Daily activity profile of the golden mantella in the 'Froggotron' - a replicated behavioral monitoring system for amphibians

Running title: ***Daily activity level of golden mantellas***

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Abstract

Research on threatened species in zoos can provide vital information to inform conservation planning and implementation in the field. This is particularly important for rare and cryptic species with behavior patterns that are difficult to observe in the wild. The Critically Endangered golden mantella (*Mantella aurantiaca*) is an iconic, endemic frog confined to mid-altitude subhumid forest in Moramanga District, Madagascar. Ecological and behavioral data for this highly threatened species are sparse, and conservation work will need to be informed by both in situ and ex situ research on behavior and habitat preferences. This study utilized environmental information gathered in the field to design a system where behavior and microhabitat use could be measured in captivity. Using replicated climatically controlled chambers (the “Froggotrons”), we analysed the 24-hour activity profile of the golden mantella in relation to temperature and humidity. Golden mantellas showed a bimodal pattern of activity during the day with much less activity during the night. Frogs kept at warmer temperatures (20-25ºC) were more active than those kept under cooler conditions (16-19ºC). However, the bimodal pattern was retained under the different temperatures, although the second peak occurred slightly earlier under warmer conditions. Most activity was observed when humidity levels were above 85%, although less than half of the mantellas were active outside leaf microhabitats during peak periods. These findings can inform ongoing field surveys through determining the optimum times of day to either capture or count golden mantellas for further conservation actions.

Keywords: amphibian decline, behavior, habitat preference, Madagascar, *Mantella aurantiaca*

Research Highlights

- Golden mantellas displayed bimodal activity during daytime.
- The activity rhythm was influenced by temperature and humidity.
- ‘Froggotrons’ allow observations of behaviour of cryptic species that may not be possible in the wild.

Introduction

Although once regarded as quite separate entities, in situ and ex situ approaches are becoming increasingly integrated within the 'One Plan Approach' to conservation management (e.g, Dickie, Bonner & West, 2007; Pritchard, Oldfield & Harrop, 2012; Traylor-Holzer, Leus & Bauman, 2019). Indeed, combining ecological and behavioral data from field and captive populations can provide complementary information that strengthens species management plans. For example, obtaining rigorous population assessments in the field may depend on an understanding of behavior of the target species that can only be obtained in captivity. This is particularly the case for rare and cryptic species for which it is difficult to obtain fundamental natural history data. Threatened amphibians are a case in point, as they often have highly seasonal activity patterns that depend on rainfall, humidity and temperature (Edmonds, Adamovicz, Rakotoarisoa, Soamiarimampionona & Harris, 2020). An understanding of both daily and seasonal activity patterns can therefore inform the design of population assessment protocols for conservation planning, but these may be difficult to assess in the wild. Observations on animals in zoos can play a vital role in filling these gaps, but can be limited by small sample sizes, a lack of information about microhabitat conditions in nature, and insufficient standardization and replication to allow rigorous analysis.

The Critically Endangered golden mantella (*Mantella aurantiaca*) is an iconic frog endemic to the upland central-eastern rainforests of Madagascar. This species is under threat from the effects of climate change, habitat destruction, collection for the pet trade and invasive species (Piludu et al., 2015). However, golden mantellas are popular exhibits in zoos, and regular captive breeding provides an ongoing supply of animals for display, education and research. Indeed, the golden mantella has proved a useful model for comparing the fitness of captive bred and wild frogs (Passos, Garcia & Young, 2017a,b, 2018). Likewise, the seasonal activity pattern of golden mantellas has been elucidated through observations on captive animals (Edmonds et al. 2020). Nevertheless, golden mantellas are poorly studied in the wild, and the microhabitat requirements for the species have only recently been described (Edwards et al., 2019). Using this environmental information from the field, we designed replicated climatically controlled chambers (the

‘Froggotrons’) that record continuous observations of behavior that would be difficult to obtain in nature. We demonstrate how the Froggotrons were used to describe the daily activity profile of the golden mantellas under different temperature regimes.

Behavioral rhythms are driven by environmental cycles but are linked to predator-prey dynamics, avoidance of competition and thermoregulation (Andrews et al., 2009; Donati, Baldi, Morelli, Ganzhorn & Borgognini-Tarli, 2009). There are two measurable aspects of an activity rhythm: (1) phasing, which relates to where the activity occurs in relation to the imposed cycle; and (2) amplitude, a measure of how much activity is occurring during the active phase. Whereas mammals and birds have circadian rhythms driven by biological clocks that are synchronized by the light-dark cycle and are independent of temperature (Aschoff, 1981), in ectotherms the light-dark cycle may be the main synchronizer of the activity cycle, but the amplitude of activity may depend on temperature. Amphibians are intricately linked to their external environment due to their ectothermic physiology, permeable skins, reproductive cycles and life history traits (Williams, Shoo, Isaac, Hoffmann & Langham, 2008; Hoffmann, Chown & Clusella-Trullas, 2012). This means amphibians are driven to seek microhabitats where they can conserve water and thermoregulate (Raske et al., 2012).

Most behavioral rhythm studies have been conducted with mammal, bird or invertebrate species and are poorly understood in amphibians (Demian & Taylor 1977; Griffiths 1985; Hasegawa & Cahill 1998; Moraes, Poletini, Ramos, Lima & Castrucci, 2014). However, an understanding of activity patterns is important for designing effective field surveys of the target species. Here we describe the daily activity cycle of the golden mantella for the first time, using climatically controlled chambers and two temperature regimes. We relate the activity patterns to microhabitat use with a view to improving the design and interpretation of population assessments carried out in the field.

