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Two steps forward, one back: kinematic observations of a South American Small-eyed Coralsnake, *Micrurus lemniscatus* (Linnaeus, 1758), regurgitating a Brown-banded Watersnake, *Helicops angulatus* (Linnaeus, 1758)

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Animals possess numerous special abilities for survival in response to stressors (for review of the hormonal stress response see Moore and Jessop, 2003), and some of these can be co-opted for foraging and consumption of food (Horn, 2008). Vomiting, or emesis, is a forceful, active ejection of digesta that enables animals to remove toxic substances from the stomach (Divers and Stahl, 2019). The vomiting response is present in many species of fish, amphibians, reptiles, birds, and mammals (Andrews et al., 2000), but vomiting in reptiles is considered rare (Mitchell and Diaz-Figueroa, 2005). Regurgitation is the discharge of undigested contents (Divers and Stahl, 2019), and this terminology is how food ejection is more generally described for reptiles, which exhibit slow digestion relative to endothermic taxa at rates as little as one-fifth to one-seventh of a mammal of equivalent size (O'Malley, 2017).

Despite numerous reports of regurgitation in snakes (e.g., Jackson et al., 2004; Gonzalez et al., 2018; Barbosa et al., 2019; Kornilev et al., 2023), descriptions regarding the mechanics of regurgitation behaviour are scant, especially for ophiophagous (snake-eating) snakes. The most common environmental and behavioural causes for reptilian regurgitation are too large or too many food items, inappropriate postprandial handling, stress, or intraspecific interactions (Divers and Stahl, 2019). For example, snakes that are not provided secure hiding may regurgitate if disturbed or handled after eating a meal (Divers and Stahl, 2019).

Coralsnakes of the genus *Micrurus* are venomous with proteroglyphous fangs. They belong to the family Elapidae and are widely distributed throughout the Neotropics (Roze, 1996; Ávila et al., 2010; Silva, 2016). They are generally considered to be terrestrial, with a few exceptions, such as *M. lemniscatus*, which occupies swampy and semi-aquatic environments (Schmidt, 1957; Roze, 1996; Campbell and Lamar, 2004). *Micrurus lemniscatus* feeds on amphibians, blindsnakes, lizards, and fish (Amaral, 1927; Schmidt, 1957; Sazima and Abe, 1991; Martins and Oliveira, 1998; Roze, 1996; da Silva et al., 2010). However, knowledge of the natural diet and feeding behaviour of this species, let alone the act of regurgitation, is limited due to their cryptozoic and fossorial habits (Souza et al., 2011; Cavalcanti et al., 2012). We here describe a new observation of regurgitation by *M. lemniscatus*.

On 6 June 2023 at 10:45 h, we observed an adult *M. lemniscatus* regurgitate a complete, intact snake (Fig. 1). We captured this individual (snout–vent length 43.2 cm, tail length 4.3 cm) in mud and water on 5 June 2023 at 22:15 h at the Santa Cruz Research Station (Project Amazonas) in Loreto, Peru (3.5279°S, 73.1788°W; elevation ca. 120 m). The following morning, at approximately 10:22 h, we put the coralsnake into a narrow tube to draw blood for an unrelated project. After we determined the snake's weight (20.5 g), it was probed and determined to be a female, and a 0.5 ml blood sample was drawn from the ventral coccygeal vein using a 31-gauge needle and syringe at 10:32 h.

