

Hidden breeding behaviour in a still undescribed giant *Mantidactylus* frog from Betampona Strict Nature Reserve, eastern Madagascar

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Madagascar's amphibian fauna is characterised by remarkable species diversity and a high level of endemism, alongside relatively limited diversity at family and subfamily levels (Andreone et al., 2021; Antonelli et al., 2022). With over 430 described species and a significant number of candidate species awaiting formal taxonomic assessment and description (Carné and Vieites, 2024), this large island is a critical hub for amphibian biodiversity conservation (Luedtke et al., 2023). However, the associated taxonomic uncertainty, often referred to as the “Linnean shortfall” (Lomolino, 2004), poses a significant challenge to conservation planning, as emphasised in Madagascar's two Sahonagasy Action Plans for amphibian conservation (Andreone and Randriamahazo, 2008; Andreone et al., 2016; Rakotoarison et al., 2022).

Basic traits of the life history of most Malagasy frogs, including their breeding strategies, larval development, and acoustic communication, still remain largely unknown and/or undocumented. Even in taxonomically well-established species, key life-history traits are often poorly known (Glaw and Vences, 2007). A notable example is the group of large-sized species belonging to the *Mantidactylus* subgenus (genus *Mantidactylus*,

family Mantellidae). The four currently described species - *M. grandidieri*, *M. guttulatus*, *M. lovei*, and *M. radaka* - along with several undescribed lineages, are primarily found in the eastern rainforests and central highlands of Madagascar (Rancilhac et al., 2020). All these species reach a considerable size (up to 130 mm SVL), are medium- to long-lived (Guarino et al., 2019), and are commonly referred to as “radaka”, “bakaka,” or “radakabe”. Due to their large size and ease of capture, they are frequently harvested as bushmeat by local communities and often sold to restaurants as frog legs (Jenkins et al., 2009).

Early dissections of preserved females revealed unusually large eggs (Glaw and Vences, 1994), leading to speculation about a possible direct development. Schulze et al. (2016) later documented aquatic tadpoles in *M. radaka* (originally described as belonging to *M. guttulatus*). This taxonomic clarification came after molecular evidence: Randrianiaina et al. (2011) reclassified tadpoles with reduced oral structures as *M. majori*, despite them originally being attributed to *M. guttulatus* by Altig and McDiarmid (2006). Notwithstanding these advances, the adaptive significance and developmental implications of large egg size remain unresolved.

Knowledge on the acoustic ecology in this subgenus has also progressed more slowly than its taxonomy. Unlike most Malagasy frogs whose advertisement calls facilitate species identification, these species' vocalisations proved exceptionally challenging to record. Prior to this study, only a single documented call (*M. radaka*) was described for this subgenus (Vences et al., 2004). To date, neither vocalisations, nor tadpole observations exist for *M. grandidieri*, *M. guttulatus*, *M. lovei*, or any other candidate species in the subgenus *Mantidactylus*. Addressing these knowledge gaps was therefore crucial for both basic biology and conservation, particularly given increasing harvesting pressures associated to

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habitat alteration that have caused significant declines in large adults, even within protected areas (Jenkins et al., 2009; Andreone et al., 2021).

Two candidate species of the subgenus *Mantidactylus* - *M. sp. Ca55* and *M. sp. Ca56* - are known to occur in the Betampona Special Nature Reserve (Piccoli et al., 2025). This small lowland rainforest (less than 30 km²) is home to an exceptionally rich and diverse population of amphibians, with at least 87 recorded species (Rosa et al., 2011, 2012; Dubos et al., 2025; Piccoli et al., 2025; Porcel et al., 2025). The Madagascar National Parks (MNP) manages the reserve in partnership with the Madagascar Fauna and Flora Group (MFG), which oversees an extensive ecological monitoring programme focusing on biodiversity assessments, particularly of herpetofaunal and other vertebrate populations.

We recorded the reproductive behaviour of individuals attributed to *M. sp. Ca56* on an annual basis during the April-June months from 2022 through 2025 (Fig. 1). Although *M. sp. Ca55* and *M. sp. Ca56* are not yet described species, they can be distinguished based on a few chromatic and morphological characteristics: *M. sp. Ca55* has a whitish ventral side and smooth dorsal skin, whereas *M. sp. Ca56* has a yellowish ventral side and granular dorsal skin. Here, we document the unique egg-deposition behaviour of individuals attributed to *M. sp. Ca56* in the reserve. Species attribution was based on photographs of adult specimens. However, identification of eggs and tadpoles found alone (without associated adults) remained tentative, as we were unable to perform biomolecular analyses to confirm their identity.

The observations occurred around three sites, respectively Sahambendrana (17.8984°S, 49.2154°E), Sahabezoa (-17.9142°S, 49.2077°E), and Sahavarikely (-17.8540°S, 49.2017°E). We made a total of 26 observations of individuals identified as putative males (distinguished by their smaller size). Putative females were sometimes observed near or inside ground burrows, often in the presence of egg clutches and tadpoles. 20 additional records involved only eggs or tadpoles, with no parent present. These observations were consistently confirmed across multiple years, indicating recurring breeding in the dry-cold season (April-July).

Males also frequently emitted loud, bark-like, calls after sunset, quite similar to those described for *M. radaka* (Vences et al., 2004), which likely have a function in mate attraction and/or territorial defence. Egg clutches were laid on the ground, a trait typical of the Mantellinae subfamily (Glaw and Vences, 2007). The single eggs were large (with a diameter of around 5

mm), corroborating earlier observations from dissected specimens. One female was seen entering a burrow, presumably for amplexus (though this was not directly observed). In this case, both adults were observed in the burrow. The individuals exhibited high sensitivity to disturbance, freezing when detected, which made prolonged observations difficult. By June, some burrows showed presence of water, though its origin (whether actively transported by adults or from passive infiltration) remains unclear. Observations during 17–18 June 2025 at Sahavarikely confirmed the presence of advanced-stage tadpoles in water-filled burrows, implying an egg-to-hatching period of 1–2 months.

