



## Phenology and growth plasticity in a short-lived chameleon under climatic variation

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**Abstract.** Understanding species' responses to climate change is crucial for the mitigation of its effects. Few studies, however, have examined how climate change impacts timing in reptile life cycles, or how it may interact with other life history traits. Here, we explore associations between climatic variation, reptile phenology, and juvenile growth. We used the chameleon species *Furcifer labordi* as a biological model given its unusual annual life history: embryonic diapause during austral winter is followed by synchronous hatching and an extremely short adult lifespan. We sampled chameleons ( $n = 674$ ) and climate data across three field seasons between 2013–2018 in Kirindy Forest (CNFEREF), western Madagascar. Evidence of temperature and precipitation shifts have already been reported for this region. We show climate-dependent variation in the timing of hatching: it always occurred after the first rains and its onset varied by up to 32 days among years (equivalent to 12–17% of the total length of non-embryonic lifespan). Moreover, delayed rainy season onset resulted in a shortening of the period between the first rains and first hatching. Significant differences in hatching time and temperature also resulted in variation in juvenile growth, specifically faster post-hatching growth in the late-hatching cohort. Therefore, climatic variation was associated with phenological and juvenile growth plasticity in the life cycle of *F. labordi*. Implications for conservation are worrying, as complete populations could be lost if a single cohort of this annual species cannot effectively respond to increasing climatic fluctuation.

**Key words.** Squamata, Chamaeleonidae, *Furcifer labordi*, growth rate, hatching period, life history, phenological shift, western Madagascar.

### Introduction

Among vertebrates, poikilothermic taxa such as reptiles are hypothesized to be particularly dependent on environmental conditions for growth and reproduction. Together with their often-limited dispersal abilities, this constraint makes reptiles particularly vulnerable to rapid environmental shifts, and they may suffer higher extinction rates than other taxa due to climatic change (SINERVO et al. 2010, HUEY et al. 2012). In various reptiles, less dramatic effects of temperature changes have been observed for hatchling phenotypes (e.g., BOOTH 2006, SINGH et al. 2020), hatchling behaviour (DAYANANDA et al. 2017, SIVITER et al. 2017), hatching success (DÍAZ-PANIAGUA et al. 2006), post-hatching survival rate (ANDREWS et al. 2000), and, in some species, offspring

sex (e.g., JANZEN & PAUKSTIS 1991, SCHWANZ et al. 2010, BALLEN et al. 2016).

In addition, range shifts due to climatic variation have been repeatedly documented in reptiles, including lizards (HOUNIET et al. 2009, CEIA-HASSE et al. 2014), snakes (LOURENÇO-DE-MORAES et al. 2019), and chelonians (IHLOW et al. 2012). However, many populations now exist in isolated habitats without access to other potentially suitable habitats, making range shifts an unlikely response to less favourable environmental conditions. It is therefore important to better understand in situ responses to climatic variability across a wide range of taxa. Such information is interesting for understanding plasticity in life history traits and crucial for identifying species threatened by climate change for ecological forecasting and conservation planning (AKÇAKAYA et al. 2006).

Among in situ responses, modification of the timing of events in a life history can occur in response to abiotic factors exhibiting variation over time (e.g., temperature, precipitation) (BELLARD et al. 2012). Such phenological shifts are well documented in many taxa (e.g., STEFANESCU et al. 2003, RATHER et al. 2018, STEPANIAN & WAINWRIGHT 2018, STAUDINGER et al. 2019). Studies focusing on reptiles' phenological responses to climate change are scarce, but few publications (e.g., MORENO-RUEDA et al. 2009, CLARKE & ZANI 2012, LJUNGSTRÖM et al. 2015), focus on the shifts of life history traits such as growth pattern caused by higher ambient temperatures.

Here, we study variation in the phenology and growth in annual cohorts of Labord's chameleon (*Furcifer labordi*) across years with significant climatic variation. This species is characterized by an extreme life history among terrestrial vertebrates as it is thought to have the shortest lifespan (4–9 months) among tetrapods as part of an unusual annual life cycle (KARSTEN et al. 2008, ECKHARDT et al. 2019). These chameleons are almost exclusively represented in the egg stage (embryonic diapause) during the austral winter followed by synchronous hatching, extremely rapid growth, and reproduction before the onset of the next dry season (KARSTEN et al. 2008). As an entire population consists of a single, synchronous age cohort, *F. labordi* provides a unique opportunity to monitor the effects of climate fluctuations on phenology and growth for entire generations of a tetrapod species. Further, due to the extremely compressed lifespan, perturbations to timing could substantially reduce the time window available for growth and reproduction, raising questions about which components of the life history are more or less plastic.

*Furcifer labordi* is restricted to dry forest patches in western and southwestern Madagascar and is classified as Vulnerable in the IUCN Red List (IUCN 2021). Two populations have been studied: a northern population in Kirindy Forest, within the protected area of Menabe Antimena (ECKHARDT et al. 2017, 2019), and a southern population in the protected area of Ranobe (KARSTEN et al. 2008). Here, we focus on the northern population from Kirindy, where the abundance of *F. labordi* is still high (RANDRIANANTOANDRO et al. 2010) and the effects of climate change have already been observed. GOODMAN et al. (2018) analysed climatic fluctuations in the protected area of Menabe Antimena over 30 years (1985–2014). An annual increase of approximately 0.5% in precipitation has been observed and the rainy season shifted on average 10 days later in more recent years. In addition, the average minimum and maximum daily temperatures increased by 1.4°C and 0.7°C, respectively.

In this study, we estimate the timing of emergence and the growth rates of hatchlings and juveniles for three generations of *F. labordi*, spanning years with significant climatic variation. First, we hypothesized that a delayed rainy season onset would be associated with a delayed hatching date. Second, we hypothesized that juvenile daily growth rate increases in late-hatching cohorts to compensate for this delay.

## Materials and methods

### Study site and species

The present study was carried out in the dry deciduous Kirindy Forest (CNFEREF) (44°28'–44°46' E, 20°03'–20°10' S, 30–60 m a.s.l.), in the Harmonious Protected Landscape of Menabe Antimena, western Madagascar. Although originally covering 12,500 ha, the integrity of Kirindy Forest is currently threatened due to habitat loss and fragmentation (GOODMAN et al. 2018). The overall rate of deforestation within the protected area was 0.67% per year with a maximum of 2.55% between 2008 and 2010 (ZINNER et al. 2014), presumably associated with the 2009 political crisis in Madagascar.

