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Reproductive behaviour and natural history of the Long-toed Treefrog, *Leptopelis xenodactylus* Poynton, 1963, in South Africa

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Abstract. Little is known about the reproductive behaviour of frogs in the genus *Leptopelis*, and in this study of the endangered *L. xenodactylus* we offer some insights from a wetland in the KwaZulu-Natal Midlands. Males call from wetlands and change their position during the season, possibly because females become more conspicuous over time. The most active period for reproductive behaviour is under heavy cloud cover between 19:00 and 21:00 h. These frogs use axillary amplexus, with evidence of a sticky substance secreted where the male's forearms grip the female, likely to assist with maintaining grip. Up to 150 eggs are laid on top of hummocks in shallow burrows. Eggs take approximately one month to develop, with tadpoles able to wait for suitable conditions before hatching. Tadpoles develop for approximately three months before metamorphosis but show evidence of being able to overwinter. These insights can guide conservation management and perhaps be useful for studies of other members of the genus.

Keywords. Amphibians, breeding, burrows, endangered, hummocks, tadpoles.

Introduction

One of the most researched aspects of vertebrate natural history is breeding biology (Nunes-de-Almeida et al., 2021), with amphibians displaying the greatest diversity in reproductive modes of all tetrapod vertebrates (Duellman and Trueb, 1986). The reproductive modes of amphibians were first defined as a specific combination of traits, including oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling (Salthe and Duellman, 1973).

Southern Africa has an impressive frog diversity with 180 species (Frost, 2025), and 71 species have been recorded in KwaZulu-Natal Province alone (du Preez and Carruthers, 2021). African treefrogs of the genus *Leptopelis* are endemic to Africa, with 51 species currently recognised in the group (Channing and Rödel, 2019). Six occur in southern Africa and three in KwaZulu-Natal Province (*Leptopelis natalensis*, *L. mossambicus*, *L. xenodactylus*; du Preez and Carruthers, 2021).

Owing to its restricted range, specific habitat preferences, and extremely secretive nature (Kyle et al., 2024), very little is known about the life history and reproductive behaviour of the Long-toed Treefrog, *L. xenodactylus*. Much of what has been documented in the literature was informed guesswork based on other, better-studied congeneric species, but the reproductive behaviour of the genus remains poorly understood (du Preez and Carruthers, 2017). Minter et al. (2004) suggested that *L. xenodactylus* might be similar to *L. bocagii* (Günther, 1865), which breeds in shallow puddles in inundated grassland areas, while Channing et al. (2012) stated that "the eggs are laid in soft mud at the edge of swamps, and the tadpoles wriggle to the water." Carruthers and du Preez (2011) reported that members of the genus *Leptopelis* lay their egg clutches in burrows in the mud or humus in close proximity to water and the tadpoles wriggle into the water upon hatching.

Wager (1986) mentioned that the encapsulated tadpoles of *L. natalensis* (Smith, 1849) can remain dormant, long after they are mature enough to hatch, while they await suitably damp conditions to emerge and wriggle to the water where they continue their development. This author also reported that, following a rainfall event that followed a dry spell, several batches of eggs, laid at different times, hatched simultaneously.

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The *L. xenodactylus* holotype was a gravid female found in Underberg, KwaZulu-Natal, in March 1961 (Poynton, 1963), and from this specimen, a conclusion was drawn that this was an autumn-to-winter breeding species. However, a year later, Poynton further hypothesized that this was evidence for aestivation (Poynton, 1964). The eggs inside this specimen were referred to being "ripe" (Poynton, 1963). The aims of this study were to determine the breeding biology of *L. xenodactylus*, to establish their calling patterns and describe the call, determine what environmental variables affect their calling, and document the egg and tadpole development process.

Materials and Methods

Fieldwork. The majority of observations reported herein were made in a wetland at Fort Nottingham in the KwaZulu-Natal Midlands (29.4207°S, 29.9161°E) over a period of three active seasons of fieldwork (September 2020–November 2022). During 19 fieldtrips, spread throughout the months of September–December of each year, as many frogs as possible were located and captured and, where possible, sex, weight, head width, snout–vent length, situation and time of capture, air temperature, water temperature, wind, moon phase, and cloud cover were recorded. Measurements were taken using digital callipers, weights were measured using a digital jewellery scale, and the temperature was measured using a digital thermometer, at approximately 1 m above ground level if not stated otherwise. Their situation was recorded as either subterranean, at ground level, or above ground in vegetation. Wind was recorded as either none, light, gusty, or strong. Moon phase was retrieved from a lunar calendar for each date. Cloud cover was a best estimate, made by the same investigator each time to ensure consistency.

