



Evidence of seasonal reproduction, laying site fidelity, and oviposition synchronicity in the critically endangered endemic Manapany Day Gecko (*Phelsuma inexpectata*) from Reunion Island (western Indian Ocean)

ARTHUR CHOEUR^{1,2}, JOHANNA CLÉMENCET³, MATTHIEU LE CORRE¹ & MICKAËL SANCHEZ^{2,3}

¹) UMR ENTROPIE, 15 Avenue René Cassin, 97400, Saint-Denis, La Réunion, France

²) Nature Océan Indien, 46 rue des Mascariens, 97429 Petite-Île, La Réunion, France

³) UMR PVBMT, 15 Avenue René Cassin, 97400, Saint-Denis, La Réunion, France

Corresponding author: ARTHUR CHOEUR, e-mail: Arthur.choeur@univ-reunion.fr

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Abstract. The reproductive phenology of tropical geckos varies considerably between species. We investigated the reproductive timing of *Phelsuma inexpectata*, a critically endangered tropical squamate endemic to Reunion Island (western Indian Ocean). From February 2018 to August 2020 (30 months), we carried out monthly monitoring of laying sites. *Phelsuma inexpectata* exhibited a seasonal reproductive pattern, with breeding activity from the end of the austral winter to the end of the austral summer. We observed intra- and interannual synchronicity of oviposition in September. The seasonal reproductive pattern appears to be synchronized with optimal environmental conditions (temperatures, food resources) for the survival of eggs and hatchlings. Females deposited their eggs in communal laying sites (up to 9 eggs) and exhibited interannual laying site fidelity (50% of the laying sites were reused in the second breeding season). Minimum and maximum incubation periods (\pm SD) were 69 ± 24 days and 115 ± 25 days, respectively. Our study provides the first description of the Manapany Day Gecko reproduction in the wild and highlights for the first time the very high synchronicity of oviposition in the genus *Phelsuma*. These results will be very useful to improve the conservation of this species, in particular with regard to the timing of predator control, designing monitoring protocols for breeding and survival parameters, and implementing a captive rearing program for hatchlings.

Key words. Squamata, Gekkonidae, *Phelsuma inexpectata*, breeding biology, incubation period, reproductive phenology.

Introduction

Reproductive phenology (i.e., time of mating, egg production, oviposition, egg incubation and hatching) of tropical geckos varies considerably between species (VITT 1995, VITT & CALDWELL 2013). Some species reproduce seasonally (VINSON 1975, COLLI et al. 1997, MIRANDA & ANDRADE 2003), while others breed throughout the year (GARDNER 1984, VITT 1986, OTA 1994, ANJOS & ROCHA 2008). Timing of reproduction in lizards is related to biotic and abiotic determinants maximizing individual fitness (VITT 1990, COLLI 1991, WATLING et al. 2005, VITT & CALDWELL 2013). The observed phenological patterns may result from local environmental conditions but may also reflect the evolutionary histories of species (VITT & CALDWELL 2013). In tropical geckos, temperature, food resource and rainfall patterns are the main factors that explain reproductive

phenologies. Reproduction typically takes place virtually year-round in unseasonal environments and is concentrated during the warmer and rainy months in seasonal regions (BAUER 2013).

The genus *Phelsuma* belongs to the family Gekkonidae, with 52 species being distributed on most islands of the western Indian Ocean (ROCHA et al. 2010). Oviparous and mainly arboreal, these geckos use cavities in tree trunks or rocks, leaf axils of palm tree species, or man-made structures as oviposition sites (VINSON 1975, AUGROS et al. 2017, SANCHEZ & PROBST 2017). As “egg-gluer species”, the *Phelsuma* of the Mascarene Archipelago (Réunion, Mauritius, Rodrigues) firmly attach their eggs to a substrate in laying sites that are shared by several females (VINSON & VINSON 1969, VINSON 1975, GARDNER 1984, HENKEL & SCHMIDT 2000, GLAW & VENCES 2007, SANCHEZ & PROBST 2017, ROESCH et al. 2021). Their eggs have hard and cal-