Regarding local climatic conditions, the study area lies in a transitional zone. The seasonally dry climate typical of the west coast of Madagascar dominates in the northern part of the protected area. In contrast, the sub-arid climate typical of southwest Madagascar dominates in the southern portion (GOODMAN et al. 2018). Rainfall averages 954mm per year (1981–2017), of which 96% falls between November and April. Temperature ranges from a mean daily minimum of 20.0°C to a mean daily maximum of 30.3°C. June to August is the coolest period (min, 12.4°C) and September to November the hottest (max, 33.4°C). Kirindy Forest is characterized by intra-annual variation (i.e., extreme seasonality) and unpredictable inter-annual variation in climate (KAPPELER & FICHTEL 2012), providing an opportunity to study the effects of substantial climatic changes over short time scales.

### Vegetation cover measurement: Normalized Difference Vegetation Index (NDVI)

NDVI, calculated by the reflection rate of red light (RED) and near infrared light (NIR) [ $NDVI = (NIR - RED) / (NIR + RED)$ ], is strongly correlated with aboveground net primary productivity (MYNENI et al. 1995; see also <http://daacmodis.ornl.gov>). Here, NIR and RED are the rates of near infrared light and red light that are reflected by the vegetation and recorded by the satellite sensor. The formula results from the fact that chlorophyll absorbs RED, whereas NIR is re-emitted. To compare seasons, we measured the proportion of vegetation cover in the middle of the dry season (Jul.–Aug.), the late dry season (Sep.–Oct.), and the wet season that covers the hatching time and period of juvenile growth (Nov.–Dec.) in 2013, 2015 and 2017. For analysis of NDVI, we selected a square of 3km<sup>2</sup> around the centre of our study site.

### Climate data analysis

Temperature and precipitation data were collected from 2013 to 2018 automatically each day, every 10 minutes, with a weather station (Lambrecht meteo GmbH, Göttingen, Germany) at the research camp in Kirindy Forest. We ex-

amed temperature and precipitation fluctuations during the field seasons using Kruskal-Wallis test, and visualized the variation via heatmaps.

#### Chameleon sampling

Chameleon sampling took place over three field seasons that cover the hatchling and juvenile growth phases in the *F. labordi* life cycle: 18 November 2013 to 14 February 2014; 12 October 2015 to 17 December 2015; and 11 November 2017 to 20 December 2017, 16 January 2018 to 14 February 2018. Chameleons were searched using a headlamp and a Maglite torch at night as they perch on distal ends of vegetation and display a conspicuous pale or vivid colour when lit (JENKINS et al. 1999). Two different transects were surveyed alternately between 7 pm and midnight. Individuals were captured by hand or removed from higher branches using an extendable pole or stick to which they were encouraged to grip. We scheduled a recurring order of 10 nights of sampling followed by a break of four nights within each field season.

For each individual, capture location was marked with an individually numbered coloured flag and coordinates were collected using a GPS. Age class (hatchling, juvenile,

or adult) was recorded using the following features: (i) individuals with a distinct small opening in the abdominal wall were classified as hatchlings, (ii) individuals lacking the abdominal opening but not yet sexually mature were classified as juveniles, and (iii) sexually mature adults were recognized by the appearance of a colourful mating pattern in females and the presence of a distinct hemipenis bag (bulge at the base of the tail) and a hard, ossified rostral appendage in males. The rostral appendage is already present in the juvenile stage but is not fully developed until the adult stage (Fig. 1). The abdominal opening in hatchlings is caused by a former connection with the yolk sack and is visible for about one week after hatching. Sex was determined in juveniles based on the presence/absence of the rostral appendage, and in adults based on the presence/absence of the hemipenis bag and rostral appendage. Snout-vent length (SVL) was measured with a calliper to the nearest 0.1 mm. All individuals were released at the exact point of capture following manipulation.

#### Hatching date and climate

We estimated the date of hatching of *F. labordi* for each year from the first date hatchlings were observed during