These observations reveal unique reproductive traits, including burrow use, terrestrial egg deposition and potential biparental care. The presence of large tadpoles in the water pools within burrows suggests that the deposition of large eggs led to the birth of tadpoles already in an advanced developmental stage. However, key interrogatives still remain regarding the origin of burrows (by direct excavation vs. cavity use), the mechanisms by which water is maintained, and the ways in which tadpoles disperse to aquatic habitats. Confirmation of biparental care would also be crucial, as this behaviour is currently only documented in cophyline microhylids among Malagasy frogs (Blommers-Schlösser and Blanc, 1991; Köhler et al., 1997; Glaw et al., 2020; Scherz et al., 2022). Our findings emphasise the urgent need for continued research on Madagascar's endemic amphibians. A better understanding of their ecological and behavioural traits is essential to inform effective conservation strategies in the face of mounting environmental threats.

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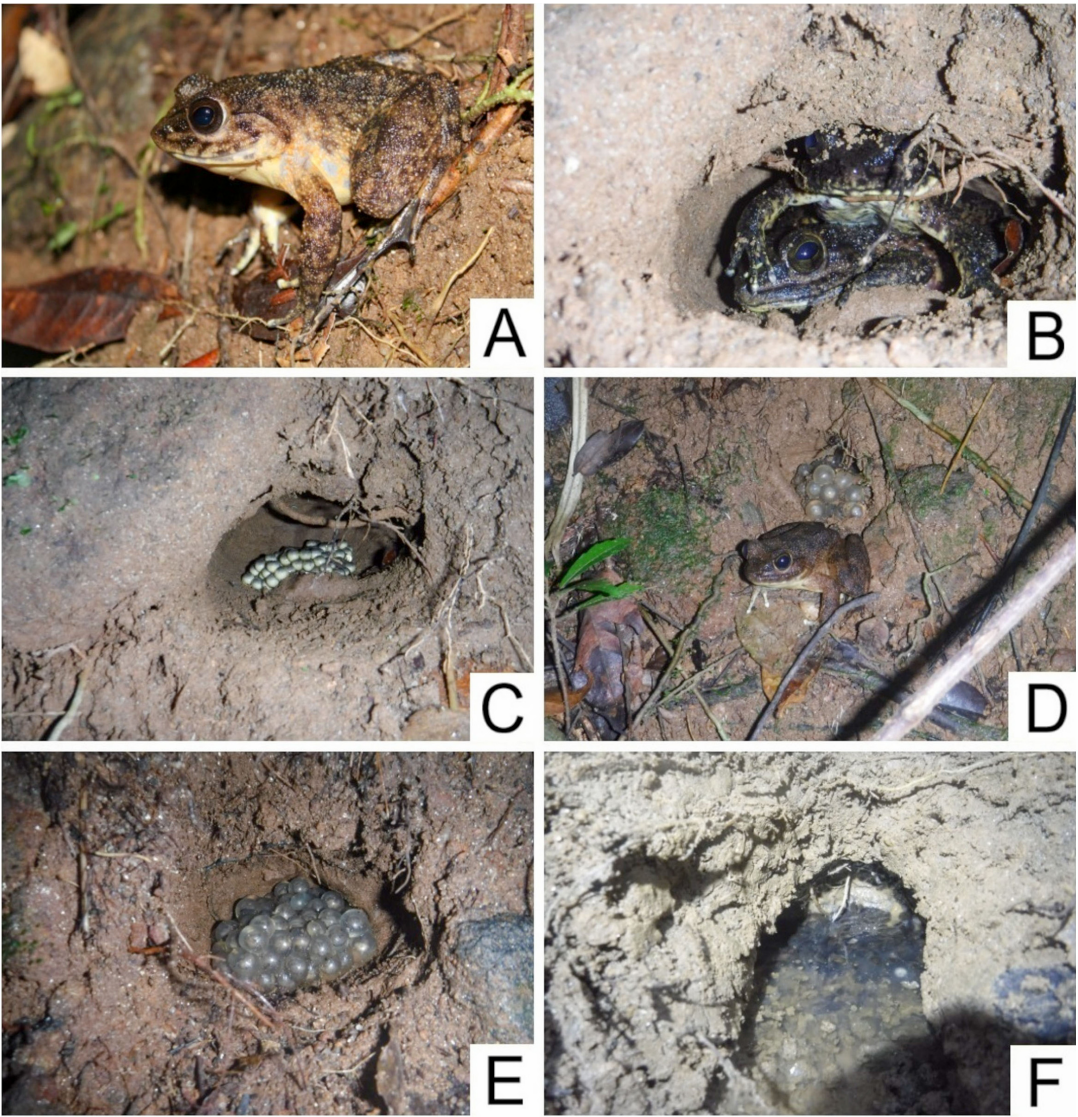


Figure 1. Observations of breeding behaviour and egg development in *Mantidactylus* sp. Ca56, Betampona Strict Nature Reserve, Eastern Madagascar. (A) Male (Sahambendrana campsite, 11 June 2023). (B) “(B) Female and male within a burrow (Sahabefoza campsite, July 2022). (C) Egg-clutch within the soil cavity (Sahabefoza campsite, 07.2022). (D) Male if front of the burrow and eggs (Sahavarikely campsite, 17 June 2025). (E) Burrow with egg-clutch, showing their large size (Sahavarikely campsite, 17 June 2025). (F) Burrow with water and developing tadpoles (Sahavarikely campsite, 18 June 2025). Photos by H. Lava.

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