cified shells (GARDNER 1984). Despite much information being available from captive breeding (reproductive behaviours, egg gestation, maximum reproductive effort per year, etc.) (e.g., RUNDQUIST 1994, HENKEL & SCHMIDT 1995, 2000, GLAW & VENCES 2007, BERGHOF 2014), the reproductive biology in their natural habitats is poorly known for most species. For their native range on Round Island (Mauritius), VINSON (1975) suggested seasonal summer breeding for the two native species *P. guentheri* and *P. ornata*, whereas in the Seychelles, two other native species *P. sundbergi* and *P. astriata*, have an aseasonal breeding cycle (GARDNER 1984). In Hawaii, the two introduced Malagasy species, *P. grandis* and *P. laticauda*, also do not have a definite seasonal reproductive cycle (GOLDBERG & KRAUS 2009, GOLDBERG 2011). Likewise, DAS (2002) and CHANDRAMOULI (2020) reported that *P. andamanensis*, an endemic species of the Andaman Islands (northeastern Indian Ocean), breeds throughout the year.

Here, we analysed the reproductive biology of the Manapany Day Gecko, *Phelsuma inexpectata*, a species endemic to the southern coast of Reunion Island (western Indian Ocean) and classified as Critically Endangered in the IUCN Red List (AUSTIN et al. 2004, SANCHEZ 2021). This species is highly threatened by habitat loss and alien predators and competitors (SANCHEZ & PROBST 2011). Knowing the reproductive biology of the species in its natural habitat is a prerequisite to designing adapted monitoring protocols and to implementing conservation measures such as captive rearing or targeted alien species control. In this context, we investigated the breeding phenology, incubation period, and oviposition site fidelity in this endemic and poorly known species.

Materials and methods

Species and study site

Phelsuma inexpectata is arboreal, insectivorous, nectarivorous and frugivorous. It is a diurnal gecko that can reach a total length of 13 cm (SANCHEZ et al. 2009). In their natural habitats, these geckos are strongly associated with patches of native coastal vegetation (SANCHEZ & PROBST 2011). Females lay one or two eggs per clutch inside cavities (tree trunks or rocks) or in the leaf axils of palm trees (SANCHEZ et al. 2009) (Supplementary Fig. S1). After hatching, the calcareous shells of their eggs remain stuck to the support for many years, facilitating the detection of old laying sites (Supplementary Fig. S2). Apart from *P. inexpectata*, there were no other *Phelsuma* or egg-glueing species in our study area.

Our study was focused on a population of geckos located on the southern coast of Reunion Island (21°06' S, 55°36' E). This population is confined to a small patch (0.24 ha) of native coastal vegetation (thickets of *Pandanus utilis*, *Scaevola taccada* and *Psiadia retusa*) surrounded by alien vegetation (thickets of *Schinus terebinthifolius* and *Flacourtia indica*, among others). It has been monitored since 2015, and the abundances of adults were estimated at

35 (29–41 CI 95%) males and 19 (16–23) females in October 2018, and 26 (19–33) males and 10 (7–14) females in October 2019 (A. CHOEUR unpubl. data).

The climate of Reunion Island is seasonal and characterized by a hot and humid austral summer from November to April (mean monthly temperature: 26°C, mean monthly precipitation: 146 mm) and a dry austral winter with cooler temperatures and less rain from May to October (22°C, 96 mm) (Météo France 2021a). The cliffs where the geckos live are orientated to the south, so that the area receives more sun in austral summers (approximately 8 h) compared to austral winters (approximately 5 h) (A. CHOEUR, unpubl. data). During the summer, the island is regularly impacted by tropical storms and cyclones (28 tropical cyclones from 2000 to 2021) (Météo France 2021b).

Fieldwork

From February 2018 to August 2020, one observer searched for oviposition sites on three consecutive days every month. Each visit consisted of one hour of search/day. We defined a laying site as a site with eggs or remnants of shells that had once been glued to a support structure. We defined a laying area as a cluster of oviposition sites at distances of less than 4 m from each other (e.g., a rocky outcrop). We inspected the local vegetation from the ground to the top of the canopy and as many natural cavities as possible using a flashlight. Each laying area and site was identified in the field by a unique number (area) and letter (site). Some natural cavities without traces of eggs but near a laying site were also monitored monthly. The content of each laying site was photographed and each egg was identified by a unique number with a soft pencil whenever possible or on the photos with photo-editing software (Microsoft Paint, version 21H1). Eggs were classified into two categories: (i) eggs recently laid (discovered the first time in an already known cavity, in that case oviposition must have occurred between the previous monthly monitoring visit and the date of discovery of the egg), and (ii) eggs without information on the laying date (discovered the first time in a new cavity; the date of deposition was therefore unknown). We assumed that an egg had hatched if it had the crack in the shell characteristic of hatching (Supplementary Fig. S3). We assumed that an egg had not hatched if it had completely disappeared (supposedly destroyed by bad weather or predators).