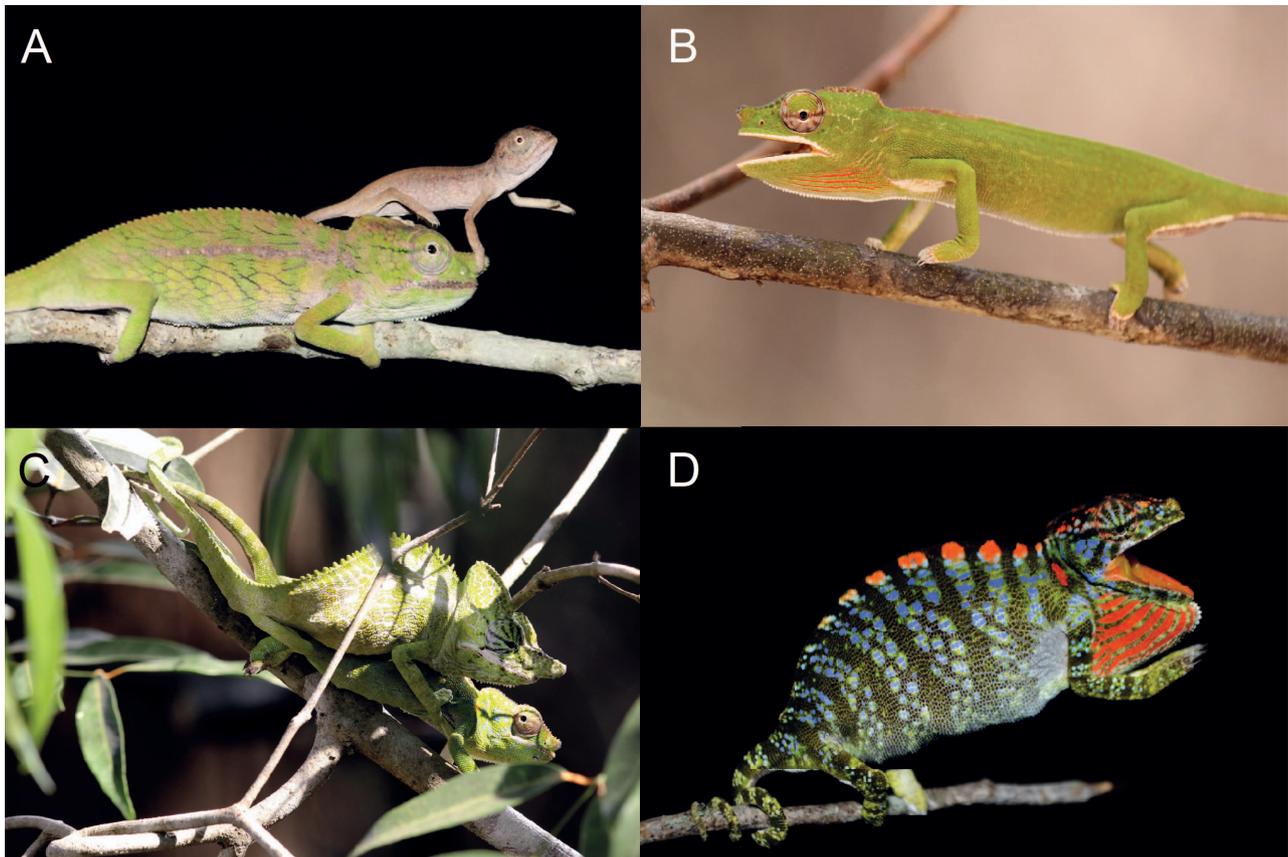


Figure 1. Individuals of *Furcifer labordi* in life: (A) hatchling climbing over a juvenile male that is several weeks older; (B) juvenile female short before change to adult coloration; (C) adult male and female during mating; (D) adult female displaying stress coloration.

the nocturnal surveys and from estimates of growth rates for hatchlings and juveniles (described below). To account for the possibility that unobserved hatching occurred prior to the first observation of hatchlings, we use growth models to determine the probable number of days since hatching for juveniles of a given size. To examine the relationship between timing of hatching and rainfall in this population, we compared the estimated date of first hatching with the start date of the rainy season (as defined by the first date with measurable rainfall) for 2013, 2015, and 2017.

### Analysis of growth patterns

Due to fluctuations in body mass with variation in stomach contents, fat storage, and reproductive status in lizards, length is more appropriate to measure growth than weight (ANDREWS 1982, HAENEL & JOHN-ALDER 2002). Therefore, our analysis of growth focuses on SVL. For each field season, we defined the date of observation of the first hatchling as day zero. After checking the assumptions of parametric tests, growth was estimated by fitting  $\log(\text{SVL})$  (response variable) on days since day zero (predictor variable) for each year's cohort of hatchling and juvenile chameleons. Data analyses and data visualization were carried out using the software R 4.0.5 (R Core-Team 2021) and the significance level was set at  $P < 0.05$ .

## Results

### Vegetation cover measurement:

#### Normalized Difference Vegetation Index (NDVI)

Comparisons across years for a given season revealed that 2013 and 2017 were consistently characterized by less vegetation cover than 2015, with 2013 showing the lowest values in general (Table 1). The higher values of vegetation cover in 2015 probably result from heavier rainfall in the previous rainy season. Reviewing average vegetation cover from 2008 until 2017, we found that the vegetation cover calculated for 2013 and 2017 was around average in the dry season and at the end of the dry season, whereas 2015 was above average. Concerning the vegetation cover during the beginning of the rainy season (main time of hatching), 2013 and 2017 were below average, whereas 2015 was above average.

### Climatic variation

The average daily temperature (Kruskal-Wallis:  $\chi^2 = 282.04$ ,  $df = 4$ ,  $P < 0.001$ ) and precipitation (Kruskal-Wallis test:  $\chi^2 = 117.91$ ,  $df = 4$ ,  $P < 0.001$ ) differed significantly during the study period (Fig. 2). The lowest monthly mean minimum temperature ( $23.7^\circ\text{C}$ ) was recorded in December 2015, whereas the highest monthly mean maximum temperature ( $30.28^\circ\text{C}$ ) was recorded in January 2018.

Table 1. Averaged NDVI for the onset of the dry season (Jul.–Aug.), end of the dry season (Sep.–Oct.), and the rainy season covering hatching and juvenile growth period (Nov.–Dec.).

Year	Jul./Aug.	Sep./Oct.	Nov./Dec.
2013	0.6153±0.04	0.5888±0.03	0.5945±0.05
2015	0.7197±0.03	0.641±0.01	0.6864±0.09
2017	0.6633±0.03	0.5796±0.02	0.6213±0.09
2008–2017	0.6309±0.05	0.5677±0.05	0.6415±0.125

### Chameleon sampling

During the field surveys conducted for this study, we sampled 674 individuals of *Furcifer labordi*. Of these, 73 (11%) were hatchlings, 421 (62%) were juveniles, and 181 (27%) were adults (Table 2). Hatchlings were observed from mid-October to December, except one hatchling found in January 2018, most likely an outlier. Juveniles were mainly found from November to January. Adults were observed from January onwards, apart from one adult female found in October 2015, most likely a survivor from the previous active season (Fig. 2). Indeed, although the adults of *F. labordi* generally die at the onset of the relatively cold dry season, a small number of females might survive until a second breeding season when the rainy season is unusually long (ECKHARDT et al. 2017). In terms of sex ratio, we found a male-bias in adults for the 2013–2014 cohort (Chi-squared:  $\chi^2 = 5.26$ ,  $df = 1$ ,  $P < 0.05$ ). Males are significantly larger than females in both juveniles (Wilcoxon test:  $W = 14076$ ,  $P < 0.05$ ) and adults ( $W = 69$ ,  $P < 0.05$ ) (Table 2).