Amplexus and development. On 12 October 2022 we found an amplecting pair of *L. xenodactylus* in a shallow burrow on top of a hummock. The frogs were removed carefully and transferred to a terrarium constructed inside a 25-l black plastic bucket with damp soil and grass tufts to simulate natural habitat. There was no standing water. The terrarium was kept off-site to allow continued observation and monitoring of egg development. Eggs were measured using digital callipers. The terrarium was kept at room temperature inside a building. After the eggs hatched simultaneously, tadpoles were divided into two batches as a precautionary measure and placed in separate glass aquaria filled with rainwater and aquatic vegetation, which was changed weekly. The aquatic vegetation was supplemented once a week with commercially available fish food (Aqua-Plus Tilapia Grower).

Tadpoles. Each week, fifteen tadpoles were selected from among the group and measured. These were placed in a few drops of water on a flat ceramic plate, where they were straightened and measured using digital callipers. Two additional *L. xenodactylus* tadpoles were captured at a site close to the main Fort Nottingham site (29.3948°S, 29.9025°E) and kept off-site to observe development.

Call measurements. Passive acoustic monitoring (PAM) using a Wildlife Acoustics SM4 Song Meter with on-board, omnidirectional microphones was conducted at the Fort Nottingham study site. Distinct calls were selected from the recordings and call parameters measured using Raven Pro v1.6 (64-bit version, Cornell Laboratory of Ornithology, Bioacoustics Research Program 2019) and were then measured using the R coding platform (R Core Team, 2024). *Seewave* (Sueur et al., 2008) and *tuneR* (Ligges et al., 2018), with all their dependencies, were the two R packages used for the measurement analysis and graphic representations of the calls. *Seewave* was used for analysing the call patterns and acoustic properties. Measurements made were call duration (s), number of notes per call, note duration (s), and inter-note interval (s). *Seewave* was also used to obtain spectral properties of the call by applying a Fast Fourier Transform (FFT) to determine the fundamental and dominant frequencies.

Statistical analysis. We summarised the data using descriptive statistics from the base R package (R Team, 2024). To test for significant relationships between frog activity and weather conditions, we used the Kruskal-Wallis test, Chi-squared goodness-of-fit test, Pairwise Chi-squared test with Bonferroni correction, and two-proportion *Z*-tests.

Results

Call site. Over the three-year study period, the calling positions of 132 male *L. xenodactylus* were recorded. A change in calling position was observed during the September–November calling activity, with more males (63%, $n = 12/19$) calling from underground locations in September. By November, 83% ($n = 36/43$) of males found were using elevated perches (Fig. 1). On 27 September 2020, five of seven males encountered were found in shallow surface burrows. The air temperature was 6°C, while the water and mud temperatures were 11°C. Furthermore, the mobility of males increased: they remained in a single position at the beginning of the season and moved more in later weeks.

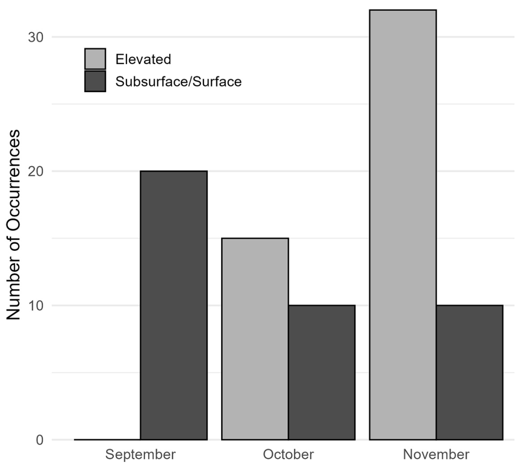

Figure 1. Positions of calling male *Leptopelis xenodactylus* over a three-month survey period (September–November in the years 2020–2022) at Fort Nottingham, KwaZulu-Natal, South Africa.

