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Short Communication

Spawning site plasticity in *Cycloramphus boraceiensis* (Anura: Cycloramphidae)

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Reproductive biology is likely the most studied subject in amphibian natural history (e.g., Womack *et al.* 2022). In part, this observation is explained by the conspicuous and easy-to-observe breeding behavior of amphibians, but also because a standardized classification system exists for amphibian reproductive modes (recently reviewed by Nunes-de-Almeida *et al.* 2021). This classification lists 74 reproductive modes (RM) for amphibians, and 71 RM for anurans (Nunes-de-Almeida *et al.* 2021). Based on the variation in the number of RM proposed by different authors (e.g., Duellman and Trueb 1986, Haddad and Prado 2005, Nunes-de-Almeida *et al.* 2021), it is clear that given the diversity of reproductive strategies, more information will be valuable.

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The reproductive strategies of species in the genus *Cycloramphus* Tschudi, 1838 roughly fall into two categories: terrestrial, in which tadpoles are nidicolous (Lutz 1944, Heyer and Crombie 1979, Almeida-Silva *et al.* 2019, Verdade *et al.* 2023) or semi-terrestrial, in which tadpoles are saxicolous, exotrophic, and mostly associated with streams (Heyer 1983a,b, Haddad and Sazima 1989, Lima *et al.* 2010, Silva and Overnay 2012, Nunes-de-Almeida *et al.* 2016, Verdade *et al.* 2019). Terrestrial reproduction has evolved independently multiple times from saxicolous species according to the phylogeny of the genus (Sá *et al.* 2020). Variation observed in the reproduction of saxicolous species are classified under RM 17, in which females lay eggs on humid rock surfaces or inside rock crevices above the water in streams, and RM 19 for *Cycloramphus dubius* (Miranda-Ribeiro, 1920), in which eggs are deposited on wet rocks or between roots at the edges or within streams, according to Nunes-de-Almeida *et al.* (2021).

The semi-terrestrial tadpoles of *Cycloramphus* spp. were thought to have restricted microhabitats, but recent observations in the field (e.g., *C. boraceiensis* Heyer, 1983; Pedrozo *et al.* 2024) and in captivity (e.g., *C. bandeirensis;* Verdade *et al.* 2019) have expanded our knowledge of their microhabitats and other features. Egg site deposition, development, and diet of *Cycloramphus* tadpoles are more variable than once thought. Egg masses of saxicolous species of *Cycloramphus* have been found on humid rocks, or more rarely, on plant stems near the splash zone of waterfalls within streams. We present herein natural history observations made in the field that increase our knowledge of variation of spawning sites of *C. boraceiensis*.

We conducted observations in the Projeto Dacnis private reserve, an area of 136 ha located within lowland Atlantic Forest in the municipality of Ubatuba, state of São Paulo, Southeastern Brazil (23°27'46" S, 45°07'58" W; WGS-84; 15–500 m a.s.l.). The region is characterized by paludal forests (patches of forests with waterlogged soil) in lowland areas and patches of primary and secondary dry forests on steep terrain. Climate in the region is classified as humid subtropical without distinct seasonality (Rolim *et al.* 2007). In 14 years monitoring the area, we found two saxicolous species in forest streams: *Thoropa taophora* (Miranda-Ribeiro, 1923) and *C. boraceiensis,* both with semi-terrestrial tadpoles that can be diagnosed by differences in body shape, position of eyes, and color pattern (Heyer *et al.* 1990, Moura *et al.* 2019, Colaço *et al.* 2021).

We monitored three spawning events, one in a cavity in the soil (Figure 1A–D) and two in a hole in a liana stem (Figure 2A–B). We encountered the first mass of eggs of *C. boraceiensis* on 13 October 2015 and observed the development of the embryos in three visits over two weeks. Forty eggs were laid on soil in a dry cavity in a vertical ravine 2 m from the stream. An adult male was observed near the clutch (Figure 1B). After six days, the larvae remained in the egg capsules but with visible eyes and body pigmentation (Figure 1C). After another six days, the tadpoles were well developed, moving among the gelatinous mass from the empty egg capsules (Figure 1D). Following a heavy rain on 28 October 2015, neither the eggs, tadpoles, nor the adult male were seen at the spawning site, having been washed away.

On 4 May 2023, we observed a second egg mass of *C. boraceiensis* inside a hole in a liana stem that was hanging approximately 30 cm above a dripping rocky wall. The spawning site was kept consistently humid by a small trickle of water running down the liana and by spray from a nearby small waterfall. We counted 36 eggs at a very early stage of development (Figure 2B). We visited the site another three times. On 8 May 2023, we observed eye pigmentation and the emergence of gills on the embryos inside the egg capsules (Figure 2C). After 7 days, free-living tadpoles were clustered inside the liana hole (Figure 2D), and from 19 May 2023 onward tadpoles were found on the rocky wall bellow the liana stem (Figure 2E). An adult *C. boraceiensis* remained close to the spawning site inside a small crevice on the rocky wall throughout the observation period. Seven months later, on 14 December 2023, another egg mass was located in the same liana hole, again with an adult nearby. Unfortunately, we were unable to determine if it was the same frog observed in May. Site fidelity is a possibility in stream-associated *Cycloramphus* spp., as high quality reproductive sites may be a limiting resource.

