

Male parental care in Malagasy stream-dwelling frogs of the *Mantidactylus femoralis* group (Anura: Mantellidae: *Ochthomantis*)

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The first report of parental care in anurans dates back to 1705, in a behavioural description of *Pipa pipa* (Linnaeus, 1758), a frog from Suriname that keeps its eggs on its back until tadpoles complete metamorphosis (Merian, 1705). Multiple forms of parental care have evolved independently throughout the course of amphibian evolution (e.g., caecilians: Bei et al., 2012; Kupfer et al., 2016; salamanders: Takahashi et al., 2017; frogs: Delia et al., 2020), yet the description and research of this complex behaviour has rapidly increased only since about 1950 (Schulte et al., 2020). A recent review (Schulte et al., 2020) recognised 28 different types of parental care in nine different modes among frogs and concluded that egg attendance is the most common parental care strategy across the order. A similar pattern was also reported by Furness and Capellini (2019), who noted adult attendance in 330 of 410 species of amphibians that exhibited parental care.

In frogs, egg attendance can last until tadpole emergence or even until the froglet stage (Oneto et al., 2010). A range of parental strategies are now well documented, with eggs and larvae guarded either exclusively by males (Noronha and Rodrigues, 2018; Garavito-David et al., 2020), by females (Sorokin and Steigerwald, 2018; Cassiano-Lima et al., 2020), or by both sexes (Brown et al., 2010). When egg attendance is performed by both sexes, this generally occurs in an alternating way (Simon, 1983; Bourne, 1998; Lehtinen, 2003), although a pair of *Platypelis barbouri* in Betampona Strict Nature Reserve, eastern Madagascar, was found guarding its nest in a tree hole in 2013 (Glaw et al., 2020; A. Crottini, pers. obs.). During egg attendance, adults may directly defend (Consolmagno et al., 2016), clean (Valencia-Aguilar et al., 2012), or hydrate their eggs (Delia et al., 2017). Formal demonstration of a resulting increase in fitness is lacking, but some experiments have shown an important increase in egg mortality when the adult is deprived of the possibility to perform egg guarding (e.g., Delia et al., 2013; Bravo-Valencia and Delia, 2016; Consolmagno et al., 2016). The increase in egg survival conveyed by attendance may constitute a selective advantage to the offspring, even though it likely represents a considerable investment for the parent(s). The physiological investment associated with egg attendance can be characterised by parental loss of body mass due to reduced foraging activity and, in the case of male egg guarding, a reduction of mating opportunities (Trivers, 1974; Townsend, 1986; Pröhl and Hödl, 1999). The physiological and biological cost of attendance may be compensated by a better survival of the guarded eggs (Townsend, 1986).

Madagascar is a hotspot of amphibian diversity, with currently more than 370 described species of frogs (caecilians and salamanders are absent; AmphibiaWeb, 2021). Parental care has now been documented for several Malagasy frogs, especially in the microhylid subfamily Cophylinae (*Anodonthyla*: Blommers-Schlösser, 1975; *Madecassophryne*: Blommers-Schlösser and Blanc, 1991; *Platypelis*: Blommers-Schlösser, 1975; Rakotoarison et