Analyses

Our study covered two breeding seasons: austral summers 2018/2019 (BS1) and 2019/2020 (BS2). In order to describe reproductive phenology, we characterized three stages: (i) the oviposition period, beginning with the discovery of the first recently laid egg and ending with the discovery of the last recently laid egg, and (ii) the hatching period, beginning with the discovery of the first hatched egg and ending with the discovery of the last hatched egg. Based on the

mum two eggs), these observations suggest that several females used the same (communal) laying site. Within a breeding season, the number of eggs laid per laying site was 3.53 ± 2.44 (range 1 to 9) (Fig. 2 and Table 1). In total, 40% of the laying sites hosted more than two eggs at the same time (Table 1). During one breeding season, one laying site had on average $10.52 \pm 7.33\%$ of the total number of eggs laid in the study area (range 2.94 to 27.27%).

The majority of the eggs (67.2%) were detected in laying sites that had already been used before (i.e., with traces of previously glued-on shells), whereas 16.4% of the eggs were detected in otherwise empty cavities (without such traces). Concerning the remaining 16.4%, it was not possible to determine whether the respective sites had been used before or not, given that these eggs were discovered in cavities that had never been inspected before. Among the laying sites used during BS1 ($N = 8$), 50% were reused during BS2. Hatching success during BS1 was not significantly different between reused (77% of success) and presumably non-reused laying sites (100% of success) (Chi-squared test; $\chi^2 = 0.30$, $P = 0.59$). The number of eggs laid during BS1 was significantly higher in laying sites reused during BS2 (Wilcoxon test; $W = 16.00$, $P = 0.027$).

Based on the 41 eggs monitored from deposition until hatching, estimates of the incubation periods averaged 69 ± 24 days at a minimum (min.–max.: 31–130 days) to 115 ± 25 days at a maximum (min.–max.: 65–181 days) (Table 1).

Discussion

Our study provides the first description of breeding biology of *Phelsuma inexpectata* in its natural environment. This

species has a clear seasonal breeding regime from the end of the austral winter to the end of the austral summer. As has been recorded from other tropical squamates (FITCH 1982, BROWN & SHINE 2006, RIGHI et al. 2012), this pattern appears to be synchronized with optimal abiotic and biotic conditions. Egg production and incubation begin in August and September, respectively, when temperatures and insolation increase (Météo France 2021a), which probably offers optimal conditions for vitellogenesis, embryogenesis, and the satisfaction of the energetic needs of the laying females (ZUG 1993). Like *Phelsuma borbonica* on Reunion Island, incubation occurs mainly before the cyclone season (SANCHEZ & GÉRARD 2017) and this may be an adaptive strategy to avoid the destruction of eggs (flooding of cavities, ambient moisture due to heavy rains, and strong winds that may destroy cavities in trees) (COLE et al. 2014, SANCHEZ & GÉRARD 2017). Hatching occurs during the wet season (November–April), when water and food resources (fruits of *P. utilis* and arthropods) are abundant for juveniles (LEVINGS & WINDSOR 1982, NICOLL 1982, A. CHOEUR, unpubl. data). Their abundance and ease of access may be beneficial to inexperienced juveniles, but also to adult females that need to recover from the strains of egg production.