### Hatching time variation

The first hatchlings were observed on 20 November in 2013, 17 October in 2015, and 18 November in 2017 (Fig. 2). However, in 2013, juveniles were observed on the same date as the first hatchlings. As an almost exclusively annual species (with the rare exceptions noted above), populations of *F. labordi* consist of single, yearly cohorts such that generations do not overlap. This means the juveniles seen on 20 November 2013 likely indicate the existence of earlier hatching that occurred prior to the start of sampling in 2013 (on 18 November). Using the estimated average daily growth derived from growth models (Fig. 3) and the SVLs of the first juveniles observed, we estimate that hatching in 2013 likely occurred around 27 October.

In 2015 and 2017, the first observations of hatchlings were preceded by more than 5 days of careful searching that resulted in no observed hatchlings. The first juveniles were observed 18 to 31 days after the observation date of the first hatchlings. From growth models, the estimated date of hatching is 13 October to 22 October, and 1 November to 18 November, respectively, for 2015 and 2017.

Table 2: Number and mean snout–vent length (SVL) in mm of detected *Furcifer labordi* individuals per age class and sex in 2013, 2015, and 2017. Sex not determined for 8 juveniles (NA).

Year	n	Hatchlings	Juveniles			Adults	
			F	M	NA	F	M
2013–2014	362	14	119	144	0	30	55
2015	142	46	44	43	8	1	0
2017–2018	170	13	35	28	0	44	50
SVL (mean±SD)	674	26.6±2.3	44.6±12.7	51.9±13.6	NA	73.5±3.3	94.0±9.3

Hatching time and climate

In order to investigate the relationship between hatching time and climate, the date of hatching was mapped onto the onset of the rainy season (Fig. 2). Hatching always occurred after the first rains. The rainy season started on 2 October in 2013 (precipitation = 25.7mm), and the estimated date of hatching (27 October 2013) occurred 25 days after first rains. The interval increased in 2015, with 40 days after the first rains, which started on 8 September (precipitation = 6.9 mm). However, in 2017, hatchlings were observed just one day after the first rain on 17 November (precipitation = 2.9 mm). As with the hatching time, the start of the rainy season varied across years. The

later the start of the rainy season, the shorter is the period between first rains and first hatching. Additionally, the amount of first precipitation decreased over the studied years.

Growth rate

Hatchling and juvenile growth followed a linear regression model ( $R^2 = 0.66$ ,  $P < 0.001$ ), and the regression equations for each cohort are shown in Figure 3. Individual growth rate was significantly higher for the cohorts from 2013–2014 and 2017–2018, compared to the cohort from 2015 (ANOVA:  $F_{2,487} = 7.55$ ,  $P < 0.001$ ).

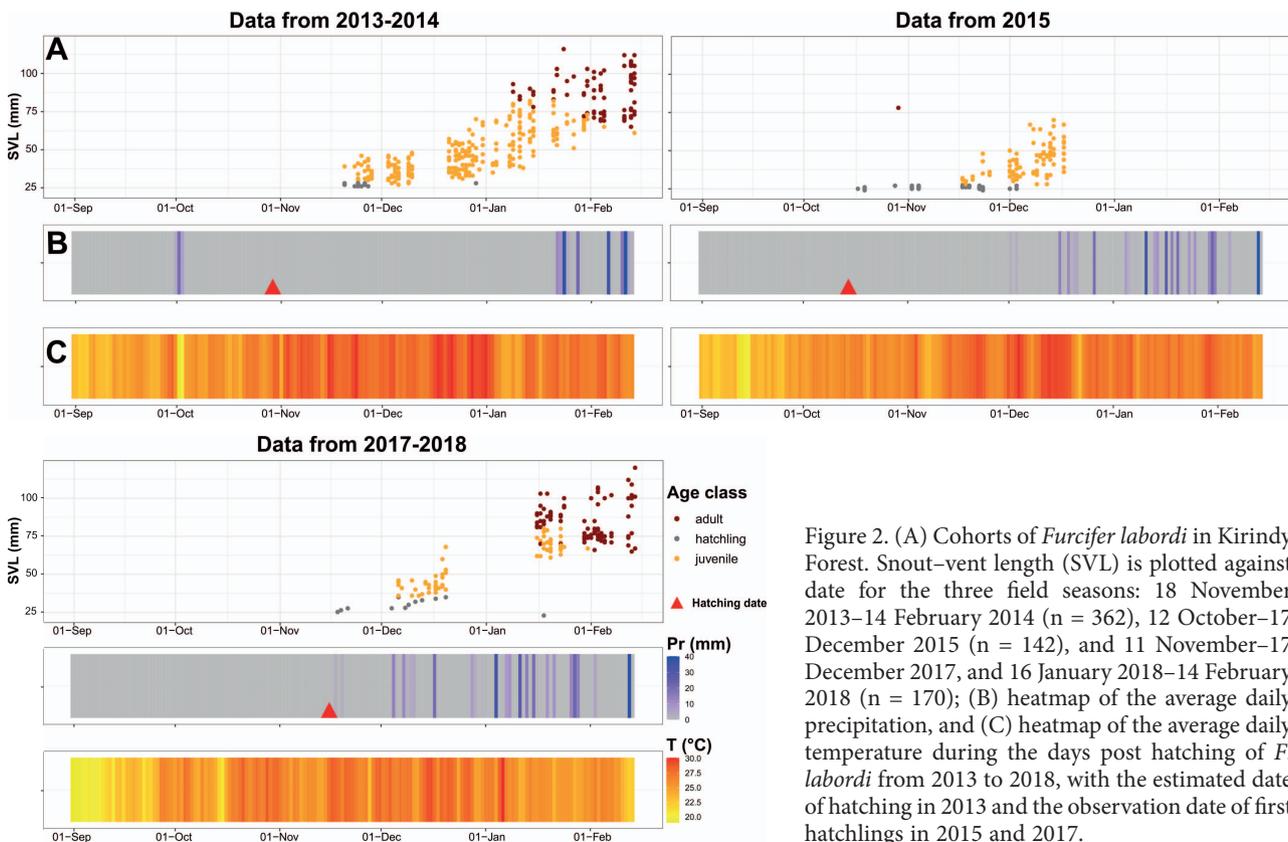


Figure 2. (A) Cohorts of *Furcifer labordi* in Kirindy Forest. Snout–vent length (SVL) is plotted against date for the three field seasons: 18 November 2013–14 February 2014 ( $n = 362$ ), 12 October–17 December 2015 ( $n = 142$ ), and 11 November–17 December 2017, and 16 January 2018–14 February 2018 ( $n = 170$ ); (B) heatmap of the average daily precipitation, and (C) heatmap of the average daily temperature during the days post hatching of *F. labordi* from 2013 to 2018, with the estimated date of hatching in 2013 and the observation date of first hatchlings in 2015 and 2017.