Weather conditions. Weather data gathered during fieldwork revealed that *L. xenodactylus* were found calling at a variety of air temperatures, with 28% (n = 31/112) found calling at 6–9°C, 15% (n = 17/112) at 10–12°C, 30% (n = 33/112) at 13–15°C, and 27% (n = 30/112) at 16–18°C. A Kruskal-Wallis test showed that all temperatures were equally likely to sustain calling activity ($p = 0.4432$). Similarly, water temperature also produced no differences ($p = 0.4373$), with 31% (n = 20/64) of frogs found at water temperatures of 11–13°C, 28% (n = 18/64) at 14–16°C, 19% (n = 12/64) at 17–19°C, and 22% (n = 14/64) at 20–21°C. In contrast, cloud cover appeared to have a much stronger impact on frog activity, with 78% (n = 86/109) found when the sky was overcast (100% cloud cover), compared to 8% (n = 9/109) found in 50–99% cloud cover, 2% (n = 2/109) found in 1–49% cloud cover, and 11% (n = 12/109) found on clear nights. A Chi-square goodness-of-fit test followed by a pairwise Chi-square test with Bonferroni correction showed that 100% cloud cover supported significantly greater frog activity (p = 0.001) than the other categories. Wind also appeared to significantly impact activity levels, with 84% (n = 75/90) of frogs found active on nights that were either still or with a light breeze, while 16% (n = 14) were found in gusty winds (winds that were strong, but irregular), and only one was found on a very windy night. We used a two-proportion Z-test to determine if there was a significant difference between the number of frogs found during either "none" or "light" wind compared to "gusty" or "strong" conditions and found a significant difference ($\chi^2 = 77.356$, $df = 1$, $p < 0.05$). Moon phase did not appear to have much influence on calling activity ($\chi^2 = 10.744$, $df = 7$, $p = 0.1502$), with 22% (n = 19/86) of frogs found on a waxing gibbous moon, 14% (n = 12/86) on waning crescent and new moon, and 13% (n = 11/86) on a waning gibbous moon, with the remaining 37% spread through the remaining four categories (waxing crescent, first quarter, full moon, and third quarter), and only 6% (n = 5) found on a full moon. The vast majority (81%, n = 86/107) of the frogs found during the project were found between 19:00 and 21:00 h, with only 7% (n = 7/107) before this and 12% (n = 13/107) found later.

Breeding. The call of *L. xenodactylus* is typical of the genus with two different parts, a short loud vocalisation and a longer, quieter buzz. The mean note length of the buzz calls (n = 33) is 0.826 s ± 0.321 s. Spectral parameters showed a mean fundamental frequency of 1867 ± 122 Hz (n = 6), a dominant frequency of 3323 ± 124 Hz (n = 6), and a bandwidth of 849–2363 Hz (n = 20). There was some indication that the buzzing part of the call may be aggressive, as it was given by a male in close proximity to a female in response to a second, approaching male. Gravid females (Fig. 2A) were located from 23 October–4 December, indicating a prolonged oviposition period.

On 12 October 2022 at 19:30 h, a pair of *L. xenodactylus* was found in axillary amplexus. The frogs were located on the top of a vegetated hummock that protruded ca. 15 cm above the surrounding substrate and was ca. 45 cm across. There was little standing water surrounding the hummock, but the substrate was saturated and there were similar hummocks all around. Hummocks were covered with several different types of grasses, forbs, and sedges. The frogs had excavated a depression at the base of the vegetation into which their bodies fit precisely. Both animals' heads protruded above the ground (Fig. 2C). The frogs ceased any previous activity whilst being observed, hunkering down into the hollow and closing their eyes.

We carefully removed the entire hummock and fit it into the base of a 25-l bucket. We closed the lid, which left the frogs undisturbed. They remained in place for the 60-km drive back to base and appeared unchanged at 22:30 h. They were left undisturbed until 07:00 h the next morning, when they were further investigated. At that time, they remained in amplexus and had filled the entire depression with eggs, to the extent that they were perched on top of the egg clutch and their bodies were raised above ground level. By 08:30 h they had separated, with the male moving to the edge of the bucket and attempting to escape. The female remained on top of the eggs (Fig. 2D). By 10:30 h the female had left this position and was situated above the eggs in the grass, and by 11:45 h she had moved to the edge of the bucket. Once the pair had separated, we observed that the female had the remains of a substance on her sides, in places where the male's forelegs had clasped her. This substance was also visible in the other amplecting pair (Fig. 2B), suggesting males may exude a secretion to assist with maintaining amplexus. A female located at the field site, with eggs visibly distending the abdominal region, inflated her body upon capture and remained puffed up for the entire duration of handling, measuring, and photography (Fig. 2A).

