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First observation of *Tropidophis boulengeri* mating in the field (Squamata: Serpentes: Tropidophidae)

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Studying the biology and ecology of snakes in the field is challenging. Many species are specialized on eating comparatively large prey and thus only rarely need to be active and are 'easier' to observe (Shine 1995, Greene 1997, Pough et al. 2016). Many species are generally elusive, for instance by being well hidden or camouflaged ambush predators, by moving underground, in dense leaf-litter, or high up in the canopy, and thus in summary are hard to detect and even harder to study. Consequently, little is known about their biology, which is the case of most neotropical snake species. This also applies to *Tropidophis boulengeri* (Peracca, 1910) (e.g. Köhler 2003), although the many common names: 'Northern Eyelash Boa', 'Rough Scaled Boa', 'Boulenger's Pygmy Boa', 'Sleepy-headed Boa', or 'Snail Snake' (Arteaga 2021, Rodríguez-Guerra et al. 2021), indicate that it is well-known to herpetologists and amateur naturalists. Recently the snake's original genus, *Trachyboa,* was synonymized with *Tropidophis* (Zaher et al. 2024; see also Reynolds et al. 2014).

Tropidophis boulengeri ranges from Panama, where it seems to be very rare, through western Colombia, to north-western Ecuador (Smith 1958, Stimson 1969, Peters & Orejas-Miranda 1970, Pérez-Santos & Moreno 1988, 1991, McDiarmid et al. 1999, MECN 2010, Wallach et al. 2014, Ray 2018). It is a terrestrial to semi-aquatic species that lives along small to larger streams in lowland to mid-altitude rainforests (Castaño-Mora et al. 2004, Cisneros-Heredia 2004, Castro-Herrera & Vargas-Salinas 2008, Rodríguez-Guerra & Guerra-Correa 2020, Arteaga 2021, Arteaga et al. 2024). More is known about its anatomy and phylogenetic relationships (e.g. Bellairs 1950, Brongersma 1951, Szyndlar & Georgalis 2023, Zaher et al. 2024), than its biology. These snakes feed on fish and amphibians, are ovoviviparous, and exhibit a variety of anti-predator behaviours including stiffening of the body (Lehmann 1970, Arteaga 2021), enrolling the body to a flat disc (Burger 2011; Fig. 1a), emptying stink glands (Lehmann 1970), and autohaemorrhaging with blood pressed in the mouth and below the eye scales (Rödel et al. 2023). In contrast to the statement in Pérez-Santos & Moreno (1988, 1991), they are not aggressive and they do not bite (MECN 2010). Some captive snakes were reported to feed on mice (Arnett et al. 1992), and Pérez-Santos & Moreno (1988, 1991) mention lizards and birds as prey. However, this seems highly unlikely at least under natural conditions (authors' own observations). With few exceptional field observations (Dwyer et al. 2018, Griesbaum et al. 2023), most feeding and all reproductive data stem from museum vouchers (Barbour 1937) and captive animals (Lehmann 1970, 1974, Burger 2011, Arnett et al. 1992). Gestation extends over minimum ten months (Lehmann 1970), and females give birth to about six young (Barbour 1937, Lehmann 1970, Arnett et al. 1992). Nothing has been reported on reproduction timing and mating behaviour, neither from captivity nor from the field. Herein we report the first mating data of this species, which were collected during an assessment of riparian herpetofauna in the Canandé Forest Reserve, Esmeraldas Province, Ecuador.

On 30 August 2024, at 12:05, one of us (MLMW) encountered two individuals of *T. boulengeri* in what proved to be a copulation. The snakes laid on gravel and leaf litter, one meter away from the edge of a small forest stream (0.529 N, 79.209 W, 299 m a.s.l.). Where the mating couple was found the regenerating forest (appr. 29 years of regeneration after use as cacao plantation) had an open canopy

and only sparse vegetation in lower strata. The stream had a width of 102 cm, the water was 2.5 cm deep and water flow speed was 0.1 m/s. Water temperature at the beginning of the observations was 23 °C, air temperature ranged between 24.1–24.3 °C from 12:00 to 12:45, with 95.1–95.7% relative humidity (from Onset HOBO U23-001A Pro V2 Data Logger). The weather was cloudy, with no wind, and it had rained heavily the night before. The couple was laying in a slight depression on the forest floor, below a fallen tree trunk.

The male's posterior body half and tail were coiled twice around the female (Figs 2b, 3b), the male's left hemipenis inserted in the female's cloaca (Fig. 3c); both snakes being pressed together along their bellies (Fig. 3a). The heads of the two individuals were facing in opposite directions. Apparently disturbed by being photographed and filmed, the two snakes slowly separated (12:15), but quickly (12:18) stopped moving and then remained motionless, approximately 2 cm apart.

