the Florida Keys (Lewis and Schroeder, 2003). In our observations we were able to identify in two different expeditions that the target prey were mugilids (*Mugil* sp.), possibly white mullets (*Mugil curema*), according to reports by local fishermen of the most commonly caught fish in the fixed traps and by the identification of the species through our footage. A remarkable difference observed between species is that for Guiana dolphins the ring-maker role can be shared, with two individuals actively creating the mud ring at the same time, which does not occur in bottlenose dolphins.

Discussion

Our results support the hypothesis that environmental features may contribute to shape foraging behaviour adaptations for dolphins worldwide (Würsig and Pearson, 2014; Methion and Díaz López, 2019). Both the shallow protected waters and prey

Table 1. Similarities between the mud ring feeding described here for Guiana dolphins to both mud plume and mud ring feeding described for bottlenose dolphins (Lewis and Schroeder, 2003; Torres and Read, 2009; Engleby and Powell, 2019; Ramos *et al.*, 2021)

Species and occurrence site	Group size	Presence of calves	Water depth	Ring-makers	Substrate type	Mud shape	Target prey	Reference
Guiana dolphins in Cananéia estuary	2 or 3	Yes	<1 m	1 or 2	Mud banks	Circular or spiral	<i>Mugil</i> sp.	In this paper
Bottlenose dolphins in Florida Keys	1	No	0.9 m	1	Seagrass flats	Linear or curvilinear	<i>Hemiramphus brasiliensis</i> and others	Lewis and Schroeder (2003)
Bottlenose dolphins in Florida Bay	Up to 6	No	0.88 m	1	Mud banks	Circular	<i>Mugil</i> sp.	Torres and Read (2009)
Bottlenose dolphins in Chetumal-Corozal Bay	'Small groups'	Yes	<1 m	1	Mud banks	Circular or spiral	<i>Mugil</i> sp.	Ramos <i>et al.</i> (2021)

behaviour could be factors driving the development of the same behaviour between two different species in geographically separated locations. Even with this preliminary assessment, our records contribute to the evidence for Guiana dolphin's behavioural plasticity (Monteiro-Filho, 2008; Deconto and Monteiro-Filho, 2013; Leão *et al.*, 2016).

Within the same species, we see great variation in behaviours among different populations and even among individuals (Shane, 1990; Nowacek, 1999; Gubbins, 2000; Sargeant and Mann, 2009). The mean group size of Guiana dolphins in the Cananéia estuary is within the range of 1 to 3 individuals, larger groups commonly occurring when the smaller ones come together for specific and ephemeral circumstances, such as foraging tactics that benefit from a greater number of individuals working together (Monteiro-Filho, 1991, 1992). The small group size and composition of the Guiana dolphins observed performing mud ring feeding recurrently at the same site, and this being such a specific behaviour, can suggest that this tactic is performed by a subset of dolphins within this population. Yet, considering the numerous mud banks along the estuary and the wide occurrence of mugilids, this behaviour may not necessarily be restricted to this single location. Indeed, over more than forty years of study in the region, various researchers on our team have documented Guiana dolphins with patches of mud on their back and sides along the estuary. Also, our records only show the white mullet as the target prey, but the generalist diet of Guiana dolphins in estuarine regions and the diversity of similar prey species in the Cananéia estuary suggests the possibility of predation of a wider list of target species using this tactic (Cremer *et al.*, 2012; Ferro de Godoy *et al.*, 2020; Teixeira *et al.*, 2023).

As mud ring feeding behaviour depends on a muddy substrate to be performed, it is possible that this behaviour occurs in other populations in this species' distribution, especially those that share a similar habit of residency, such as the Paranaguá estuary and the Caravelas River, on the south and northeast coast of Brazil respectively. Indeed, Guiana dolphins have already been observed with mud patches on their bodies in the Caravelas River, which has been suggested to be associated with bottom foraging behaviours (Rossi-Santos and Wedekin, 2006).

An important feature of the Cananéia estuary is the presence of fixed traditional fishing traps (*cercos-fixos*; Radasewsky, 1976). The fact that most of the mud rings registered were created near to these traps, may indicate the advantage of physical barriers to this behaviour. By using the *cercos-fixos* as an additional barrier with the mud ring, prey escape routes are reduced, enhancing both predation and cooperation between individuals, with an individual chasing the fish inside the mud ring while another chases them between the ring and the *cercos-fixos* wall.

Tool use in cetaceans can be defined as the use of either an object from their habitat or the manipulation of environmental

features such as waves, bubbles, water jets and mud to achieve an objective, generally associated with foraging behaviours (Mann and Patterson, 2013). In addition to creating mud rings, bottlenose dolphins also use sponges and shells to facilitate foraging (Smolker *et al.*, 1997; Allen *et al.*, 2011; Krützen *et al.*, 2014; Wild *et al.*, 2020). Other cetacean species such as humpback whales and orcas (*Orcinus orca*) have also been observed using the sediment as a tool to increase their foraging success (Hain *et al.*, 1995; Rossbach and Herzing, 1997; Visser, 1999). Social interactions between differently aged individuals during behaviours involving tool use in cetaceans may lead to observational learning and attempts of imitation by younger individuals (Galef and Giraldeau, 2001; Laland, 2004; Kuczaj and Yeater, 2006).

The calves observed along with adults during the mud ring behaviour were swimming in close proximity to their mothers which exposes them to this tactic that can eventually be used in later stages in their life (Link, 2000; Spinelli *et al.*, 2002; Lodi, 2003; Monteiro-Filho, 2008). Like many other specialized foraging behaviours, the mud ring feeding displayed by Guiana dolphins may be socially learned – i.e. maternally by vertical transmission rather than by a horizontal or oblique learning mechanism among individuals, since there was no evidence of multiple groups interacting during this behaviour (Nowacek, 2002; Mann and Sargeant, 2003; Wells, 2003; Whitehead *et al.*, 2004; Krützen *et al.*, 2005; Bender *et al.*, 2009; Torres and Read, 2009). Another potential indicator of vertical social learning is the presence of infants even though the shallow water (<1 m) presents a risk of stranding to inexperienced calves (Rautenberg and Monteiro-Filho, 2008).

Our findings contribute to the already rich list of foraging behaviour displayed by Guiana dolphins and builds upon existing records of mud ring feeding behaviour in cetaceans. The fact that these behaviours are displayed by different delphinid species with a great geographic distance between them, demonstrates a strong adaptive behaviour that may increase the foraging success for both species.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S002531542400078X>.

Data. The data that supports this finding is available online in the Supplementary materials section of this article.

Acknowledgements. We thank the Instituto de Pesquisas Cananéia (IPEC) for the logistical support. We also thank Marcelo Ferri from the Terra da Gente TV programme who graciously provided his aerial footage andIVALDO Neves, a local fisherman who helped identify the fish species.

Author contributions. All authors designed the study, JP performed the research and wrote the first draft of the manuscript, JP and MN collected data, CL and EMF provided materials for data collection and accuracy and all authors contributed substantially to revisions.

Financial support. This research received no specific grant from any funding agency, commercial or non-profit sectors.

Competing interests. The authors declare none.

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