Eggs and tadpoles. The eggs are relatively large, round, creamy white spheres, typical of the large yolk sac found in the genus but lacking any further pigmentation (Fig. 3A; Poynton and Broadley, 1987). They were found to be adhesive, sticking to each other and the surrounding substrate. Because they were laid in a dense clutch, it was impossible to count them individually and accurately without disturbing them. From a sample of

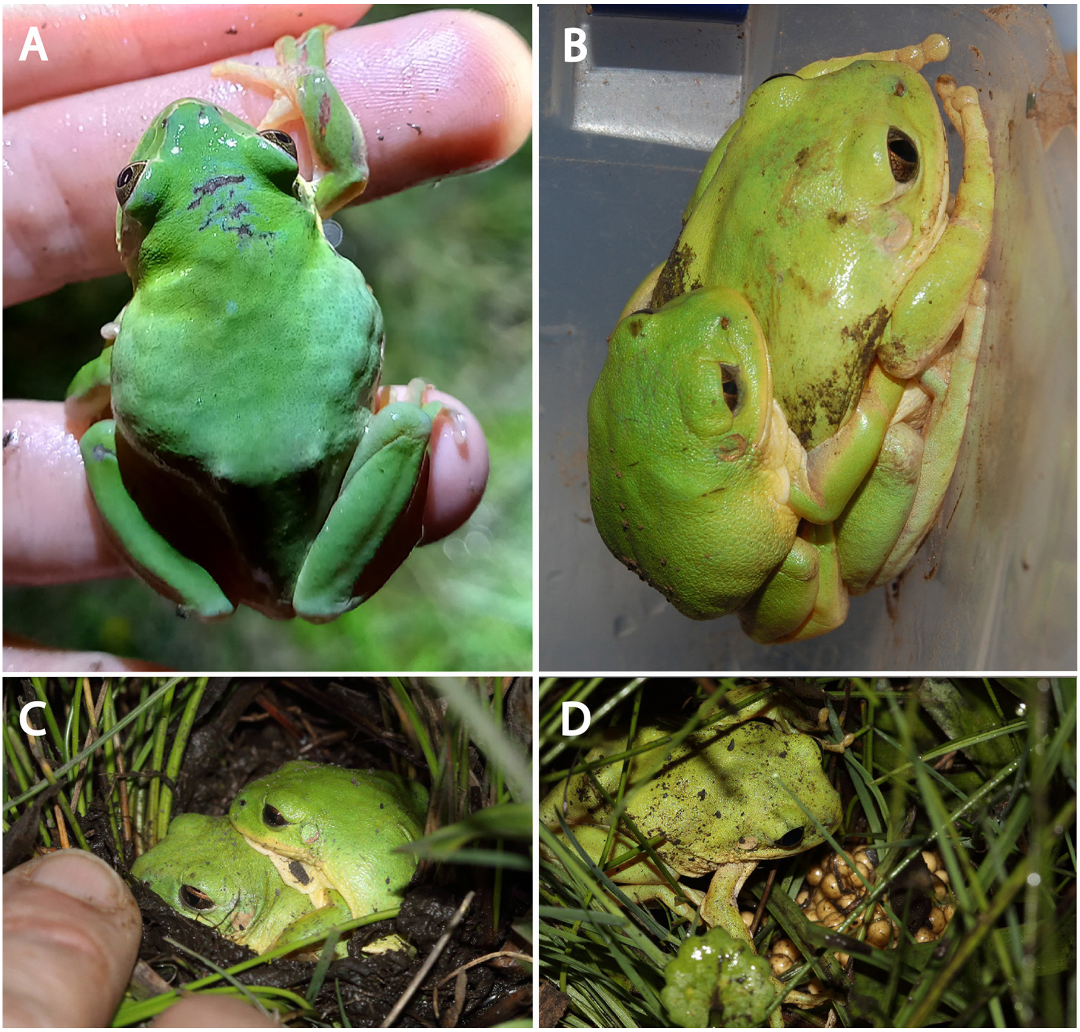

Figure 2. Reproduction in *Leptopelis xenodactylus* in wetlands at Fort Nottingham, KwaZulu- Natal, South Africa. (A) A gravid female, showing the presence of large oviductal eggs through the skin. (B) A pair in amplexus. The secretions covered by dirt visible near the male's arms are indicative of an adhesive substance to assist with his grip. (C) An amplexed pair in a nest, a depression in the grass on the top of a hummock. (D) A female perched over her eggs. Photos by Kirsty Kyle (A, C, D) and James Harvey (B).

ten eggs that could be measured, they had an average diameter of 3.6 ± 0.1 mm. By Day 14 of development the measurable eggs had increased in diameter to 4.2 ± 0.1 mm, with early developmental stages of small tadpoles (between Gosner Stage 14 and 17; Gosner, 1960) attached to the yolk sacs visible inside the eggs (Fig. 3B). By Day 28 the tadpoles and their yolk sacs were clearly visible in the eggs (Fig. 3C). The tadpoles twitched inside the eggs in response to stimulation with a bright light from a torch or the vibration of the bucket lid being opened. Several eggs were infertile (Fig. 3C), but the majority contained developing tadpoles.