After the individuals separated, we recorded their length and weight, confirmed their sex (using a sex probe set), and photographed them. Snout–vent length (SVL) and tail length (TL) were measured with a flexible measuring tape (accuracy ± 1 mm) appressed to the snakes' bodies; SVL + TL male: 27.2 cm + 3.3 cm; female: 33.5 cm + 3.2 cm. Weight was measured with a Pesola spring balance (max. 100 g,

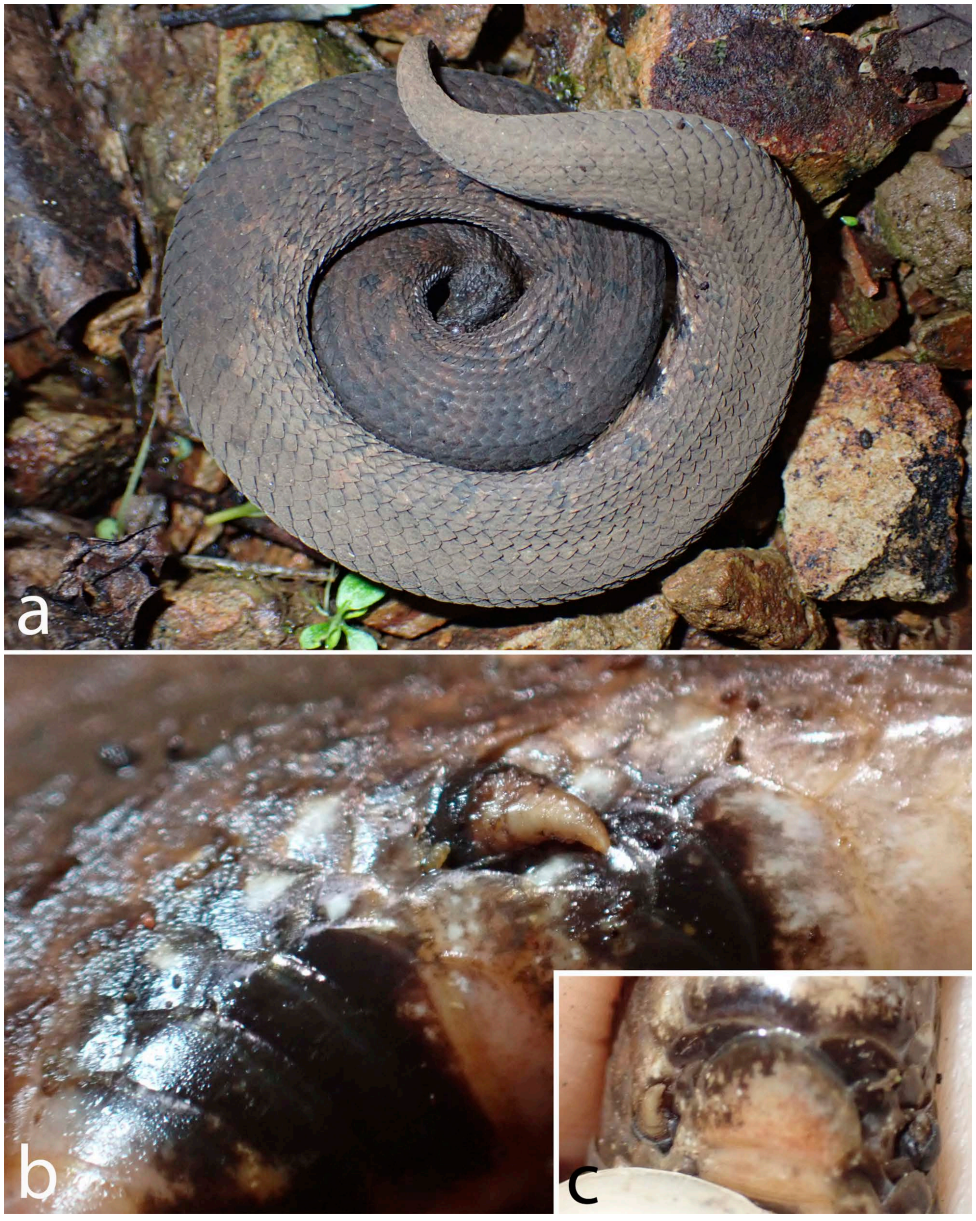

Figure 1. *Tropidophis boulengeri* male, coiled up in defence (a); and detailed views of pelvic spurs (b, c). Photographs by M. L. M. Wiedebusch.

accuracy ± 0.5 g; male: 30 g; female: 46.5 g). The male's sex was known due to the visibility of one hemipenis during copulation, and small but distinct anal spurs on either side of the cloaca; the right spur was approximately 1 mm long, the left 2 mm long (Figs 1b, c). For comparison and to confirm the female's sex, both snakes were palpated. In the male the probe head could be inserted 9–10 subcaudal scales deep; in the female the depth was only 3 subcaudal scales. The male was first handled at 12:19, and again from 12:45 to 12:55. During the second handling he began to coil up (Fig. 1a). At 12:44 and after covering them with some leaves (in the hope that they would stay hidden), the snakes were left alone in the same spot; the male still coiled, and the female stretched out.