We observed intra- and interannual synchronicity of oviposition in September. For BS1 and BS2, considering adult female abundance (19 in September 2018 and 10 in September 2019), clutch size (between one and two eggs), and the number of eggs laid over two days (seven eggs in September 2018 and four in September 2019), we can estimate that between 21–37% and 20–40% of the females laid their eggs in less than 48 hours in September, respectively. This very high degree of synchronicity was confirmed dur-

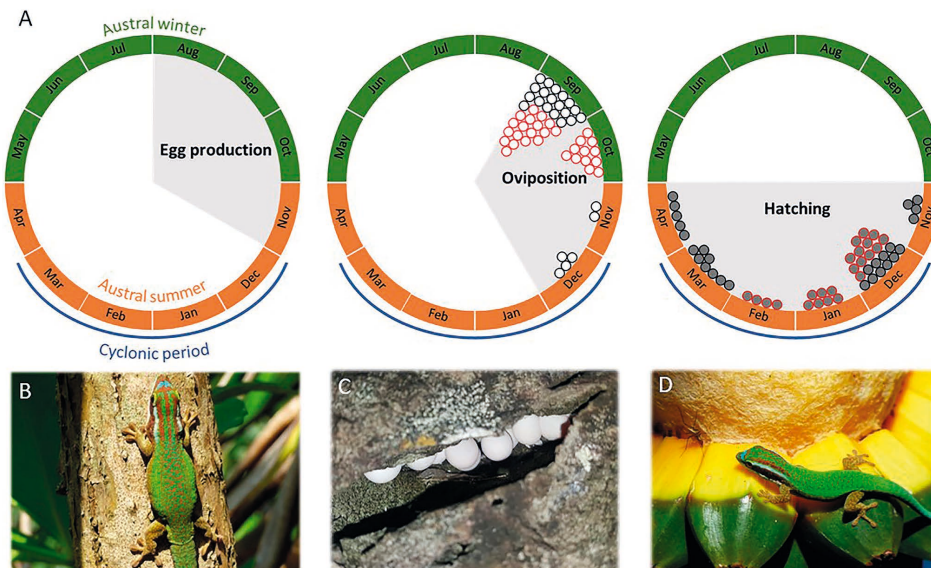


Figure 1. Reproductive phenology of the Manapany Day Gecko (*Phelsuma inexpectata*) in a wild population in the south of Reunion Island monitored from February 2018 to August 2020. (A) Each circle corresponds to a detected egg (black outline: breeding season 2018/2019; red outline: breeding season 2019/2020; white inside: eggs laid; dark grey inside: eggs hatched). Austral summer is shown in orange and austral winter in green. (B) gravid female, (C) laying site 1A with recently laid eggs, and (D) juvenile on a fruit of *Pandanus utilis*.

ing the following breeding season (2020/2021, A. CHOEUR, unpubl. data). Monthly oviposition synchronicity has already been documented for other reptile species (BOCK & RAND 1989, BURGER & ZAPPALORTI 1992, WIEWANDT 1992). However, to our knowledge, it is the first time that oviposition synchronicity has been recorded in the genus *Phelsuma* and at such a fine (daily) scale. This phenomenon could be driven by environmental cues (e.g., photoperiod, temperature) (OSADNIK 1984) as to match reproduction with optimal environmental conditions (BOCK & RAND 1989). Synchronicity behaviour may also favour the survival of gravid females, eggs and hatchlings through a dilution effect (TURNER & PITCHER 1986).

Our study provides the first estimate for the incubation period in *P. inexpectata* in the wild (69–115 days) and it is similar to other *Phelsuma* species (GARDNER 1984, GLAW & VENCES 2007, ROESCH et al. 2021). Incubation periods seem to be different between laying sites (range 65–181 days), which may be due to temperature variations that influence embryo development (ZUG 1993, KÖHLER 2005, ROESCH et al. 2021). However, the precision of the incubation period estimates is limited due to our monitoring at monthly intervals, and could be refined by selecting shorter intervals.

Female *P. inexpectata* used communal laying sites as has also been reported for this species in urban areas (SANCHEZ et al. 2009) and for other *Phelsuma* species (VINSON & VINSON 1969, VINSON 1975, GARDNER 1984, SANCHEZ & PROBST 2017, ROESCH et al. 2021). Rela-