## Discussion

The results of our study showed climate-dependent variation in the timing of hatching of *F. labordi*, in which a delayed onset of the rainy season resulted in a shortening of the period between first rains and first hatchings. Additionally, significant differences in hatching time and ambient temperature caused differences in juvenile growth, in which faster post-hatching growth occurred in the late-hatching cohort.

Previous studies of the southern population of *F. labordi* in Ranobe showed a synchronous hatching at the onset of the rainy season (KARSTEN et al. 2008). Our results from the northern population in Kirindy showed that hatching occurred after the first rains and hatchlings can generally be detected for over a month. A single hatchling was also found at the end of December in 2013 and around mid-January in 2018. We therefore observed an extended hatching period in Kirindy. As the hot rainy season is longer in Kirindy compared to Ranobe (GOODMAN et al. 2018), food resources are more abundant and available for a longer period.

We also observed variation in the hatching time of *F. labordi* that follows a pattern similar to the rainfall schedule. The hot rainy season started earliest in 2015, followed by 2013 and 2017, and the earliest observed hatching of *F. labordi* followed the same order. Based on growth models, estimated hatching time only differed by 10 days between 2013 and 2015. Moreover, we found that first juveniles appeared around the same period. However, over a month separated the hatching time in 2017 compared to 2015. Juveniles were also observed approximately three weeks apart, actually indicating delayed hatching in 2017. The relatively long time span between the detection of the

first hatchlings and juveniles might be due to the fact that hatchlings from one clutch emerge synchronously and sleep in the proximity of the nest in the first night(s) and are therefore easier to detect than those that already dispersed. Additionally, at the beginning of the rainy season the probability to detect small juveniles is rapidly decreasing due to increasing foliage growth.

Delayed hatching can occur when environmental conditions are not suitable (DOODY, 2011). A delayed rainy season accompanied by a decreased amount of rainfall in 2017 have probably resulted in the later emergence of hatchlings. The eggs of chameleons are sensitive to ecological conditions during incubation, especially variation in temperature and moisture (DÍAZ-PANIAGUA et al. 2002, DÍAZ-PANIAGUA & CUADRADO 2003). In fact, their eggs are flexible-shelled as they contain a minimal calcareous layer (PACKARD et al. 1982), making them more permeable and more vulnerable to hydric conditions during incubation (e.g., PACKARD 1991, 1999). As the eggs are buried underground and rainwater filters through the soil to reach the nest, the soil should be moist enough for hatchlings to be able to crawl and find a way through to reach the surface (MEASEY et al. 2014).

Henceforth, the observed variation in the onset of the rainy season induces a temporal shift in the hatching time of *F. labordi*. Nevertheless, as temperature also plays a role in the activation of embryonic development and ending of diapause (ANDREWS et al. 2008), there is also a need to investigate the relationship between timing of hatching and temperature fluctuation. The observed changes in the phenology of *F. labordi* may indicate that climate change is affecting living systems in negative ways (e.g., PARMESAN & YOHE 2003). At the population level, the observed shortened interval between the onset of the rainy season and the hatching date from 25 days in 2013 to one day in 2017 suggests a possible risk of future mismatches between the two events, resulting in decreased hatching success.

Climate change might also have additional effects on this species. For instance, within the population in Kirindy, male adult body size differed significantly within years (ECKHARDT et al. 2017). This observation was linked to inter-annual climate fluctuations, suggesting a relatively fast adaptation to shorter reproductive seasons concerning adult body size. This assumption is underpinned by the observation that males in Kirindy were significantly larger compared to those in the population of Ranobe (ECKHARDT et al. 2017). Therefore, the reduction of adult body size might be an answer to climate change in this species as well. Moreover, BALLEEN et al. (2016) observed that the sex of hatchlings in the Veiled chameleon *Chameleo calyptratus* is affected by the interaction of egg mass and temperature. This phenomenon might be more widespread within chameleons and climate change might additionally lead to a sex bias in *F. labordi*. ECKHARDT et al. (2019) observed a strong sexual bias towards males in juvenile *F. nicosiai* that might be ascribed to partial temperature sex determination in this species. At the community level, three sympatric *Furcifer* species are observed in the Kirindy Forest and

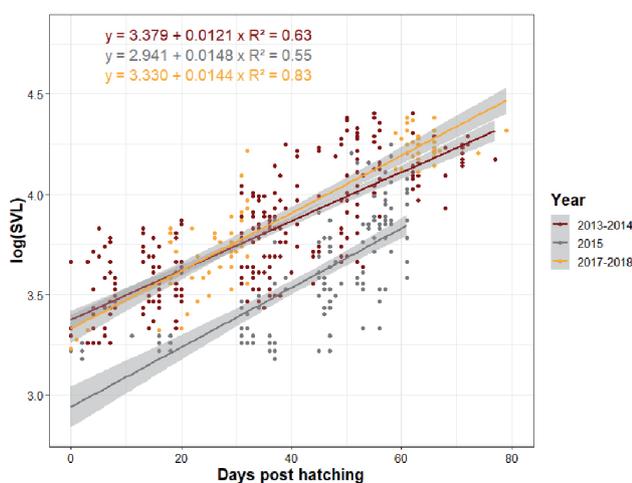


Figure 3. Graph showing linear regression model of hatchling and juvenile growth of *Furcifer labordi* on time in Kirindy Forest. Depicted is log-transformed snout-vent length (log(SVL)) against days post hatching for the three cohorts (2013–2014, 2015 and 2017–2018).

they probably partition the resources by the temporal shift in species-occurrence of hatching, with *F. labordi* hatching the earliest (ECKHARDT et al. 2019). Therefore, the observed delayed hatching of *F. labordi* may increase competition for food and space resources between the three sympatric species. However, further analyses are required to clearly document the impacts of climate change on species interactions (e.g., FORCADA et al. 2006, YANG & RUDOLF 2010). These are preliminary results, but long-term studies with experimental demonstration are necessary to obtain results that are more conclusive. Moreover, data from additional generations are needed to determine if these patterns hold across a larger sample of years. Furthermore, the shift in the onset of the rainy season and precipitation patterns that we observed might be highly linked to the Indian Ocean Dipole (IOD) that is responsible for irregular oscillation of the sea surface temperatures, but long-term recordings are obligatory to investigate a clear correlation. The IOD has only been recognized about two decades ago (WEBSTER et al. 1999), making it much less studied than other climate patterns. However, increased frequency of extreme IOD events due to greenhouse warming are predicted in the study of CAI et al. (2014), leading to extreme climate and weather events in regions that are affected by the IOD, such as Madagascar.

