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Evidence-based practice

Influence of seasonal temperature fluctuation on successful reproduction of the Gorongosa girdled lizard *Smaug mossambicus*

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Abstract
Climatic seasonality has allowed species to evolve to use such variation to their advantage. Correct timing of breeding and parturition can be an essential factor in species survival, and adaptations to geographic seasonal changes can assist in preparation for a successful breeding season. The Gorongosa girdled lizard *Smaug mossambicus* is a little-known cordylid lizard from Mozambique, for which there is very limited information regarding its natural history and breeding habits. Through keeping this species at Drayton Manor Resort, UK, it was apparent that seasonal climatic changes may have an impact on the successful reproduction of this species. Using data collected at Drayton Manor Resort and additional data collected from both private and professional institutions via a questionnaire, the climatic factors affecting reproduction in this reptile were investigated. The results suggest that seasonal temperature variation may have some influence on captive breeding success, although this is likely to be in conjunction with other factors such as variance in photoperiod, humidity and rainfall. There is evidence of strictly seasonal reproductive behaviour by *S. mossambicus*, which corresponds with many other species from southern Africa: producing a single litter annually, breeding in winter with parturition in summer. Litter size varied between one and six individuals. Future research should focus on exploring further climate variables that may influence the breeding habits of *S. mossambicus*. This study builds a foundation for understanding the breeding behaviour of *S. mossambicus* and should aid in the successful maintenance and reproduction of the species.

Background

Cordylid lizards are a widely distributed group of lizards native to southern Africa (FitzSimons 1943), comprising over 80 species split between two subfamilies: Cordylinae (nine genera, viviparous) and Platysaurinae (one genus, oviparous; Reissig 2014). Early studies hypothesised that cordylid lizards were influenced by seasonal changes comparable to species of northern temperate regions which, at the time, were subjected to greater investigation. Reproductive activity was assumed to occur in spring and summer, with parturition (birth) occurring late summer/autumn (Duvall et al. 1982; Fitch 1970; Licht 1984). In contrast, Van Wyk (1989) found that vitellogenesis (yolk formation) in *Cordylus p. polyzonus* began in autumn and concluded in spring, suggesting that taxa from the southern hemisphere may follow different patterns. In addition, Van Wyk (1990) reported that testes volume of *C. p. polyzonus* peaked in winter and was at its lowest in mid-summer, which synchronises with the patterns observed by Van Wyk (1989). This has since been found to be congruent with a variety of cordylid species from southern and south-eastern Africa (Branch et al. 2005; Flemming and Van Wyk 1992; Flemming 1993a, 1993b; Van Wyk 1989, 1990, 1991).

Mozambique's climate exhibits distinct seasons: a cooler dry season followed by a hotter wet season. Mozambique is home to the Gorongosa girdled lizard *Smaug mossambicus*. Although seasonal changes have been noted to affect reproduction of other cordylid lizards, especially those native to South Africa, few studies have investigated the breeding habits or detailed natural history and ecology of *S. mossambicus* either in the wild or in captivity. With knowledge of the natural seasonal shifts in the native range of *S. mossambicus*, this paper evaluates how seasonal temperature fluctuation may affect breeding success in captive *S. mossambicus*.

Actions

Study animals

Drayton Manor Resort acquired 2.2.0 *S. mossambicus* in October 2016, sourced via a loan from a private individual. The 2.2.0 were characterised as mature individuals, based on size and colouration described in Reissig (2014), and therefore were assumed to be of reproductive age. Upon maturity, males develop an orange colouration ventrally throughout the body, and a row of obvious femoral pores on each thigh that are also seen in many other similar species (Reissig 2014). Females broadly retain the juvenile colouration (near black dorsal, slate-grey ventral) into adulthood and lack femoral pores either side of the vent; however, females do develop slight orange colouration upon maturity, limited to the lower jawline only.