On Day 47, 176 eggs hatched, but four tadpoles died soon after hatching. Newly hatched tadpoles measured (to the nearest 0.1 mm) on average 20.0 ± 2.5 (range 16.7–26.2; n = 15) in length. Four weeks after hatching (Fig. 3D) they measured 31.0 ± 1.54 (28.0–34.0), and after eight weeks 31.5 ± 1.9 (27.8–34.5). By Week 11, the first froglets emerged, while the remaining tadpoles measured 35.5 ± 3.9 (29.3–42.9). Their growth rate is illustrated in Fig. 4. On 31 May, 32 tadpoles had not yet metamorphosed, indicating that the species may be able to overwinter as tadpoles. The morphometric data of froglets (n = 14) were taken prior to their release at the site of origin.

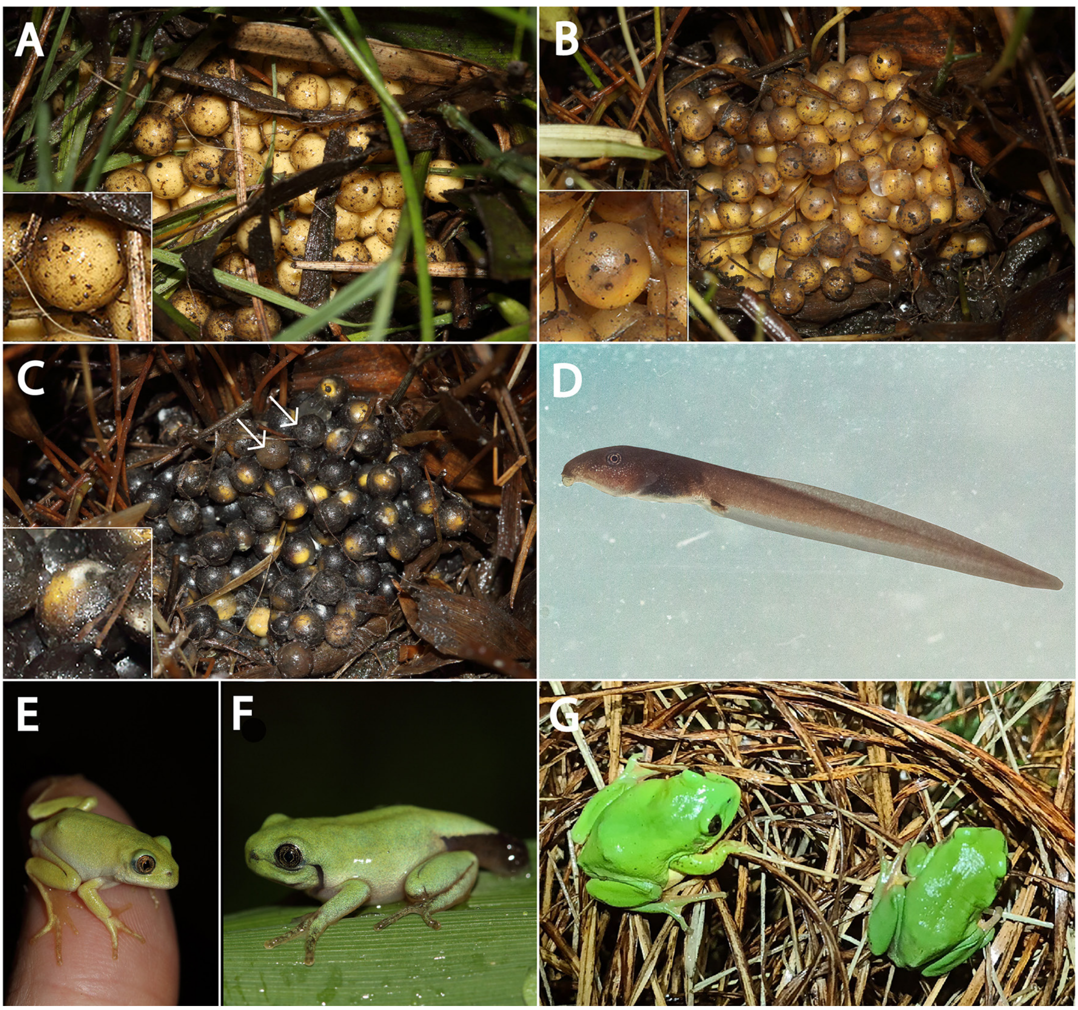

Figure 3. Developmental stages of *Leptopelis xenodactylus* in wetlands at Fort Nottingham, KwaZulu-Natal, South Africa. (A) A clutch shortly after oviposition. (B) The same clutch after two weeks, with some visible tadpole development. (C) A clutch with eggs just prior to hatching, tadpoles fully developed. Note that some eggs show no development (arrows). (D) Tadpole at four weeks (Gosner Stage 35). (E) Newly metamorphosed froglet. (F) Early metamorph, with tail and gill slit still visible. (G) Size comparison of female (left) and male (right) adults. Photos by Kirsty Kyle.