Our observations are the first to describe an egg mass of a saxicolous stream-associated species of *Cycloramphus* in a dry cavity on soil away from wet rocks or the splash zone of a waterfall. Our observations of spawning on the stems of lianas confirm those reported for *C. boraceiensis* (Pedrozo *et al.* 2024). Based on the current reproductive mode classification system of Nunes-de-Almeida *et al.* (2021), *C. boraceiensis* would be categorized in RM 17 (for saxicolous species of the genus), RM 19 (previously known only for *C. dubius*), and RM

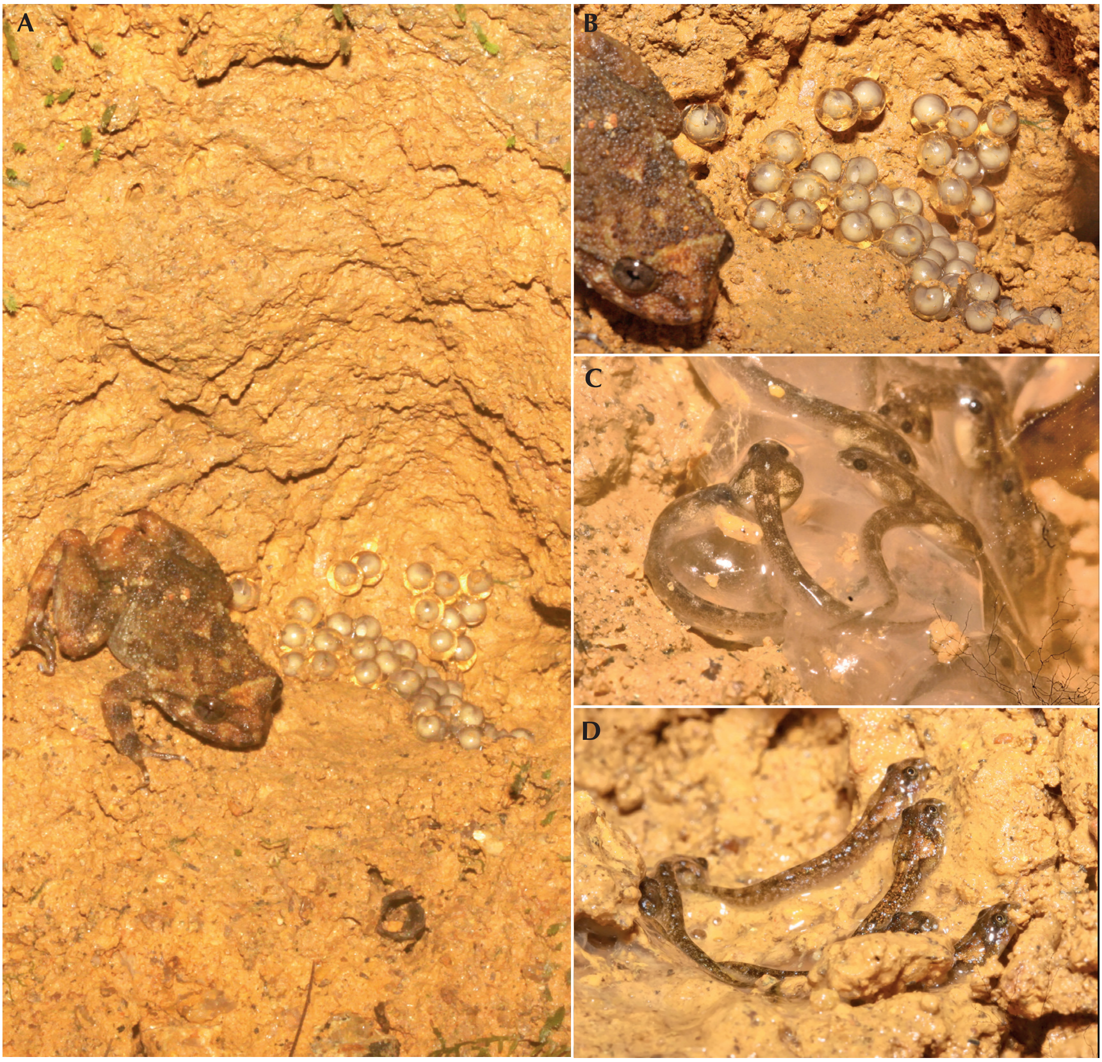

Figure 1. (**A**) Egg mass of *Cycloramphus boraceiensis* in a permanently dry ravine cavity; (**B**) a male guarding eggs in an early stage of development; (**C**) larvae with visible eyes and body pigmentation; (**D**) hatched tadpoles still in the gelatinous mucus inside the ravine cavity.

32 (reported here for the first time) by depositing eggs in dry cavities on soil.

Our observations expand those of Pedrozo *et al.* (2024) on the use of humid cavities in the soil at the steep edges of streams for reproduction in *C. boraceiensis*. The plasticity in spawning sites observed in *C. boraceiensis* indicates how little we know about the requirements associated with high quality sites for reproduction, and how the limitation of this resource could lead to differential survivorship of eggs and tadpoles. Understanding selective pressures induced by humidity levels, risk of displacement by heavy rainfall, and effective

Figure 2. (**A**) Egg mass of *Cycloramphus boraceiensis* within a consistently humid vine hole situated above a rock wall with a continuous water layer; (**B**) an egg mass with embryos at an early stage; (**C**) larvae with ocular pigmentation and gills; (**D**) hatched tadpoles still within the liana cavity; (**E**) tadpoles adhered to the rocky wall.

parental care are crucial to understanding the evolution of terrestrial reproduction in the genus. The future of populations of *Cycloramphus* spp. may include a scenario of climate change that may affect rainfall volume and periodicity.

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