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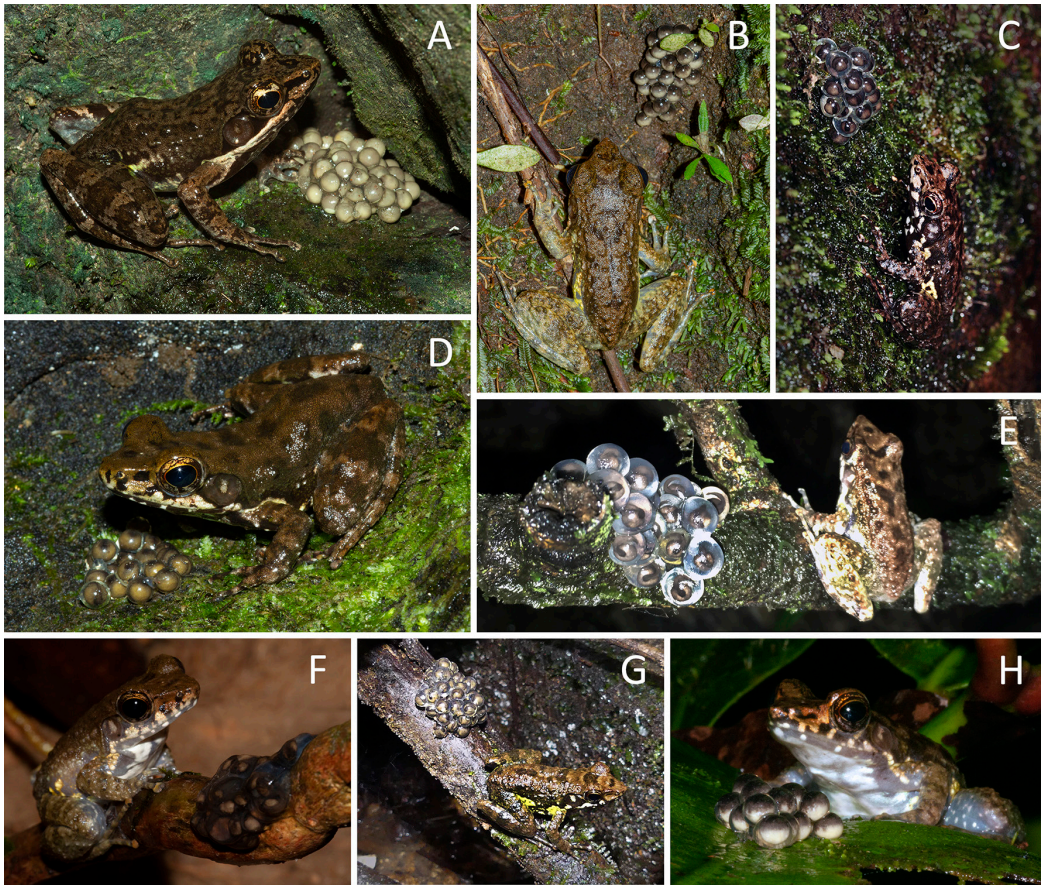


Figure 1. Egg-guarding behaviour in adult males of the *Mantidactylus (Ochthomantis) femoralis* species group in Betampona Strict Nature Reserve, Madagascar. (A–D) show males guarding eggs on rocks or crevices. (E–G) show males guarding eggs perching on branches. (H) shows a male guarding an egg clutch on a leaf. Specific identifications of individual frogs are provided in Table 1.

al., 2012; Glaw et al., 2020; *Plethodontohyla*: Blommers-Schlösser, 1975; Vences et al., 2003; *Rhombophryne*: Köhler et al., 1997; *Stumpffia*: Glaw and Vences, 1994; Rakotoarison et al., 2017).

All species of the subfamily Mantellinae (family Mantellidae) lay eggs outside water (Glaw and Vences, 1994, 2007), and Lehtinen (2003) observed egg attendance in *Guibemantis wattersoni* (reported as *G. bicalcaratus*) and *G. annulatus* (reported as *G. punctatus*). Egg guarding has also been documented for species of *Blommersia* (e.g., Glaw et al., 2019), *Mantidactylus majori* (Vences and de la Riva, 2005), *Mantidactylus (Maitsomantis) argenteus* (Glaw and Vences, 2007), and *Gephyromantis webbi* (Glaw and Vences, 2007). Similarly, Wolf (2013) observed a male from an unspecified *Mantidactylus (Ochthomantis)* guarding eggs on a branch and hypothesised that egg attendance by males might be widespread in this subgenus. Here we document egg guarding (Mode A9 of Schulte et al.,

2020) in male stream-dwelling frogs of the *Mantidactylus (Ochthomantis) femoralis* group (Fig. 1).