In general, short-lived species invest more energy into growth and reproduction at the expense of health maintenance (e.g., SMITH & FRENCH 2017). We confirmed the predicted increased investment in individual growth to compensate for delayed hatching in this study. Several other species also exhibit faster post-hatch growth in late hatching (e.g., BENOWITZ-FREDERICKS & KITAYSKY 2005, NEWTON 2008, WALLUS & SIMON 2008, BALDASSARRE 2014). A faster growth is necessary for these hatchlings to reach the stage of sexual maturation quickly. As observed throughout the field seasons, gravid females appeared around the same period despite the observed variation in hatching time. Thus, juvenile growth provides a mechanism to flexibly adjust the life history schedule of late-hatched cohorts, but the clock they use to calibrate their short life cycle remains elusive. In addition, the main egg-laying period likely remains constant, whereas elongated rainy seasons can lead to extended egg-laying periods (ECKHARDT et al. 2017).

Concerning the average vegetation cover within the growth period of *F. labordi*, 2015 showed the highest values, indicating that more water and insect food were available for the growing juveniles. However, in this season, juveniles grew more slowly compared to the other two seasons. The daily temperature and precipitation varied significantly during the study period. Variation in growth is associated with climatic conditions, especially temperature, and the effects are particularly pronounced in reptiles. For example, juvenile snapping turtles (*Chelydra serpentina*) grow slowly in a cool (19°C) versus a warm (28°C) ambient temperature (RHEN & LANG 1999). In addition, lizards mature earlier during longer hot seasons (ADOLPH & PORTER 1996). Other factors should also be considered, such

as the availability of food resources. Their contribution to the individual growth rate in *F. labordi* should be quantified to separate direct effects of temperature on growth. The current study is also limited by the fact that we did not follow individuals over time, but rather considered population averages.

In conclusion, the current study suggests that climatic variation induces variation in hatching time and juvenile growth rate of chameleon species. A delayed rainy season induced by climate change promotes late hatching, prompting neonates to grow faster in compensation. Such changes probably affect embryonic diapause and hatching success. Annual species, such as *F. labordi* might be particularly vulnerable to climate change as a whole population could be lost if a single cohort cannot adjust their phenology with the year-to-year climatic fluctuations. Since the population in Ranobe has much shorter lifespan (KARSTEN et al. 2008), it is highly likely that southern populations will vanish first. *Furcifer labordi* is an extreme example for short lifespan among tetrapods, but other chameleon species seem to have an annual life history as well (ANDREONE et al. 2005, TOLLEY et al. 2010, GLAW et al. 2020). Therefore, several chameleon species, especially those from highly seasonal habitats in western Madagascar, may suffer from unexpected extreme weather conditions and might even become extinct due to temporary non-appearance of rainy seasons.

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#### References

- ADOLPH, S. C. & W. P. PORTER (1996): Growth, seasonality, and lizard life histories: age and size at maturity. – *Oikos*, **77**: 267–278.
- AKÇAKAYA, R. H., S. H. M. BUTCHART, G. M. MACE, S. N. STUART & C. HILTON-TAYLOR (2006): Use and misuse of the IUCN red list criteria in projecting climate change impacts on biodiversity. – *Global Change Biology*, **12**: 2037–2043.
- ANDREONE, F., F. M. GUARINO, J. E. RANDRIANIRINA (2005): Life history traits, age profile, and conservation of the panther chameleon, *Furcifer pardalis* (Cuvier, 1829), at Nosy Be, NW Madagascar. – *Tropical Zoology*, **18**: 209–225.
- ANDREWS, R. M. (1982): Patterns of growth in reptiles. – pp. 273–320 in: GANS, C. & F. H. POUGH (eds): *Biology of the Reptilia*, Vol. 13. – Academy Press, New York.
- ANDREWS, R. M., C. DÍAZ-PANIAGUA, A. MARCO & A. PORTEHAULT (2008): Developmental arrest during embryonic development of the common chameleon (*Chamaeleo chamaeleon*) in Spain. – *Physiological and Biochemical Zoology*, **81**: 336–344.