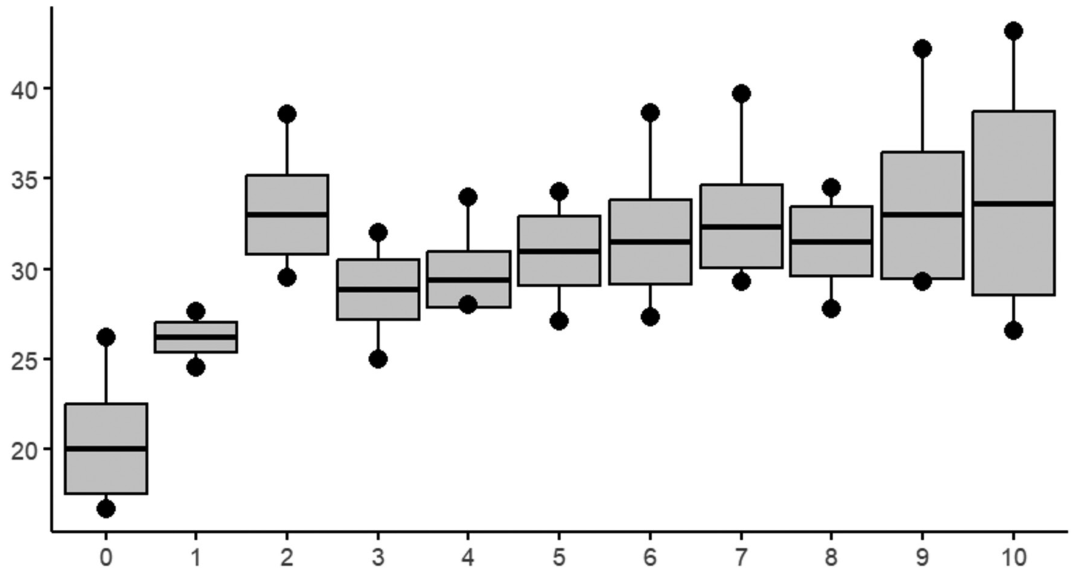

Figure 4. Tadpole growth (in mm) from hatching to metamorphosis for *Leptopelis xenodactylus* from Fort Nottingham, KwaZulu-Natal, South Africa. Indicated are mean, maximum and minimum, and standard deviation values at hatching and at the end of each week, with millimetres on the y-axis and weeks on the x-axis.

The snout–vent length (SVL) of these froglets was 10.7 ± 0.4 mm (10.0–11.5) with a head width of 4.8 ± 0.4 mm (4.2–5.3 mm).

On 26 December 2019, tadpoles were found at a site near Fort Nottingham (29.3962°S, 29.9025°E). Two were located in a small area of open water in the wetland and these were taken into captivity. On 2 January 2020 they were approximately 38 mm and 50 mm in length, respectively, with small hindlegs present in the larger tadpole, which was estimated to be at Stage 35, with the smaller one at Stage 25. They were fed commercial fish flakes and grew rapidly. By 4 February, both were released where they had been found, one as a fully formed froglet (Fig. 3E) and the other as a metamorph (Fig. 3F).

Sexual dimorphism. While it is usually difficult to differentiate between males and females of this species in the field, males reached a maximum SVL of 43 mm. In contrast, females can be considerably larger, with the largest female reaching 54 mm. Females also appear to have a more pointed snout, while male snouts are more rounded (Fig. 3G). Measurements taken from 85 calling frogs, confirming that they were males, revealed the mean weight of a male to be 4.9 ± 1.5 g (range 1.6–8.2 g), while the mean head width was 13.7 ± 2.5 mm (6.0–21.5 mm) and the mean SVL was 35.3 ± 5.2 mm (23.0–43.0 mm). Only four females were measured during the course of the project, with a mean weight of 8.15 ± 1.0 g (6.6–9.0 g), mean head width of 16.3 ± 2.2 mm (14–20 mm), and mean SVL 45 ± 5.2 mm (41–54 mm).