Observations were made sporadically between 2007 and 2019 at Betampona Strict Nature Reserve (between 17.25° and 17.92°S and 49.20° and 49.25°E) on the east coast of Madagascar. Betampona is a small relict of lowland humid forest where amphibian and reptile populations have been regularly monitored since 2009 (Dubos et al., 2020; Porcel, 2020). We observed egg guarding on ten separate occasions and in two candidate species (sensu Vieites et al., 2009), *Mantidactylus* sp. Ca38 and *Mantidactylus* sp. Ca44 (Table 1). In all cases, males were attending eggs (Figs. 1, 2) in clutches positioned overhanging water, and on at least three occasions we confirmed that egg attendance was prolonged, lasting several days (Fig. 1G). Individuals were identified as males by the presence of conspicuous femoral glands (Fig. 2; Glaw and Vences, 2007).

Table 1. Records of egg-guarding behaviour for stream-dwelling frogs of the *Mantidactylus* (*Ochthomantis*) *femoralis* group in Betampona Strict Nature Reserve, Madagascar. Ca38 and Ca44 are candidate species (sensu Vieites et al., 2009), to which our observed frogs were assigned genetically or morphologically. Records of unattended egg clutches did not allow identification to species, but our other observations lead us to conclude that they belong to either *Mantidactylus* sp. Ca38 or *Mantidactylus* sp. Ca44. They are listed as unassigned below. Tissue samples used in species identification were analysed in Rosa et al. (2012). Species identifications based on morphology only are identified by asterisks (*). For each of the observations, we reference a specific figure in this report. Embryo stages were defined following Gosner (1960) and Scheld et al. (2013). Collections are abbreviated using the following acronyms: Museo Regionale di Storia Naturale, Torino, Italy (MRSN); field numbers of Franco Andreone (FAZC) and Angelica Crottini (ACZC); and field numbers of the Betampona 2019 expedition (bet).

Species	Figure	Date	Time (h)	Site	GPS Coordinates (°S, °E)
Ca38*	1H, 3C	8 Feb 2007	21:30	Sahambendrana	17.8987, 49.2152
Ca38*	1F, 3A	7 Mar 2007	20:00	Sahabefoza	17.9143, 49.2086
Ca38	1A, 2A, 3B	5 Dec 2007	23:50	Betakonana	17.9135, 49.2154
Ca44	3D	18 Nov 2007	10:27	Maintimbato	17.8954, 49.2268
Ca44	2B, 3G	5 Dec 2007	11:20	Betakonana	17.9128, 49.2161
Ca44*	1C	20 Oct 2010	10:10	Sifaka	not available
Ca44*	1B, 3E	16 Nov 2013	20:50	Betakonana	17.9113, 49.2146
Ca44*	1D, 3F	23 Nov 2013	09:00	Maintimbato	17.8937, 49.2236
Ca44*	1G	23–26 Jul 2019	10:00–22:00	Sahambendrana	17.8987, 49.2152
Ca44*	1E	31 Jul 2019	20:07	Sahabefoza	17.9143, 49.2086
unassigned	4A, B	2 Mar 2007	10:30	Vohitsivalana	17.8862, 49.2027
unassigned	4D, E	14 Nov 2007	21:30	Sahaïndrana	17.8963, 49.2019
unassigned	4C	5 Dec 2007	9:30	Betakonana	17.9131, 49.2151