- ANDREWS, R. M., T. O. M. MATHIES & D. A. WARNER (2000): Effect of incubation temperature on morphology, growth, and survival of juvenile *Sceloporus undulatus*. – *Herpetological Monographs*, **14**: 420–431.
- BALDASSARRE, G. (2014): Ducks, geese, and swans of North America, Vol. 1. – Johns Hopkins University Press, Baltimore.
- BALLEN, C. J., R. SHINE, R. M. ANDREWS & M. OLSSON (2016): Multifactorial sex determination in chameleons. – *Journal of Herpetology*, **50**: 548–551.
- BELLARD, C., C. BERTELSMEIER, P. LEADLEY, W. THUILLER & F. COURCHAMP (2012): Impacts of climate change on the future of biodiversity. – *Ecology Letters*, **15**: 365–377.
- BENOWITZ-FREDERICKS, Z. M. & A. S. KITAYSKY (2005): Benefits and costs of rapid growth in common murre chicks *Uria aalge*. – *Journal of Avian Biology*, **36**: 287–294.
- BOOTH, D. T. (2006): Influence of incubation temperature on hatchling phenotype in reptiles. – *Physiological and Biochemical Zoology*, **79**: 274–281.
- CAI, W., A. SANTOSO, G. WANG, E. WELLER, L. WU, K. ASHOK, ... & T. YAMAGATA (2014): Increased frequency of extreme Indian Ocean Dipole events due to greenhouse warming. – *Nature*, **510**(7504): 254–258.
- CEIA-HASSE, A., B. SINERVO, L. VICENTE & H. M. PEREIRA (2014): Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. – *Ecography*, **37**: 1–10.
- CLARKE, D. N. & P. A. ZANI (2012): Effects of night-time warming on temperate ectotherm reproduction: Potential fitness benefits of climate change for side-blotched lizards. – *Journal of Experimental Biology*, **215**: 1117–1127.
- DAYANANDA, B., B. R. MURRAY & J. K. WEBB (2017): Hotter nests produce hatchling lizards with lower thermal tolerance. – *Journal of Experimental Biology*, **220**: 2159–2165.
- DÍAZ-PANIAGUA, C., A. C. ANDREU & C. KELLER (2006): Effects of temperature on hatching success in field incubating nests of spur-thighed tortoises, *Testudo graeca*. – *Herpetological Journal*, **16**: 249–257.
- DÍAZ-PANIAGUA, C. & M. CUADRADO (2003): Influence of incubation conditions on hatching success, embryo development and hatchling phenotype of common chameleon (*Chamaeleo chamaeleon*) eggs. – *Amphibia-Reptilia*, **24**: 429–440.
- DÍAZ-PANIAGUA, C., M. CUADRADO, M. C. BLÁZQUEZ & J. A. MATEO (2002): Reproduction of *Chamaeleo chamaeleon* under contrasting environmental conditions. – *Herpetological Journal*, **12**: 99–104.
- DOODY, J. S. (2011): Environmentally cued hatching in reptiles. – *Integrative and Comparative Biology*, **51**: 49–61.
- ECKHARDT, F., P. M. KAPPELER & C. KRAUS (2017): Highly variable lifespan in an annual reptile, Labord's chameleon (*Furcifer labordi*). – *Scientific Reports*, **7**: 11397.
- ECKHARDT, F., C. KRAUS & P. M. KAPPELER (2019): Life histories, demographies and population dynamics of three sympatric chameleon species (*Furcifer* spp.) from western Madagascar. – *Amphibia-Reptilia*, **40**: 41–54.
- FORCADA, J., P. N. TRATHAN, K. REID, E. J. MURPHY & J. P. CROXALL (2006): Contrasting population changes in sympatric penguin species in association with climate warming. – *Global Change Biology*, **12**: 411–423.
- GLAW, F., D. PRÖTZEL, F. ECKHARDT, N. A. RAHARINORO, R. N. RAVELOJAONA, T. GLAW, K. GLAW, J. FORSTER & M. VENCES (2020): Rediscovery, conservation status and genetic relationships of the Malagasy chameleon *Furcifer voeltzkowi*. – *Salamandra*, **56**: 342–354.
- GOODMAN, S. M., M. J. RAHERILALAO & S. WOHLHAUSER (2018): Les aires protégées terrestres de Madagascar: Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota. – *Association Vahatra, Antananarivo*.
- HAENEL, G. J. & H. B. JOHN-ALDER (2002): Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulatus*. – *Oikos*, **96**: 70–81.
- HOUNIET, D. T., W. THUILLER & K. A. TOLLEY (2009): Potential effects of predicted climate change on the endemic South African Dwarf Chameleons, *Bradypodion*. – *African Journal of Herpetology*, **58**: 28–35.
- HUEY, R. B., M. R. KEARNEY, A. KROCKENBERGER, J. A. M. HOLTUM, M. JESS & S. E. WILLIAMS (2012): Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. – *Philosophical Transactions of the Royal Society B*, **367**: 1665–1679.
- IHLow, F., J. DAMBACH, J. O. ENGLER, M. FLECKS, T. HARTMANN, S. NEKUM, H. RAJAEI & D. RÖDDER (2012): On the brink of extinction? How climate change may affect global chelonian species richness and distribution. – *Global Change Biology*, **18**: 1520–1530.
- IUCN (2021): *Furcifer labordi*. The IUCN Red List of Threatened Species. Version 2021-1. – Available at: <http://www.iucnredlist.org>. Accessed on 30 April 2021.
- JANZEN, F. J. & G. L. PAUKSTIS (1991): Environmental sex determination in reptiles: Ecology, evolution, and experimental design. – *The Quarterly Review of Biology*, **66**: 149–179.
- JENKINS, R. K. B., L. D. BRADY, K. HUSTON, J. L. D. KAUFFMANN, J. RABEARIVONY, G. RAVELOSON & J. M. ROWCLIFFE (1999): The population status of chameleons within Ranomafana National Park, Madagascar, and recommendations for future monitoring. – *Oryx*, **33**: 38–46.
- KAPPELER, P. M. & C. FICHTEL (2012): A 15-year perspective on the social organization and life history of sifaka in Kirindy Forest. – pp. 101–121 in: KAPPELER, P. M. & D. P. WATTS (eds): Long-term field studies of primates. – Springer, Heidelberg.
- KARSTEN, K. B., L. N. ANDRIAMANDIMBIARISOA, S. F. FOX & C. J. RAXWORTHY (2008): A unique life history among tetrapods: An annual chameleon living mostly as an egg. – *Proceedings of the National Academy of Sciences of the United States of America*, **105**: 8980–8984.
- LJUNGSTRÖM, G., E. WAPSTRA & M. OLSSON (2015): Sand lizard (*Lacerta agilis*) phenology in a warming world. – *BMC Evolutionary Biology*, **15**: 206.
- LOURENÇO-DE-MORAES, R., F. M. LANSAC-TOHA, L. T. F. SCHWIND, R. L. ARRIEIRA, R. R. ROSA, L. C. TERRIBILE, P. LEMES, T. F. RANGEL, J. A. F. DINIZ-FILHO, R. P. BASTOS & D. BAILLY (2019): Climate change will decrease the range size of snake species under negligible protection in the Brazilian Atlantic Forest hotspot. – *Scientific Reports*, **9**: 8523.
- MEASEY, G. J., A. RASELIMANANA & A. HERREL (2014): Ecology and life history of chameleons. – pp. 85–113 in: TOLLEY, K. A. & A. HERREL (eds): The biology of chameleons. – University of California Press, London.