One 1.1.0 pair was housed together on-exhibit (Figure 1) and an additional 1.1.0 together off-exhibit. The 1.1.0 pairs were maintained separately to avoid potential male-male aggression that may occur within this species in captivity. Although little wild-group dynamic data exist for this species, maintaining pairs separately provides certainty of parentage of any future young. The male on exhibit was maturing upon acquisition and so was assumed to be approximately 1–2 years old, and this is supported by subsequent growth rates of captive juveniles produced at Drayton Manor Resort (T.G. Baker personal observation). It was not possible to accurately estimate the age of the other 1.2.0, though individuals were suspected to be three or more years of age, and therefore sexually mature based on the features of mature individuals outlined above.

On-exhibit enclosure

The dimensions of the on-exhibit enclosure were 220 × 94 × 113 cm (length × width × height) (Figure 1), and half of the available height within the enclosure was furnished and therefore accessible to the animals. A full range of temperature and humidity gradients, UV provision (0 UVI in shade and up to 3 UVI at basking areas, based on FZ2; Baines et al. 2016) and multiple hiding places within rock crevices were provided within the enclosure. The glass viewing panels at the front of the enclosure allowed keepers to monitor behaviour of the individuals and adjust parameters where necessary to meet the putative needs of the species.

Although unintentional upon the outset, the on-exhibit enclosure, due to its position within the Reptile House, fluctuated in temperature throughout the year. These fluctuations corresponded to the mean annual fluctuations in Gorongosa Mountain, Gorongosa National Park, Mozambique, the type locality of the species (Climate Data 2020; FitzSimons 1958). The on-exhibit enclosure was sprayed once each morning with water, including for longer durations in summer to ensure hydration. However, it was not possible to record detailed humidity readings throughout the study period. Access to natural outdoor light cycles was limited, due to the positioning of the on-exhibit enclosure within the Reptile House. However, due to daylight savings and institutional requirements until January 2020, the photoperiod of enclosures varied between approximately 8–10 hours in April–November and 7–8 hours in December–March. From February 2020 onwards, all artificial lighting was operated on time switches and the photoperiod was extended to 12 hours in March–October and 10 hours in November–February to more accurately reflect annual daylight fluctuations of the type locality (Climate Data 2020).

Off-exhibit enclosure

Dimensions of the off-exhibit enclosure were 150 × 70 × 70 cm (length × width × height). The same range of temperature and humidity gradients, UV provisions and access to hiding places were afforded to the off-exhibit enclosure as those for the on-exhibit enclosure. Similarly, half of the enclosure was furnished and accessible to animals and glass viewing panels at the front of the enclosure were present for monitoring purposes.

As was the intention for the on-exhibit enclosure, the off-exhibit enclosure had little substantial variation in environmental conditions. Husbandry of this species was still being studied and therefore seasonal fluctuation had not been added into the intentional husbandry at this stage. However, conditions appeared appropriate for successful maintenance of the animals based on the excellent body condition maintained throughout the observation period. The off-exhibit enclosure was sprayed once each morning using the same method as in the on-exhibit enclosure. The light and heating for the off-exhibit enclosure was kept constant (12 hours on, 12 hours off) using an automated timer throughout the study period with limited and indirect exposure to natural light.

Diet

The same dietary regime (food items and frequency) was maintained for animals in both enclosures throughout the study. Diet consisted of invertebrates in the *Gryllus, Schistocerca, Blaptica, Tenebrio, Galleria, Zophobas, Oniscus, Philoscia, Trichoniscus* and *Porcellio* genera, either scatter-fed or placed in bowls and made available three to four times weekly.

Data collection

Relevant animal observations were recorded in the Drayton Manor Resort Reptile House section diary and on the Species 360 Zoological Information Management System (ZIMS; Species360 2020). Pertinent information on reproductive activity observations (copulation events, birthing events and litter size) were accessed in ZIMS.

Figure 1. The on-exhibit enclosure housing 1.1 *Smaug mossambicus* at Drayton Manor Resort.