Species	Microhabitat	Height (m)	Embryo Stage	Eggs (n)	Tissue	Voucher	GenBank
Ca38*	leaf above water	1.60	11	21	FAZC 13560–61	MRSN A6638	–
Ca38*	branch above water	0.60	22	> 30	none taken	–	–
Ca38	rock crevice	1.20	11	62	FAZC 13948–49	–	HM364728
Ca44	branch above water	0.80	22	27	FAZC 13899	–	HM364677
Ca44	rock slope	1.00	22	18	FAZC 13941–42	–	HM364679
Ca44*	rock wall	0.20	19	20	ACZC3610	–	–
Ca44*	rock wall	1.10	10	34	ACZC 5997	–	–
Ca44*	rock wall	0.80	13	18	none taken	–	–
Ca44*	branch above water	0.20	9–18	36	Bet_061	–	–
Ca44*	branch above water	0.80	19	22	none taken	–	–
unassigned	rock wall	0.75	22	62	none taken	–	–
unassigned	rock wall	0.65	20	21 / > 40	none taken	–	–
unassigned	rock wall	0.50	20	> 110	FAZC 13940	–	–

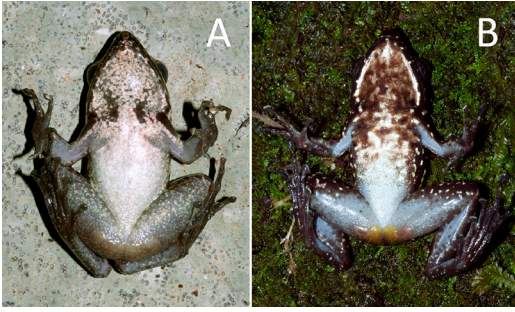


Figure 2. Ventral views of two adult male individuals of the *Mantidactylus (Ochthomantis) femoralis* species group from Betampona Strict Nature Reserve, Madagascar, showing their femoral glands. (A) Candidate species Ca38, also shown guarding eggs in Fig. 1A. (B) Candidate species Ca44, also shown guarding the egg clutch in Fig. 1G.

In the first observation, made on 18 November 2007, a male *Mantidactylus* sp. Ca38 was observed on a leaf above water (Fig. 1H) guarding a clutch of 21 eggs (Fig. 3C). The male was positioned less than a few centimetres

from the clutch, in close proximity to a stream. In other cases, we found individuals perching on branches (such as a male *Mantidactylus* sp. Ca44; Fig. 1E, G), on rocks, in a crevice (Fig. 1A), or in a more exposed position, such as on rock faces (Fig. 1B, C). Animals were perching from about 0.20–1.50 m above the ground/water level (Table 1). This behaviour was recorded all year round, both during the day and at night.

We observed male-guarding of eggs at different developmental stages for both species (Fig. 3), from early development (Stage 9, Gosner, 1960; Scheld et al., 2013; Figs. 1B, 3E) to embryo hatching (Stage 22, Gosner, 1960; Scheld et al., 2013; Figs. 1F, 3A). A focal observation of one of the males (Fig. 1G) by our team revealed that a large amount of time is invested in this behaviour (at least 10–12 h per day, although we did not follow the male overnight, so this amount could be an underestimation) over at least five days. The male was found sitting near the eggs and moved only in the case of direct disturbance but would always return after a few minutes. We directly observed the individual guarding