- MORENO-RUEDA, G., J. M. PLEGUEZUELOS & E. ALAMINOS (2009): Climate warming and activity period extension in the Mediterranean snake *Malpolon monspessulanus*. – *Climate Change*, **92**: 235–242.
- MYNENI, R. B., F. G. HALL, P. J. SELLERS & A. L. MARSHAK (1995): The interpretation of spectral vegetation indexes. – *IEEE Transactions on Geoscience and Remote Sensing*, **33**: 481–486.
- NEWTON, I. (2008): *The migration ecology of birds*. – Academic Press, London.
- PACKARD, G. C. (1991): Physiological and ecological importance of water to embryos of oviparous reptiles. – pp. 213–228 in: DEEMING, D. C. & M. W. J. FERGUSON (eds): *Egg incubation: its effects on embryonic development in birds and reptiles*. – Cambridge University Press, Cambridge.
- PACKARD, G. C. (1999): Water relations of chelonian eggs and embryos: Is wetter better? – *American Zoology*, **39**: 289–303.
- PACKARD, M. J., G. C. PACKARD & T. J. BOARDMAN (1982): Structure of eggshells and water relations of reptilian eggs. – *Herpetologica*, **38**: 136–155.
- PARMESAN, C. & G. YOHE (2003): A globally coherent fingerprint of climate change impacts across natural systems. – *Nature*, **421**: 37–42.
- R Core-Team (2021): *R: A language and environment for statistical computing*. – The R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- RANDRIANANTOANDRO, C., B. RAZAFIMAHATRATRA, M. SOAZANDRY, J. RATSIMBAZAFY & R. K. B. JENKINS (2010): Habitat use by chameleons in a deciduous forest in western Madagascar. – *Amphibia-Reptilia*, **31**: 27–35.
- RATHER, R. N., A. A. WANI, M. KASHTWARI & Z. A. BEIGH (2018): Phenological shifts due to climate change and the associated conservation threats. – *Climate Change*, **4**: 80–86.
- RHEN, T. & J. W. LANG (1999): Temperature during embryonic and juvenile development influences growth in hatchling snapping turtles, *Chelydra serpentina*. – *Journal of Thermal Biology*, **24**: 33–41.
- SCHWANZ, L. E., F. J. JANZEN & S. R. PROULX (2010): Sex allocation based on relative and absolute condition. – *Evolution*, **64**: 1331–1345.
- SINERVO, B., F. MÉNDEZ-DE-LA-CRUZ, D. B. MILES, B. HEULIN, E. BASTIAANS, M. V. CRUZ, R. LARA-RESENDIZ, N. MARTÍNEZ-MÉNDEZ, M. L. CALDERÓN-ESPINOSA, R. N. MEZA-LÁZARO, H. GADSDEN, L. J. AVILA, M. MORANDO, I. J. DE LA RIVA, P. V. SEPULVEDA, C. F. D. ROCHA, N. IBARGÜENGOYTÍA, C. A. PUNTRIANO, M. MASSOT, V. LEPETZ, T. A. OKSANEN, D. G. CHAPPLE, A. M. BAUER, W. R. BRANCH, J. CLOBERT & J. W. SITES (2010): Erosion of lizard diversity by climate change and altered thermal niches. – *Science*, **328**: 894–899.
- SINGH, S. K., D. DAS & T. RHEN (2020): Embryonic temperature programs phenotype in reptiles. – *Frontiers in Physiology*, **11**: 35.
- SIVITER, H., D. C. DEEMING, J. ROSENBERGER, O. H. P. BURMAN, S. A. MOSZUTI & A. WILKINSON (2017): The impact of egg incubation temperature on the personality of oviparous reptiles. – *Animal Cognition*, **20**: 109–116.
- SMITH, G. D. & S. S. FRENCH (2017): Physiological trade-offs in lizards: Costs for individuals and populations. – *Integrative and Comparative Biology*, **57**: 344–351.
- STAUDINGER, M. D., K. E. MILLS, K. STAMIESZKIN, N. R. RECORD, C. A. HUDAK, A. ALLYN, A. DIAMOND, K. D. FRIEDLAND, W. GOLET, M. E. HENDERSON, C. M. HERNANDEZ, T. G. HUNTINGTON, R. JI, C. L. JOHNSON, D. S. JOHNSON, A. JORDAAN, J. KOCIK, Y. LI, M. LIEBMAN, O. C. NICHOLS, D. PENDLETON, R. A. RICHARDS, T. ROBBEN, A. C. THOMAS, H. J. WALSH & K. YAKOLA (2019): It's about time: A synthesis of changing phenology in the Gulf of Maine ecosystem. – *Fisheries Oceanography*, **28**: 532–566.
- STEFANESCU, C., J. PEÑUELAS & I. FILELLA (2003): Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. – *Global Change Biology*, **9**: 1494.
- STEPANIAN, P. M. & C. E. WAINWRIGHT (2018): Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. – *Global Change Ecology*, **24**: 3266–3275.
- TOLLEY, K. A., R. N. V. RAW, R. ALTWEGG & J. MEASEY (2010): Chameleons on the move: Survival and movement of the Cape dwarf chameleon, *Bradypodion pumilum*, within a fragmented urban habitat. – *African Zoology*, **45**: 99–106.
- WALLUS, R. & T. P. SIMON (2008): *Reproductive biology and early life history of fishes in the Ohio River drainage: Elasmobranchs and Centrarchidae*, Vol. 6. – CRC Press, Florida.
- WEBSTER, P. J., A. M. MOORE, J. P. LOSCHNIGG & R. R. LEBEN (1999): Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997–98. – *Nature*, **401**: 356–360.
- YANG, L. H. & V. H. W. RUDOLF (2010): Phenology, ontogeny and the effects of climate change on the timing of species interactions. – *Ecology Letters*, **13**: 1–10.
- ZINNER, D., C. WYGODA, L. RAZAFIMANANTSOA, R. RASOLOARISON, H. T. ANDRIANANDRASANA, J. U. GANZHORN & F. TORGLER (2014): Analysis of deforestation patterns in the central Menabe, Madagascar, between 1973 and 2010. – *Regional Environmental Change*, **14**: 157–166.