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Temperature data

Zoo keepers at Drayton Manor Resort collected minimum and maximum diurnal surface temperature data for each enclosure using an infra-red temperature gun (Etekcity Lasergrip 774), which was calibrated yearly to ensure standardisation of temperature readings. Data were collected for the on-exhibit enclosure between October 2016 and September 2021 and for the off-exhibit enclosure between January 2018 and April 2019. Prior to November 2018, attempts were made to collect temperature readings on a weekly basis. The temperature was checked an average of 3±0 times per month (range=1–5 times per month) within the on-exhibit enclosure and 4±0 times per month (range=3–5 times per month) in the off-exhibit enclosure. Protocols were altered to increase the number of temperature readings for each month, resulting in an average of 17±5 times per month (range=7–28 times per month) for the on-exhibit enclosure and 26±4 times per month (range=19–30 times per month) for the off-exhibit enclosure (Supplementary Figure 1). The temperature of each exhibit was recorded between 1100 and 1600, in an attempt to detect the warmest period of the day; however, this temporal sampling could not guarantee that the temperature recordings truly reflected the maximum daily temperature achieved. The maximum temperature at basking areas within the enclosures and minimum temperatures in the coolest areas were consistently recorded, ensuring readings were within 30 cm of the respective surface. Monthly average minimum and maximum temperatures were calculated for both on- and off-exhibit enclosures. Data were visualised in R v.3.5.3 (R Core Team 2019) and RStudio v.1.2.1335 (RStudio Team 2019), using the *ggplot2* v.3.2.1 (Wickham 2016) and *scales* v.1.1.0 (Wickham and Seidel 2019) packages. Raw data were manipulated using the R packages *dplyr* v.0.8.3 (Wickham et al. 2020) and *readr* v.1.3.1 (Wickham et al. 2018). We calculated mean values and standard errors using the *pracma* v.2.2.5 package (Borchers 2019).

Questionnaire data

A short questionnaire was created using SmartSurvey (SmartSurvey 2020) and distributed in accordance with local laws and regulations to fellow collections—both professional and private—via shared weblinks, online forums, social media platforms (Facebook) and private emails. The questionnaire aimed to ascertain any information pertinent to *S. mossambicus*, particularly involving reproductive success.

In summary, questions were asked concerning the number of individuals maintained together, and the sex ratio of these individuals (group dynamic); the temperature range at which enclosures were kept, and whether seasonality was introduced (temperature variation); the relative humidity at which enclosures were kept, and whether there was substantial variation noted (humidity); the typical photoperiods in the enclosures, and whether this varied seasonally (photoperiod variation); whether UV-B was available to animals (UV-B provided); the broad diet of the animals (diet); the dates on which reproductive events were recorded (copulation date and birth date); and how many litters were observed in the enclosure each year (litters per year). A detailed list of questions and responses can be found in Supplementary Table 1.