Discussion

Clutch deposition. Based on what was known from other *Leptopelis* species, it was presumed that *L. xenodactylus* would lay eggs in covered burrows on the periphery of the wetland, under grass litter and substrate (Channing et al., 2012). Based on our findings, this does not appear to be the case. While hummocks were already thought to be important to these frogs, they were assumed to be perches for calling males. Instead, it appears that they may also support and facilitate nesting and oviposition. The amplectic pair we encountered was situated on the top of the hummock, in an area that was presumably safe from most flooding events. The depression that was constructed was in densely compacted mud and would have taken some effort to excavate, as it was dug down into the substrate with an earthen floor. The eggs were completely exposed on the surface of the depression, which would potentially subject them to a higher risk of predation and desiccation – even though the clutch was surrounded by the dense wetland sedges, grasses, and herbs. It is possible that these risks may be mitigated by the "island" effect of the hummock emerging from the surrounding thick mud. This area is heavily trampled by cattle, which avoid the hummocks when passing through. Exposure to the elements may also afford a degree of protection from fungal and other infections, whereas a closed burrow might create conditions more conducive to pathogens that can cause morbidity and mortality.

General behaviour and movement. All females located during the project, with the exception of the amplecting individual, were found on the edges of the wetland. It is possible that females emerge from their underground overwintering sites with the first substantial rains and head to the periphery of the wetland to forage and build up energy while their eggs develop. During this period, with the wetlands perhaps not yet suitable for nesting and egg-laying, the emerging males establish their calling sites and form choruses. In October, when conditions have become suitable for successful breeding, females may descend into the wetlands and select a mate from among the calling males. This corresponds to the time when the males appear to select more elevated calling perches.

In a survey report Harvey (2007) mentioned finding seven *L. xenodactylus* tadpoles in mid-December 2006. The images in this report show the tadpoles to be at Stage 36 (Gosner, 1960) in their development. Channing (2008) described collecting three tadpoles near Franklin Vlei, KwaZulu-Natal, on 15 January 2007 from between grass hummocks in shallow water over soft mud. The larger two were at Stage 38 and the smaller one at Stage 37 (Channing, 2008). On 6 March 2015, the second author captured and photographed tadpoles between Stage 40 and 41 at Franklin Vlei.

James Harvey (pers. comm.) raised a tadpole to metamorphosis and kept the young frog in captivity for over a year. He reported that the frog began calling at one year of age, although the call was at an audibly higher pitch than the calls of larger frogs heard in the field. This confirms an observation from our fieldwork, when smaller frogs (assumed to be the previous season's metamorphs) were identifiable by the higher pitch of their calls. The young frog kept in captivity ate fruit flies as a metamorph and progressed to crickets as it grew. Van Dijk (1978) mentioned that young frogs kept in captivity ate moths.

It was apparent during our fieldwork that, early in the breeding season (September), males were often calling from below ground or ground level, while in October and November they could be found higher in the vegetation. It may be that early in the season males are likely calling from close to their overwintering spots, in sections of wetland that are most suited to burrowing, while later in the season they start to disperse to other areas in the wetland. Frogs also became considerably easier to locate later in the breeding season, frequently calling from high up in vegetation and from exposed perches. Throughout the season, males responded to auditory prompts, most likely stimulated by the emerging chorus.

It was also apparent that these males often aggregate, displaying this behaviour throughout the breeding season. This could be due to the behaviour of calling individuals (Calsbeek et al., 2022), or it could suggest that a well-defined set of optimally suitable microhabitat parameters exists. These parameters may include vegetation type and water depth, and microhabitat conditions could also contribute to the seasonal movement of the frogs. As the season advances, with the increase in rainfall and the growth of vegetation, more areas become suitable habitats, and dispersal ensues. From data collected at Fort Nottingham and other sites, *L. xenodactylus* do not appear to utilise the entire wetland and avoid sections that to the human eye appear similar to parts they favour. Thus, there are likely some subtle but essential parameters that dictate which areas are, and are not, suitable.

Another possible explanation for the seasonal increase in mobility and elevation in perch height is temperature. Early in the season, when the ambient temperature is coolest, frogs would be sheltered from cool conditions, including wind, by calling from underground burrows or surface calling sites, as was evidenced by the five of seven frogs found calling underground on 27 September. Our data revealed that early in the season (September) proportionately more males were calling from underground positions, whereas late in the season (November) proportionately more males were calling from elevated positions. This has implications for fieldwork as it shows that males of this species tend to call from higher up in the vegetation later in the season and would therefore be easier to locate then.