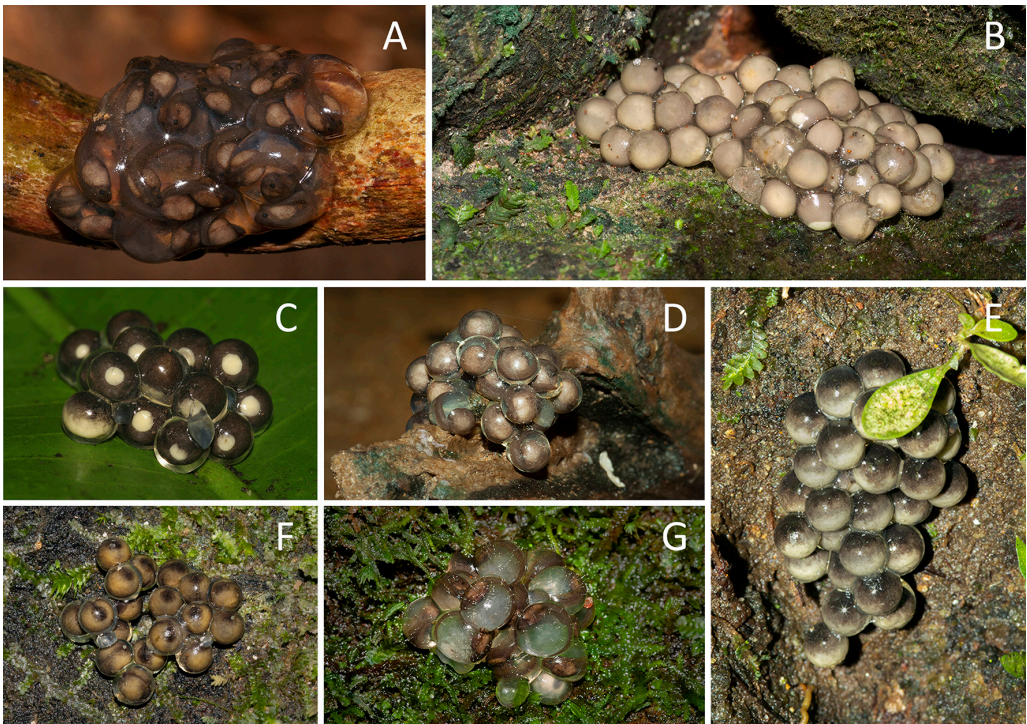


Figure 3. Attended egg clutches of the *Mantidactylus (Ochthomantis) femoralis* species group from Betampona Strict Nature Reserve, Madagascar, showing eggs at different developmental stages. (A–C) Clutches of candidate species Ca38. (D–G) Clutches of candidate species Ca44. Shown are eggs from the male in Fig. 1F (A), the male in Fig. 1A (B), the male in Fig. 1H (C), the male in Fig. 1B (E), and the male in Fig. 1D (F). Details of species assignment and additional information are provided in Table 1.

eggs from Stage 9 to Stage 18 of development. In another instance, we observed hatching embryos (showing external gills; Stage 22) perforating the already shapeless gelatinous mass (Figs. 1F, 3A). This suggests that the same male individuals guard for the entire duration of embryogenesis, or at least until the tadpoles drop into the water. The recorded number of eggs per clutch ranged from < 20 (Fig. 3F, G) to > 110 (Fig. 3B; Tables 1, 2).

On a few occasions we encountered unattended egg clutches with no adult individuals detected in the immediate area (Fig. 4; Table 2). Based on egg and tadpole morphology, we expect that these clutches belong to *Mantidactylus* sp. Ca38 or *Mantidactylus* sp. Ca44, or, alternatively, to a species of the subgenus *Hylobatrachus*. On one of these occasions, two clutches were located that had been deposited < 1 cm apart. Both clutches comprised eggs at apparently the same developmental stage (Stage 20; Fig. 4D). All three of these observations were documented during 2007.

Based on our assumption that the egg clutches belong to a species in the subgenus *Ochthomantis*, there are three possibilities for how we came upon unguarded clutches. The guarding male may (1) have been temporarily

absent due to a feeding excursion or prior disturbance; (2) be permanently absent after having been killed in a predatory encounter (e.g. Rosa et al., 2016); or (3) have abandoned the clutch, possibly because the embryos were about to hatch. Notably, all unattended egg clutches were at a late stage of development ($\geq$ Stage 20), suggesting there is a trade-off between the time and energy allocated to guarding eggs and the chance to re-mate.

Studies of the advantages and constraints of parental care in Malagasy frogs are limited (but see Fischer et al., 2019) and there is great scope for future work in this area. One of the most likely hypotheses is that this behaviour evolved as an anti-predator mechanism. Anuran egg clutches are consumed by a wide range of vertebrate and invertebrate predators (e.g., Drewes and Altig, 1996; Burbano-Yandi et al., 2018), and in Madagascar these include: geckos (*Phelsuma lineata*: Lehtinen, 2003), snakes (*Compsophis*: Glaw and Vences, 2007; Hutter et al., 2018), ants (Lehtinen, 2003), and wasps (*Ropalidia*: Safarek et al., 2010).