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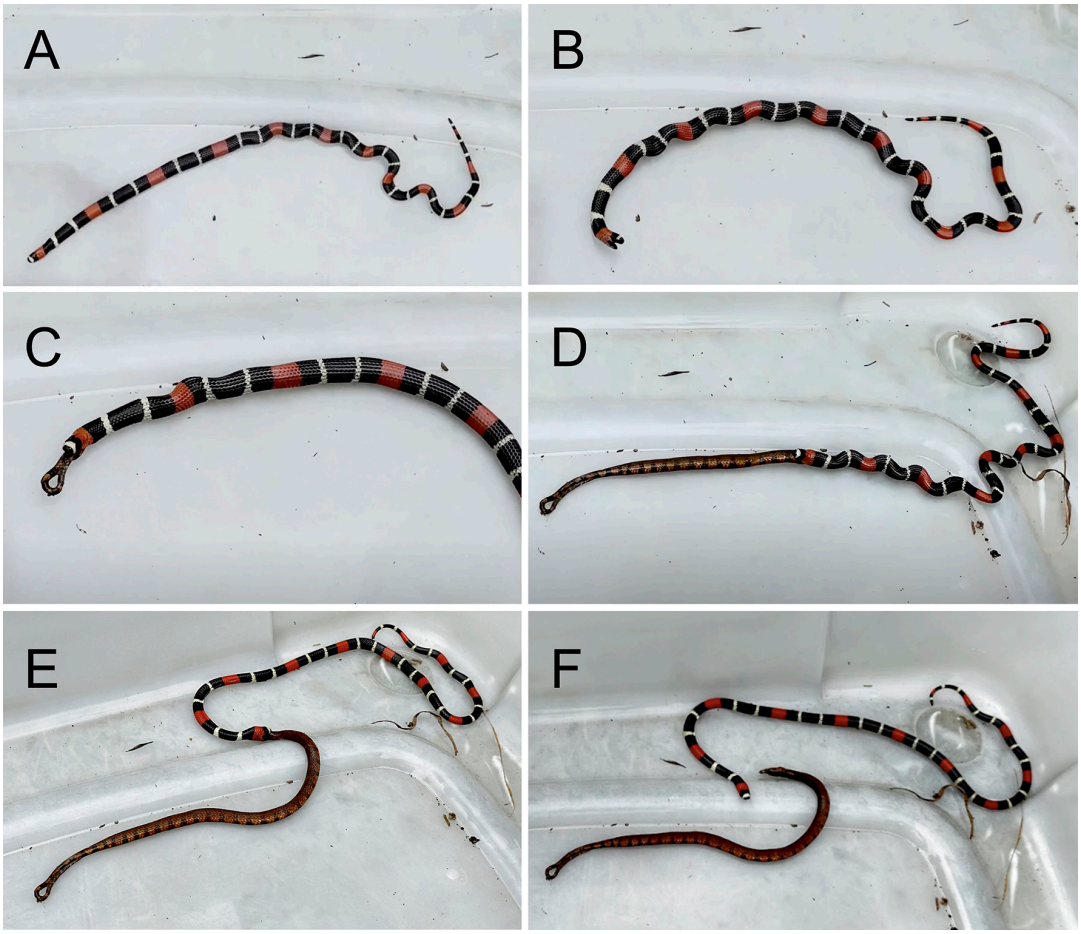

Figure 1. The coralsnake *Micrurus lemniscatus* regurgitating a watersnake (*Helicops angulatus*). (A) The coralsnake initiated regurgitation by compressing the posterior, precloacal portion of its body. (B) The compressive motion translocated anteriorly along the body. (C) The looped tail of the watersnake emerged from the coralsnake's mouth. (D–F) The coralsnake continued to contract its body to fully disgorge the watersnake.

To digitally determine its length (Astley et al., 2017), the snake was released into a large plastic bin (with approximate dimensions of 69 x 37 x 61 cm) to be photographed. Approximately 1 min after placement into the bin, the snake started telescoping the caudal portion of its body. This unusual behaviour prompted us to immediately record a standard-speed video (30 frames per second) using a digital camera on an iPhone Pro 14, and we subsequently recorded 97 s of the regurgitation event until the memory of the camera prevented further recording. Thereafter, photographs were taken periodically with the same device until regurgitation was complete. The total duration of this combined imaging, from the start of the video recording to the end of regurgitation, was 5:53 min. The video, shown in both regular and slow-motion speeds, can be viewed at https://youtu.be/g-1Tyw5HYuk.

