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The kiwi of all skinks: an unusual egg size in a species of *Madascincus* (Squamata: Scincidae) from eastern Madagascar

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In the animal world, egg, hatchling, and neonate sizes are positively correlated with adult body size, although small species usually produce a smaller number of offspring per clutch in comparison to their larger relatives (Meiri et al., 2015). Yet, natural selection has led some species to exhibit extreme traits in this regard. Kiwis (*Apteryx* spp.) are the smallest of the ratite birds, but their eggs are among the largest in proportion to body size among all birds. The ratio between egg and adult body mass is one order of magnitude larger than in other ratites, and they generally lay only one egg (maximum two) weighing about one quarter of the female body mass (Calder, 1979; Migeon, 2014). On the other hand, *Tenrec ecaudatus* (Schreber, 1778), a Malagasy mammal of the endemic family Tenrecidae, gives birth to 16.6 small neonates per litter on average (Racey and Stephenson, 1996) with a maximum litter-size of 32 neonates (Bluntschli, 1938; Louwman, 1973), the greatest number among mammals.

The negative offspring-size allometry (with smaller species producing relatively larger offspring and larger species producing smaller offspring) is quite widespread in squamates, and species showing invariant clutch sizes tend to have unusually steep offspring size allometries (Meiri et al., 2015). Squamates have evolved a variety of reproductive strategies, and a lot of attention has been given to the study of their reproductive investment (e.g., Vitt, 1992; Calsbeek and Sinervo, 2008). Species fitness is largely dependent on both offspring size and number (Schwarzkopf, 1993). Egg and offspring size are generally constrained by a trade-off with their number (Ji et al., 2009), with shifts depending on female (Schwarzkopf, 1992) or environmental conditions (Jin and Liu, 2007), or resource availability (Ferguson et al., 1990; Laurie, 1990; Ji and Wang, 2005; Dubos, 2017).

Because of their almost ubiquitous distribution and the high diversity of habitats they occupy, skinks have developed a plethora of reproduction strategies: oviparity (Ma, 2018; Vergilov and Natchey, 2018), viviparity (including three types of chorioallantoic placenta and a real placenta similar to that of mammals; Weekes, 1935; Stewart and Thompson, 1996; Cornelis et al., 2017), and bimodal reproduction where either can be used depending on the local conditions (Brown Wessels, 1989; Smith and Shine, 1997). Their reproduction is also characterised by a variety of reproductive cycle patterns, from annual to triennial clutching depending on the species (Edwards et al., 2002; Holmes and Cree, 2006), and with some species even having developed different forms of parental care (Huang, 2007, 2008; Pike et al., 2016). Skink clutch size generally varies from 2–17 eggs/neonates (Telford, 1959; Cree, 1994; Thompson, 1994; Du, 2004; Somma and Fawcett, 2011; Ma, 2018), although single-egg

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clutches have been observed in a few instances (Greer and Parker, 1968, 1974; Greer, 1976; Mys and Greer, 1987).

In November 2013 we had the opportunity to observe two females of a miniaturised species of endemic Malagasy skink (genus *Madascincus* Brygoo, 1981), referred to hereafter as *Madascincus* sp. (Fig. 1A), which each carried a single, unusually large egg. These observations were made in Betampona Strict Natural Reserve (ca. 17.8898°S, 49.2261°E), a small forest fragment on the eastern coast of Madagascar. This patch of lowland humid forest sustains a remarkably diverse amphibian community (Rosa et al., 2012; Dubos et al., 2019; Porcel, 2020) and it is known to host a rich squamate community, with 38 species currently listed (Goodman et al., 2018). This candidate species of skink is relatively abundant in Betampona, and molecular data showed that it is closely related, although different, to another candidate species, *Madascincus* sp. "baeus" from Andasibe (Glaw and Vences, 2007; Miralles et al., 2016; A. Crottini, unpublished data). One female (ACZCV 0267) measuring 31.3 mm snout–vent length (SVL) was found carrying one large egg about 8 mm long and 3 mm wide, corresponding to one quarter of her SVL (Fig. 1B), while the second female (ACZCV 0104) was 27.8 mm in SVL and carried a single egg about 7 mm long and 3 mm wide.

Single-egg clutches are generally the consequence of the loss of an oviduct (often the left one; Greer, 1976), and this loss seems to have occurred at least nine times in skink evolution (Greer, 1976; Greer and Mys, 1987). In Madagascar, the loss of the right oviduct was reported for *M. nanus* (Andreone and Greer, 2002) and we assume that this might also be the case for *Madascincus* sp. Despite of our attempted at a minimally invasive examination of the internal anatomy of ACZCV 0104, its small size, the extremely thin, fragile and translucent walls of its genital tract, and the large size of its unique egg compressing and hiding most internal organs prevented us from confirming this hypothesis. Despite the report of single-egg in *M. nanus* (Andreone and Greer, 2002) there is no report of such great egg size relative to female size for that species, nor any other species of Malagasy skink. For comparison, an

Figure 1. (A) Dorsolateral view of *Madascincus* sp. from Betampona Strict Nature Reserve. (B) Ventral view of the gravid female of *Madascincus* sp. (ACZCV 0267), showing the large single egg with a length about one quarter of her SVL. Photos by Franco Andreone (A) and Angelica Crottini (B).

individual of *Parvoscincus sisoni* Ferner et al., 1997 – a small skink species (SVL < 34 mm) from the Philippines that also lost an oviduct and adopted a single-egg clutch strategy – was reported to bear an egg measuring 4.4 mm in length, but this egg was not shelled, suggesting a small underestimation (Ferner et al., 1997).

We interpret the loss of an oviduct as a possible consequence of the extreme miniaturisation that some skink species underwent, necessitating some rearrangement of body cavity space to provide enough room for the stomach (Greer, 1976). In addition, a decrease in clutch size allows a higher resource allocation per egg, resulting in larger eggs with enhanced individual fitness (Ji et al., 2009) because larger juveniles will have a better chance of survival (Ferguson and Fox, 1984; Brown and Shine, 2004). The reduction to one extremely large egg can be linked to the highly competitive environment and predation pressure typical of tropical areas (e.g., Tinckle et al., 1970; Andrews and Rand, 1974), where shortened life span would lead to a smaller clutch in favour of a shorter yolking time. In support of this hypothesis, it is worth mentioning that tropical species generally mature earlier compared to temperate species (Tinkle et al., 1970).

Little is known about the reproductive phenology of this species. The two females of *Madascincus* sp. observed in Betampona were collected in late November, and the two gravid females of *M. nanus* observed by Andreone and Greer (2002) were found in early December. These sampling events correspond to the early- to mid-wet season, when the majority of Malagasy squamates reproduces, and it is also the period that typically coincides with higher availability of trophic resources (Glaw and Vences, 1996). Further investigation on the breeding phenology of this species and other similarly miniaturised skinks in Madagascar is needed to assess if this species consistently lays only one egg throughout the year. The study of the number of clutches and brood per year and the age and size at the first reproduction may also help to better understand the life cycle of the species, detect potential responses to environmental change, and assess its conservation status.

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