Our observations provide additional information on the reproductive strategies of Malagasy frogs and reinforces the idea of egg attendance as a common behaviour in frogs of the subfamily Mantellinae

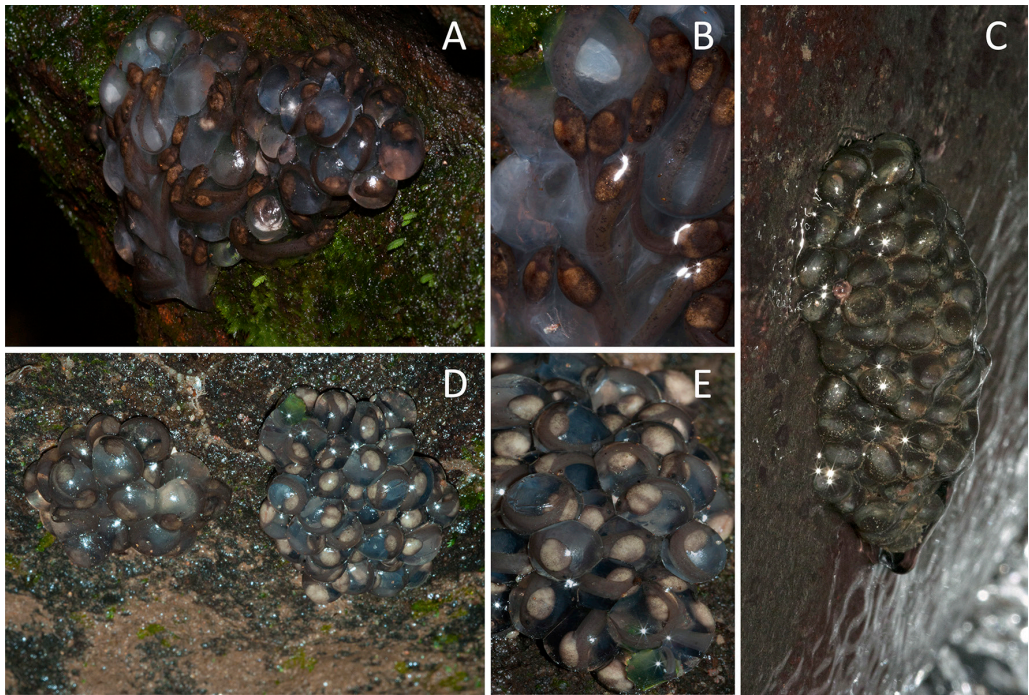


Figure 4. Unattended egg clutches likely from stream-dwelling frogs of the *Mantidactylus* (*Ochthomantis*) *femoralis* species group found in Betampona Strict Nature Reserve, Madagascar. (A) and (B) show hatching embryos. (C) is a large clutch of eggs on a rock face above the water, and (D) and (E) are two clutches on a rock face. Details of species assignment and additional information are provided in Table 1.

(Lehtinen, 2003; Vences and de la Riva, 2005; Glaw and Vences, 2007; Wolf, 2013; Glaw et al. 2019), and the subgenus *Ochthomantis* in particular, for which this behaviour was until recently poorly documented. Further investigation is needed to assess the direct benefits of this form of parental care on egg survival in these species. Increased understanding could be gained, for example, through parent removal experiments (selecting abundant and non-threatened species) or by following clutches (e.g., by direct observation or camera traps) to document potential predators and identify the nature of the advantage in the natural environment. Our observations were made during a relatively short period (max. 5 days), and we have no information on the extent of this behaviour over the entire developmental period. Following adults during reproduction would allow better characterisation of such behaviour, assessment of the extent of intraspecific variability, and could provide insight into the trade-offs between egg guarding and other costs for the males. Finally, future studies may also assess the potential variability of such behaviour in response to changing conditions.

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