The images enabled a detailed analysis of movements involved in regurgitation (Figs. 2, 3) as well as measurements (provided as mean ± standard deviation). Overall, regurgitation proceeded in rhythmic cycles that fully ejected the prey. A cycle started with movement at the caudal end of the body. After the initial few cycles, this movement was generally directed caudally, giving the appearance of the snake stretching rearward. After this movement, a large lateral bend was formed in the caudal region, followed by a series of smaller lateral bends that formed progressively in time toward the head.

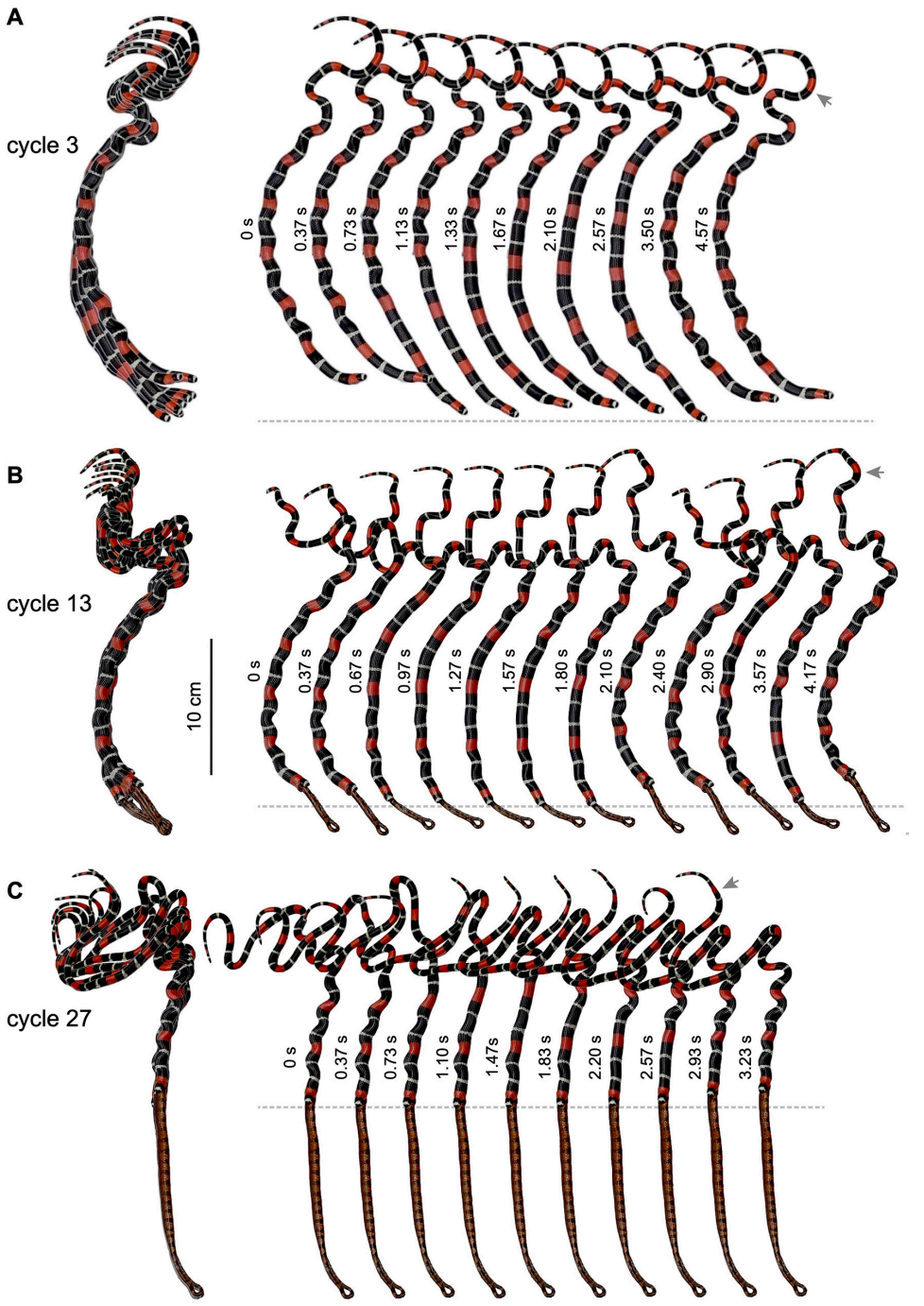

Figure 2. Kinematic details of regurgitation by the coralsnake *Micrurus lemniscatus*. Cycles 3 (A), 13 (B), and 27 (B) are shown as representatives from early, mid, and late portions of the regurgitation event. The images shown were extracted from the video frames using Adobe Photoshop and then aligned and scaled using background landmarks using Adobe Illustrator. The dashed line is for reference for gauging the relative displacement of the coralsnake during the cycle. The grey arrows indicate the location of the vent. The time