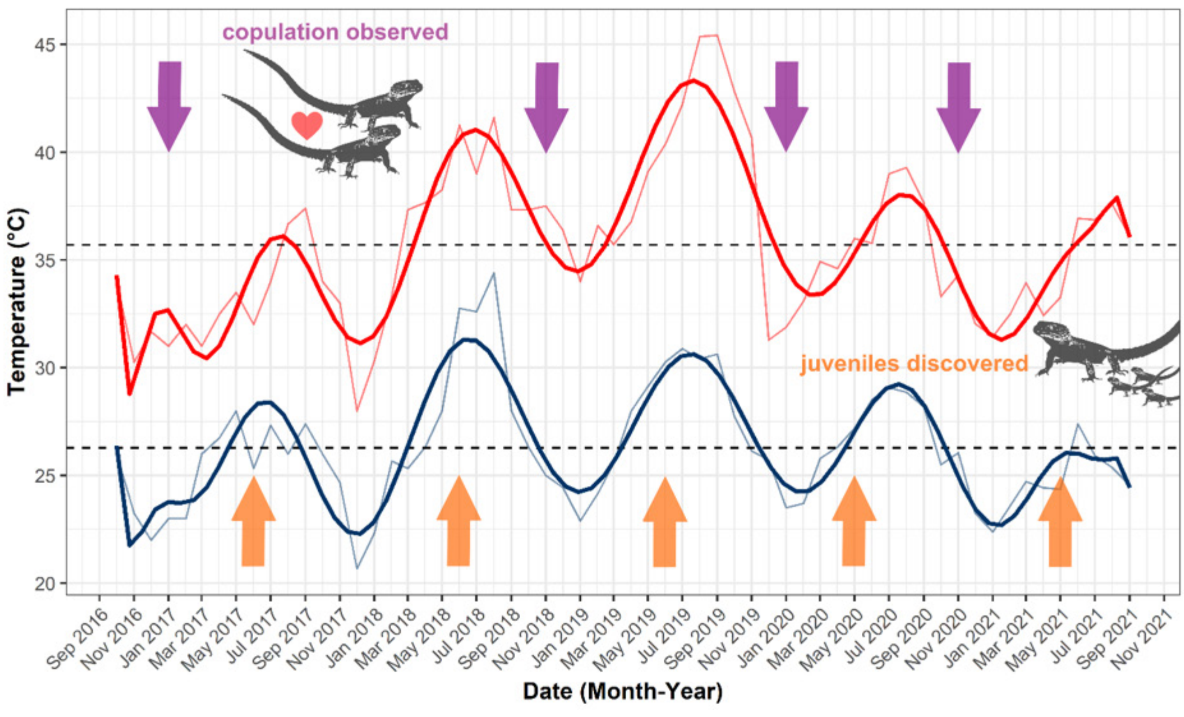

Figure 2. Seasonal variation in monthly average diurnal surface temperature across the five-year study period (2016–2021) in the on-exhibit enclosure holding 1.1.0 *S. mossambicus* at Drayton Manor Resort. Red line: maximum temperature. Blue line: minimum temperature. The bold, smoothed lines overlaying the results represent the data with a linear model (lm) and 15 degree polynomial implemented using the geom_smooth() function of ggplot2, to ease visual interpretation. Purple arrows represent the date on which copulation was observed and the orange arrows show when juveniles were subsequently discovered within the enclosure.

Table 1. A summary of results from the questionnaire providing husbandry data pertaining to *S. mossambicus* in both private and professional collections across Europe and the USA, plus data from this study (DMR). All respondents provided groups with UV-B and an insectivorous diet. Independent groups kept by the same respondent are separated via a semi-colon (group dynamic). Experience denotes the number of years for which the respondent has worked with *S. mossambicus*. Country refers to the location where the group is maintained. Birth date shows the month of the year that juveniles were discovered in the enclosure. Litters per year indicates the number of occasions in the year that new juveniles were discovered. Respondents with multiple groups report findings for all groups and enclosures in one answer, with no differentiation given per group.

Number	Experience (years)	Country	Group dynamic	Temperature variation (°C)	Humidity variation (RH%)	Photoperiod variation	Copulation date	Birth date	Litters per year
1	2	Unknown	1.2.0	Reduced in winter	Higher in winter	Reduced in winter	Not observed	June	1
2	18	United States	1.1.0; 1.2.0	Summer: 22–30 Winter: 18–24	Highest end of summer, dry winter	Reduced in winter	Not observed, assumed February	June, July and August	1
3	9	Germany	1.1.0	Summer:30–40 Winter: reduced	Higher in winter	Reduced in winter	Not observed	June, July	1
4	5	United States	3.4.0; 1.1.0	Summer:29–35 Winter: 18–24	No variation, maintained at 80	12 hours light	Not observed, assumed November	February	1
5	3	Belgium	1.1.0	Summer: 30 Winter: 22	No variation	Reduced in winter	Not observed	June	1
6	15	United States	5.8.0	No, 23–28	No variation	Reduced in winter	Not observed	May, June	Unknown
7	3	United States	2.3.0	Summer: 18–32 Winter: 18–23	Higher in winter	12 hours light	Not observed	September	1
DMR on-exhibit	5	United Kingdom	1.1.0	Summer: 30–40 Winter: 20–30	Higher in spring–summer	Reduced in winter	November, January	June	1
DMR off-exhibit	5	United Kingdom	1.1.0	No variation	Higher in spring–summer	12 hours light	Not observed	N/A	0

Data availability
Data used in this study are available on Zenodo (DOI:10.5281/zenodo.5810769), including an R script for recreating figures.

Consequences

On-exhibit enclosure
The mean maximum temperature within the on-exhibit enclosure was 35.69°C (±3.76°C) and the mean minimum temperature was 26.28°C (±2.78°C), showing consistent temperature fluctuations between low temperature winters (November–March) and high temperature summers (June–September) across multiple years (Figure 2). This variation is similar to that of the wild habitat data available for Gorongosa, with reversed seasons (Climate Data 2020). An increase in average annual temperature was observed within the on-exhibit enclosure in 2018 and 2019, likely due to differences in enclosure layout over time, replacement of heating equipment and the influence of the natural UK climate.