In relation to the moon phase, it seems unusual that these frogs do not either favour a dark moon or a bright moon, to either provide protective darkness or to assist with vision, but when taking cloud cover data into account, it becomes apparent that frogs were significantly more active on cloudy nights. Considering the prevalence of mist and rain on these high-elevation grasslands, moon phase is perhaps less relevant. The wind results were as expected, with fewer individuals found during windy nights. On windy nights, the vegetation frogs clamber through would be swaying, and because these frogs do not hop but move hand over foot from blade to blade, any strong swaying movement would make navigation difficult. Wind also provides better cover for predators by providing background noise, which likely makes it more difficult for frogs to sense approaching threats. With regard to air and water temperatures, it appears that the frogs are active across a wide range of temperatures. However, time of night is an important factor to take into account when trying to locate these frogs. For approximately 2 h, from around 19:00 h, when it first gets dark in Spring in the Midlands, these frogs are at their most active until the activity dwindles around 21:00 h. They do call before and after this time period, but from the individuals found and the data gathered, the most activity occurs within this window.

Conclusion

Leptopelis xenodactylus males start calling in the wetlands at the beginning of September, most likely to set up territories, while females are not yet seen and may be on the periphery or still underground. Females are seen in the wetlands from the end of September onwards and oviposition is likely to occur in October and November. The large, yolky eggs are laid in clutches in shallow burrows on the top of hummocks and take approximately 47 days to hatch. Tadpoles may be waiting for a sufficient rainfall event and, when conditions are suitable, break the egg casings and make their way to the water. Tadpoles are found in low numbers in shallow water.

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References

Calsbeek, R., Zamora-Camacho, F.J. Symes, L.B. (2022): Individual contributions to group chorus dynamics influence access to mating opportunities in wood frogs. Ecology Letters **25**(6): 1401–1409.

Carruthers, V., du Preez, L.H. (2011): Frogs and Frogging in South Africa. Cape Town, South Africa, Struik Nature.

Channing, A. (2008): The mud dwelling tadpole of the Long-toed Tree Frog, *Leptopelis xenodactylus* (Arthroleptidae). Herpetological Review **39**: 288–290.

Channing, A. Rödel, M.-O. (2019): Field Guide to the Frogs and Other Amphibians of Africa. Cape Town, South Africa, Struik Nature.

Channing, A., Rödel, M.-O., Channing, J. (2012): Tadpoles of Africa. Frankfurt, Germany, Edition Chimaira.

du Preez, L.H., Carruthers, V.C. (2021): Frogs of Southern Africa. Cape Town, South Africa: Penguin Random House. [Application for mobile phones]

Duellman, W.E., Trueb, L. (1986): Biology of Amphibians. New York, USA, McGraw-Hill.

Gosner, K.L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**: 183–190.

Ligges, U., Krey, S., Mersmann, O., Schnackenberg, S., Guenard, G., Ellis, D.P.W., et al. (2018). *tuneR*: Analysis of Music and Speech (v1.4.7). Available at: https://CRAN.R-project.org/package=tuneR. Accessed on 10 October 2025.

Minter, L.R., Burger, M., Harrison, J., Braack, H., Bishop, P.J., Kloepfer, D. (2004): Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland. Washington, D.C., USA, Smithsonian Institution.

Nunes-de-Almeida, C.H.L., Haddad, C.F.B. Toledo, L.F. (2021): A revised classification of the amphibian reproductive modes. Salamandra **57**: 413–427.

Poynton, J.C. (1963): Descriptions of South African amphibians. Annals of the Natal Museum **15**: 319–332.

Poynton, J.C. (1964): Southern African Amphibia. Annals of the Natal Museum **17**: 171–172.

Poynton, J.C., Broadley, D.G. (1987): Amphibia Zambesiaca 3. Rhacophoridae and Hyperoliidae. Annals of the Natal Museum **28**: 161–229.

Salthe, S.N., Duellman, W.E. (1973): Quantitative constraints associated with reproductive modes in anurans. In: Evolutionary Biology of the Anurans, p. 229–249. Vial, J.L., Ed., Columbia, Missouri, USA, University of Missouri Press.

Sueur, J., Aubin, T., Simonis, C. (2008): *Seewave*: a free modular tool for sound analysis and synthesis. Bioacoustics **18**: 213–226.

R Core Team (2024): R: a Language and Environment for Statistical Computing. Vienna, Austria, R Foundation for Statistical Computing.

Wager, V.A. (1986): Frogs of South Africa – their Fascinating Life Stories. Cape Town, South Africa, Delta Books.

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