shown above each snake image represents the duration within the cycle. The start of the cycle was identified as the frame prior to the first movement of the caudal end of the body, preceding the formation of a large bend. Scale bar for all images = 10 cm.

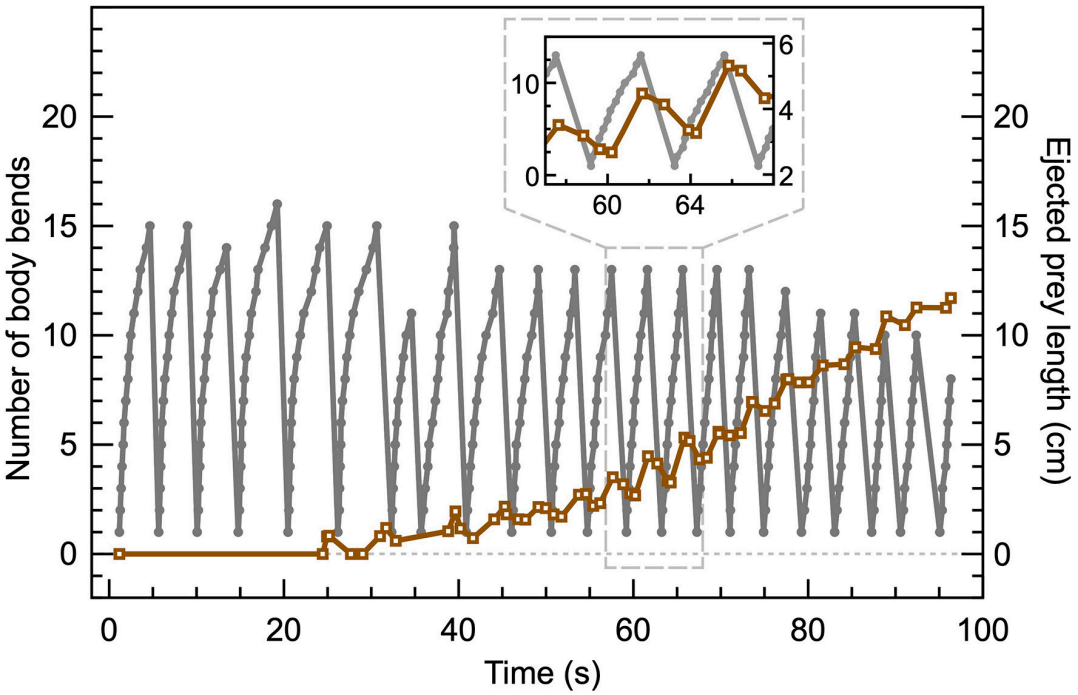

Figure 3. Relationship between the number of lateral body bends (grey) and ejected prey length (brown) vs. time during a portion of the regurgitation event. A total of 21 complete regurgitation cycles are shown here. Time zero indicates the time of the first cycle recorded, not the actual start of the regurgitation process (which was not recorded). The maximum ejected prey length shown, 11.7 cm, represents 39% of the total length of the prey item. The later stages of the regurgitation were not videorecorded. Length was measured using FIJI software (Schneider et al., 2012) using the segmented line tool and smoothed using the 'fit spline' function. Each measured frame was calibrated using a ruler as a reference, recorded concurrently with the regurgitation event. On average, the duration between successive bends was 0.24 s (n = 282 bends) with a range of 0.03–0.87 s.