During the five-year study period, excellent body condition of the 1.1.0 animals within the on-exhibit enclosure was qualitatively recorded. In addition, these animals successfully reproduced, resulting in a single litter every year. Copulation events were observed in the winter of each year, excluding 2017–2018, corresponding to periods of low temperatures, and litters of five, one, five, one and four individuals were born in June 2017, 2018, 2019, 2020 and 2021 respectively (Figure 2). The emergence of juvenile lizards was recorded in May–June across all five years (Figure 2). All juveniles were healthy upon discovery and sexes were recorded as 5.0.0, 1.0.0, 2.3.0, 0.1.0 and 2.2.0 in respective litters. Sexing is usually possible around 5–8 months of age dependent on growth rate, based upon the development of femoral pores, followed by the orange ventral colouration on males (T.G. Baker personal observation).

Off-exhibit enclosure
No substantial fluctuations in seasonal temperature were recorded (Figure 3). A mean maximum temperature of 34.42°C (±0.94°C) and a mean minimum temperature of 23.79°C (±0.54°C)

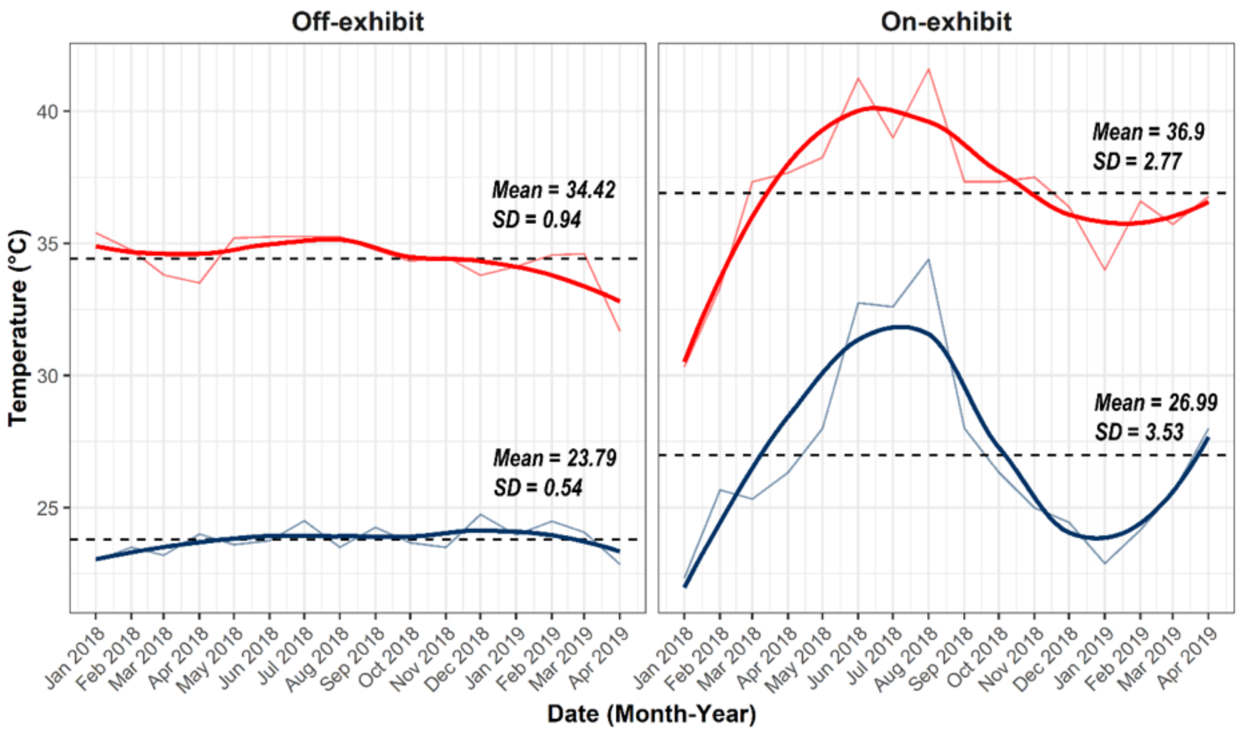

Figure 3. A temporal comparison of monthly average diurnal surface temperature in both the off-exhibit (left) and on-exhibit (right) enclosures, each holding 1.1.0 *S. mossambicus* in 2018–2019 at Drayton Manor Resort. Red line: maximum temperature. Blue line: minimum temperature. SD: standard deviation. The bold, smoothed lines overlaying the results represent the data with a linear model (lm) and 15 degree polynomial implemented using the geom_smooth() function of ggplot2, to ease visual interpretation.

were recorded in the off-exhibit enclosure throughout the study period (January 2018–April 2019). Comparatively, the on-exhibit enclosure had a mean maximum temperature of 36.9°C (±2.77°C) and a mean minimum temperature of 26.99°C (±3.53°C) within the same timeframe.

No observations of courtship, copulation, breeding and therefore emergence of juveniles were observed between 2016 and 2019 within the off-exhibit enclosure. Individuals in the off-exhibit enclosure were qualitatively assessed to have excellent body condition throughout the study period, similar to the on-exhibit pair. Although the temperature data are partially unavailable, enclosure parameters and design remained unchanged throughout the entire study period.

Questionnaire data

Data were obtained for an additional 16.23.0 animals across seven respondents from both private (six) and professional (one) collections across Europe (one Germany, one Belgium) and the USA (two California, one Texas, three undisclosed), resulting in a total of 18.25.0 animals (n=43, Table 1). Respondents reported 2–18 years of experience with *S. mossambicus* and data represent sexually mature individuals maintained in groups of 1.1 or more, all with access to UV-B light (UV-basking or tube-style lamps).