MLMW returned to the site at 14:30 and found the pair engaged in a second copulation. The individuals' identities could be confirmed by comparison of the body pattern with the photos taken before. Based on the previous experience that taking photos and videos may result in the couple separating, MLMW restricted her own movements to a minimum. The male's body was now mostly on the female, again coiled twice around the posterior part of

Figure 2. *Tropidophis boulengeri* copulation; (a) male coiled around the female's body, with his head pressing the female flank, being dragged by her very slowly; (b) male (left snake) coiled around the posterior part of the female (right snake) with the hemipenis inserted; (c) male (above) coiled around female (below), with their bellies pressed together, both snakes having their head hidden and cloacae connected. Photographs by M. L. M. Wiedebusch.

the female's body, bellies of both snakes pressed together (Fig. 2c). The female's tail was stretched, while the male's tail was coiled around. The male laid on top of the female, his head pressed against her left flank; the female's head was hidden under leaves. The snakes were left alone, but periodically checked again (15:04; 15:28; 16:00). The snakes maintained their position, but the male was breathing 'agitatedly' and very slightly moved his head. When the leaves on the female's head were removed at 16:30, both snakes moved slightly. The male positioned his head horizontally next to the female's body, and both attempted to hide their heads under leaves, still engaged in copulation. The female coiled the first part of her body slightly, while hiding her head, and the male placed his head under a leaf. The snakes were left in this position at 16:58; copulation duration at that time was 2.5 hours; air temperature ranged from 24.15–24.6 °C, with 96.2–98.0% relative humidity.

MLMW returned to the site at 22:12 (5 hours later), finding the snakes in almost the same position. The female had placed her head on her body. They remained in this position until 22:40, when the female raised her head, and the male placed his head on the female. The female then began to move very slowly, sticking her tongue out from time to time. The male remained motionless at first, while the female hid her head again under leaves. Then the male pressed his head against the female's body, still coiled three

Figure 3. *Tropidophis boulengeri* copulation; (a) both snakes being pressed together along their bellies, the male coiled around the female's posterior part and tail (b); (c) male's hemipenis inserted into the female's cloaca. Photographs by M. L. M. Wiedebusch.

times around the final and middle part of the female body (Fig. 2A). At 22:50, the male constricted the female again, his head being placed almost under the second half of the female's body. The female continued moving during these efforts and it seemed that her head was slightly swollen. During her movements the male constricted her more intensively. At 23:04, the male withdrew his head from under the female, while she continued moving very slowly (now being approximately 8 cm from their previous position at 22:12); the male flicked his tongue from time to time; and pressed his head against the female's flank. At 23:09, the male shook his head rapidly for a few seconds, while the female kept moving; the cloaca remained connected; the male being dragged by the female. At 23:11, the male began to disengage a little (slightly loosening his coils) from the female and started to move slightly (for a few seconds) alongside. He moved his head over the female and shook it rapidly for a few seconds, then lowering his head and keeping it on the right side of her body. The male breathed agitatedly, whereas the female remained calm. The female kept moving very slowly, covering about 5–8 cm, stopping from time to time, while the male was being dragged, only coiling more tightly around the female. At 23:28, the female stopped, while the male was coiled around her posterior half. At 23:34 the snakes were left alone. Before MLMW left, the female moved her head up, and the male slightly loosened his coils, while raising his head. The cloacae were still connected, the copulation had lasted already more than 9 hours. Air temperature during the night ranged from 23.4–23.9 °C, with 91.4–93.8% relative humidity.

During the observation MLMW registered another *T. boulengeri* male, twenty-five meters downstream. This snake showed however, no interaction with the couple. The next day, MLMW returned to the mating area, but could not spot any specimens of *T. boulengeri*.