In effect, these lateral bends gave the snake's body the appearance of being crinkled or crenulated. Once the bends reached their anteriormost extent (usually near the snake's head), the process started over again with a movement at the caudal end. From the start of the recording, it took approximately 20 s until the tail of the prey snake emerged from the coralsnake's mouth (at the end of cycle five; Fig. 3). The tail of the prey was looped, and it is unclear if this shape formed during or prior to the regurgitation process. With each successive movement cycle, the prey was ejected farther out of the mouth (displacement 1.04 ± 0.44 cm; Fig. 3) and then pulled back inside by a smaller amount (displacement 0.47 ± 0.26 cm). The cyclic contractions proceeded until the meal was fully disgorged. The initial eight cycles employed approximately 15 small bends, and then the number of bends decreased in steps as the cycles continued. The initial caudally directed movement at the beginning of a cycle appeared to help straighten the body out, with the small bends disappearing quickly in reverse sequence to their formation. The caudal bend that formed at the beginning of a cycle was present throughout the cycle, and it was always larger than the bends that formed near the head. This bend may have helped to prevent the prey item from moving caudally, but further research is needed to understand the mechanical function of bending timing and morphology. A total of 21 cycles were quantified, with an average duration of 4.5 s. Overall, the process described here could be roughly analogized as a concertina-type movement, but in the reverse direction seen in typical concertina locomotion in snakes (Jayne, 2020).

Once the prey item was fully disgorged, it was inspected and identified as a Brown-banded Watersnake, *Helicops angulatus*. Immediately after regurgitation, we determined that the prey weighed 9.5 g, representing a relative prey mass of 0.86 (RPM; relative prey mass = prey mass/predator mass) of the coralsnake's 11.0 g

weight. The total length of the watersnake was 30.0 cm, representing 63% of the coralsnake's total length of 47.5 cm. Neither predator nor prey were collected. An RPM of 0.86 is within the range of reported values for ingested prey of *Micrurus* (0.20–1.31; Glaudas et al., 2019). Thus, it is likely that the size of the prey item itself did not stimulate the regurgitation response. It is more likely that the stress of capture, handling, and blood draw induced the behaviour. Nevertheless, the RPM of the regurgitated snake was large and could influence other aspects of the coralsnake's life history. In other snake species, RPM can influence prey handling (Mori, 1991; Mehta, 2003; Penning and Cairns, 2016; Jayne et al., 2018), locomotion (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986; Crotty and Jayne, 2015), and antipredator behaviours (Mehta, 2006). The resulting weight gain from the meal can negatively influence endurance and sprint speeds (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986; Crotty and Jayne, 2015). Additionally, the added mass and decreased locomotor speed can promote greater usage of stationary and cryptic antipredator behaviours (Mehta, 2006).

The behaviour of feeding on large prey items relative to body size in snakes can reduce feeding frequency (Secor and Diamond, 1998). For ophiophagous snakes, 'large' can mean long relative to body length, as was observed here. To facilitate ingestion of a long item, the stomach of the predatory snake is stretched, and the body of the prey can be bent into waves (Jackson, et al., 2004). A similar phenomenon was exhibited when the coralsnake compressed its body and stomach in wave-like lateral bends to expel its previous meal, rather than ingest it. Overall, this new observation of *M. lemniscatus* disgorging *H. angulatus* contributes to our knowledge of ophiophagous behaviour and provides new insight into the biomechanics of postprandial regurgitation in snakes.

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