tive to adult female abundance (10 females), our observations indicate that between 40 and 80% of the local females laid their eggs in the same cavity in September 2019 (BS2). These females also exhibited strong oviposition site fidelity, as has previously been reported for various Gekkota (e.g., HENKEL & SCHMIDT 1995, SOMAWEERA 2009, BAUER 2013, DAS et al. 2018), but to a lesser extent for *Phelsuma* spp. (e.g., SANCHEZ & PROBST 2009). We do not know whether it was the same females that used the same sites, but it is very likely given the low number of laying sites identified. Fidelity to and communal use of laying sites could be explained by adaptive advantages such as survival benefits to females, eggs, and/or hatchlings. These behavioural expressions may be crucial for oviparous species without parental care (DOODY et al. 2009). Communal laying sites also have the advantage of providing stable and optimal abiotic conditions (especially temperature) for embryonic development (HÅKANSSON & LOMAN 2004). On the other hand, communal laying sites could have a dilution effect on predators, which may be particularly effective when laying and hatching are synchronized (TURNER & PITCHER 1986, GRAVES & DUVALL 1995). Communal laying and site fidelity may also limit inbreeding through temperature-dependent sex determination (by most offspring from the same laying site having a greater chance of being of the same sex) (SHINE 1999). It may also be explained by the use of common conspecific cues to assess the quality of a laying site (DOODY et al. 2009). These behavioural adaptations may be advantageous in terms of energy and time expenditure (to search for a site), and in terms of survival of the eggs (GIRALDEAU et al. 2002, DOODY et al. 2009). Although gleaned from only two years of observation and therefore preliminary, our results indicate that hatching success is not necessarily greater in cavities reused in subsequent seasons. Studies over a longer period and monitoring more laying sites would be required to more comprehensively investigate this question. Several authors have also suggested that in some reptile species, females may be genetically programmed to lay their eggs in their own birth sites (BROWN & SHINE 2007, WEBB et al. 2008). Apart from adaptive hypotheses, the scarcity of suitable nesting sites may be an alternative explanation to these reproductive behaviours (DOODY et al. 2009, INEICH 2010, SANCHEZ & PROBST 2017). However, it appears unlikely that *P. inexpectata* suffers from such scarcity, because rock cavities are abundant across our study area and several laying sites were not reused from one year to the next.

In conclusion, our study shows a highly synchronous and seasonal breeding pattern, the use of communal laying sites, and high laying site fidelity for *P. inexpectata*. These results will be very useful for designing conservation measures in the field (timing of predator control for instance) and for designing monitoring protocols for breeding and survival parameters (hatching success, reproductive effort, hatchling and female survival). They will be also very useful for implementing a captive rearing program for juveniles.

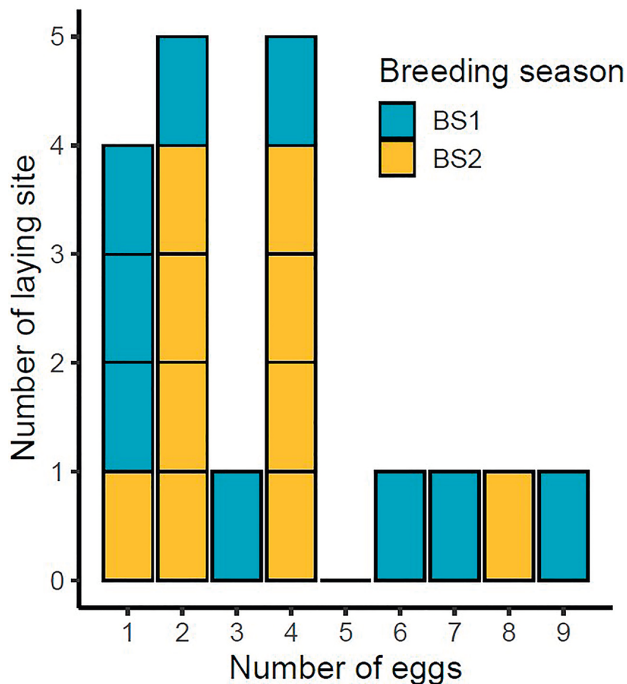


Figure 2. Laying site occupancy. Distribution of eggs in laying sites recorded for both BS1 (breeding season 2018/2019) and BS2 (breeding season 2019/2020). Each box represents one laying site during one year.

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Supplementary data

The following data are available online:

Supplementary Figure S1. Laying sites of *Phelsuma inexpectata* monitored on the southern coastal cliffs of Reunion Island (western Indian Ocean).

Supplementary Figure S2. Calcareous egg shells of *Phelsuma inexpectata* glued on the support.

Supplementary Figure S3. Laying site of *Phelsuma inexpectata* with eggs recently laid and recently hatch.

Supplementary Figure S4. Laying area of *Phelsuma inexpectata* with several laying sites.