Respondents report *S. mossambicus* to be insectivorous, accepting a wide range of food items offered (species within the *Gryllus, Schistocerca, Blaptica, Tenebrio, Galleria, Zophobas, Bombyx* and *Hermetia* genera) which is consistent with personal experience and available literature (Reissig 2014).

Questionnaire respondents reported seasonal fluctuations of warm summer periods (30–40°C) and cooler winter periods (18–30°C; reported by 80% of respondents). Respondents report both high and low relative humidity levels within their enclosures, with 50% reporting intentional seasonal fluctuations. Additionally, 80% of respondents reduce the photoperiod of enclosures during the winter months. None of the respondents have observed copulation in their captive animals but two respondents speculate an assumed copulation during the cooler winter period derived from birthing events. All respondents reported breeding activity when providing seasonal fluctuations in enclosures, with females giving birth to a single litter per year. Ninety percent of births observed by respondents occurred between May and August, with 50% occurring in June. Litter size varied between one and six individuals, but no corresponding data on age and size of breeding females are available. Since none of the respondents reported a failure to breed *S. mossambicus* when providing seasonal fluctuations within enclosures, no further information on non-breeding animals is provided in this study, other than for the off-exhibit pair housed at Drayton Manor Resort.

This study serves as a foundation for future work and introduces a hypothesis that seasonal temperature changes, similar to that of their native range, will facilitate the successful captive breeding of the Gorongosa girdled lizard. This hypothesis is based on a limited sample size and observation period, and thus requires substantial testing. There are a limited number of collections that have non-breeding groups for which data were unobtainable during this study; however future studies should attempt to include additional animals and parameters to further understanding. It would be beneficial to test single variables per year going forward while keeping all others controlled, together with more detailed additional data on variables such as humidity, to provide more accurate conclusions on this topic. Future years of breeding will provide additional valuable data, and hopefully data from new collections will be available in the future. In any future research, methods, equipment and controls for all partaking collections should be standardised to ensure consistency of results, providing more accurate comparisons and conclusions.

At Drayton Manor Resort, 24-hour temperature within the on-exhibit enclosure is now being recorded to provide a greater understanding of the effect of temperature on breeding success in *S. mossambicus*. The off-exhibit pair subsequently developed an unconfirmed fatal infection prior to moving on from Drayton Manor Resort, and are therefore unavailable for further investigation; it is unknown if this was a consequence of the lack of seasonality offered to the pair.

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