The copulation occurred on the ground and near flowing water, the habitat usually occupied by this species (Ortega-Andrade et al. 2010, Ibáñez et al. 2019, Rodríguez-Guerra & Guerra-Correa 2020, Arteaga 2021, authors' unpubl. data). In various literature sources it is mentioned that this species is (also) arboreal (Pope 1966 cited in Lehmann 1970, Pérez-Santos & Moreno 1988, 1991, Harrington et al. 2018, O'Shea 2023, Uetz et al. 2024). We confirm that *T. boulengeri* occasionally 'climb' on low vegetation (< 60 cm, see also Arteaga 2021), to avoid flooding or to ambush frogs (authors' unpubl. data). In one extreme event we also observed a snake 1.5 m in a shrub, however, that does not mean that they are arboreal. Their usual habitat is at or even in water, where they ambush fish, frogs and most likely tadpoles (compare Lehmann 1970, MECN 2010, Dwyer et al. 2018, Griesbaum et al. 2023).

Interestingly, we observed the copulation first during day, extending into the night. Although MECN (2010) mention day and night activity for the species, we observed the species as being almost exclusively nocturnal (authors' unpubl. data), a fact also reported by other authors (Lehmann 1970, Ortega-Andrade et al. 2010, Arteaga 2021). Rehak (1987) reported the copulation time in captivity for another tropidophid snake, *Tropidophis feicki,* as lasting for 2 hours and 41 minutes. The copulation duration of our snakes, lasting for nine hours or more, thus seems very long. However, we have to admit that we cannot be certain that in the five hours between later afternoon and night, where we interrupted our observation, the snakes remained continuously in copulation. They could have also been separated and reengaged again, as after their first separation due to our activities.

Lehmann (1970) reported a female *T. boulengeri* from Ecuador, giving birth to six young on 24 October 1968. He bought the female in January 1968, kept her individually, and thus concluded that gestation takes a minimum of nine months [to our knowledge, it is unknown if *Tropidophis* possess a spermatheca]. So far reproduction time of the species was unknown. Our observation is from 30 August, the end of the 'dry' season. However, we observed very small *T. boulengeri*, the size of new-borns according to Lehmann (1970) and Arnett et al. (1992), through various months (authors' unpubl. data), and thus believe that the mating time corresponds to a longer period, if not yearround.

Although there are no concrete examples of constriction during courtship and mating, some snake families exhibit coiling and sometimes muscular contractions to ensure copulation. For instance in some boid snakes, like green anacondas (*Eunectes murinus*) and carpet pythons (*Morelia spilota*), males coil around females during mating to maintain contact (Rivas & Burghardt 2001). Colubrid snakes also exhibit coiling around the female's cloaca for intromission (Shine et al. 2000). Male *Thamnophis sirtalis* (garter snakes) induce hypoxic stress in unreceptive female through caudocephalic waves (rhythmic muscular contractions), causing the female to gape her cloaca, inadvertently facilitating intromission (Shine et al. 2003). We cannot say if the *T. boulengeri* male applied a similar strategy, but at least it looked like it put some pressure to the female when constricting her.

The presence of cloacal or pelvic spurs in males is shared with other 'basal' snakes (Bellairs 1950, Underwood 1967, Anzai et al. 2023 and literature cited therein). Peracca (1910) did not discover spurs in his male, but mentions them for *T. gularis* (Peters, 1860). Bellairs (1950) provides a very detailed description of the hind-limb rudiments in *T. boulengeri*, while Boulenger (1913) and Pérez-Santos & Moreno (1988, 1991) mention pelvic vestiges in males, which are not externally visible in females. However, this character is surprisingly not mentioned in newer literature (Rodríguez-Guerra et al. 2020, Arteaga et al. 2024, O'Shea 2023). Burbrink & Crother (2011) mention that tropidophid snakes retain some pelvic elements, and Brongersma (1951) and Ortega-Andrade et al. (2022), report on cloacal spurs in male *Tropidophis melanurus* (Schlegel, 1837) and *T. cacuangoae* Ortega-Andrade, Bentley, Koch, Yánez-Muñoz & Entiauspe-Neto, 2022, respectively. Interestingly Brongersma (1951) does not mention cloacal spurs for the one *Trachyboa gularis* Peters, 1860 male he was dissecting. Dunn & Bai-

LEY (1939) mention the absence of cloacal spurs in a female *T. boulengeri*, an observation which we confirm. In boas, male snakes use the pelvic spurs to stimulate cloacal opening of the female before inserting the hemipenis (LILLYWHITE 2014, ANZAI et al. 2023). We could not observe any behaviour involving the use of the spurs. However, as we encountered the snakes already in copula, we simply may have missed that stage.

This observation of mating behaviour in *T. boulengeri* expands our understanding of the species' reproductive ecology. However, further research will be crucial for understanding the reproductive patterns and ecology of this and other snakes of the Ecuadorian Chocó.

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