Methods

Design of enclosures

Research was conducted from 12th – 21st May 2015 at the amphibian biosecure facility at Paignton Zoo Environmental Park. Eight replicated enclosures (termed "Froggotrons") were constructed using compressed plastic fibre boards, each measuring 1 m x 0.78 m x 1.2 m with a Perspex viewing/access window at either end. A 150 mm deep trough at the front of each tank was filled with water; small pebbles were placed at each end to allow the frog's safe access and exit. Enclosure lids were covered with a fine mesh to allow light in and prevent escape by frogs or the invertebrates used as live food. Each Froggotron was fitted with a misting system operated via a timer set to spray deionised water for two minutes twice daily (08:30 hrs and 16:30 hrs). The floor of each enclosure was covered in coconut matting ('Lucky Reptile' TM), and split into a 2 x 2 matrix comprising four equal sections using thin string, the fifth section made up by the water trough area. As golden mantellas are active in and around patches of leaf litter in the wild (Edwards et al., 2019), mixed deciduous leaves were placed on the floor of each tank in piles covering an area equal to approximately 50% of the total floor area (Figure 1). Each tank was fitted with a small camera (Sony HK TM 420 TVL color camera with infra-red night vision capability) connected to a digital video recorder set to record 24 hours per day.

Temperature and light regimes

Two rooms within the amphibian biosecure centre were used with four enclosures in each; one room was kept at 16-19°C (Cooler Room) and the other at 20-25°C (Warmer Room). Temperatures in both rooms were maintained by air conditioning systems. The presence of lighting and other heating systems meant that temperatures fluctuated (warmer room: 20-25 °C; cooler room: 16-19 °C), with the warmer room invariably increasing in temperature during the day. Our intention was to replicate in-situ wet season light levels for the duration of the study (Edwards et al., 2019). Therefore, light levels increased in stages in the mornings via a timer starting with small (300 mm) fluorescent tubes (Zoo Med T5 HO ReptiSun TM 10.0 UV) providing first light at 06:15 hrs. This was followed by larger fluorescent ceiling room lights activated around 08:30 hrs by keepers; and finally full daylight bulbs (150 w metal halide, Eye Color PAR36 TM) directly over each tank timer activated at 09:00 hrs. Full spectrum daylight bulbs were set to turn off at

16:00 hrs followed by ceiling room lights at 17:00 hrs, with the small fluorescent tube lights out and full darkness at 18:15 hrs. In 2014 light and temperature measurements were made at forest floor level at golden mantella sites in Madagascar. Full daytime light levels ranged between 200 ~ 400 lux (light meter CEM DT-1300™) and temperatures were between 21 – 23 °C. Camouflage netting was fitted to the lids of each tank to simulate canopy cover, taking light levels down to those recorded in the forests (Edwards et al., 2019). Both groups of mantellas were fed at the same time each day between 11:00-14:00 hrs with either fruit flies (*Drosophila melanogaster*) or hatchling crickets (*Gryllus bimaculatus*). Crickets were fed Cricket Calci-Paste (International Zoo Vet Group) and both crickets and fruitflies were dusted with Nutrobal (Vetark ™).

Behavioral monitoring

Golden mantellas were sourced from three captive collections in the UK and were all sexually mature adults (1-4 yrs old; 15-22 mm snout-vent length; golden pigment fully developed). Eighty captive-bred golden mantellas were split into two groups of 40, each group (now called Group 1 and Group 2) were again separated into sub-groups of 10 frogs (4 males, 6 females), and each of the sub-groups were placed in identical Froggotrons. Group 1 was allocated to the warmer room; Group 2 was allocated to the cooler room. Our priority was to ascertain the diel activity patterns of the frogs by recording behavior continuously for 24 hours each day over a period of 10 consecutive days. We reviewed the recorded material via instantaneous scan sampling at 30 min intervals, noting the number of mantellas visible, area of the enclosure and the type of substrate used (leaves or coconut mat). We determined a mantella to be active if it had emerged from hiding within leaves (Gunderson & Leal, 2016), but we did not attempt to reliably distinguish individuals or sexes from the video footage. Each enclosure was allocated a temperature and humidity data logger (EL-USB-2™) set to record every 30 minutes, and timing was synchronised with the video recording system. Research was carried out with approval from The Wild Planet Trust's Animal Welfare and Ethics Committee and in compliance with "Guidelines for the use of animals in research" (Association for the Study of Animal Behavior, 2015).

Data analysis

Non-parametric tests were used as the number of mantellas active were shown to deviate significantly from a normal distribution (Shapiro-Wilk test: $p \leq 0.05$). After the initial twenty-four-hour activity budget was analysed, data were then separated to represent day (06:30-18:00 hrs) and night (18:30 -06:00 hrs). As activity was minimal during the night, activity, temperature and humidity relationships during daylight were only analysed further. Daytime data recorded for activity, temperature and humidity across all four tanks in each room were averaged, warm and cool room means were then compared using a Wilcoxon Signed Rank Test. Further, the total number of mantellas observed were combined across all eight tanks at 30-min intervals between 06:30–18:00 hrs over 10 days and plotted against temperature and humidity levels (Fig. 3). Statistical analyses were carried out using Excel™ and the R program ™ (R Core Team, 2016). Data analysis followed the protocol developed by Zuur Leno, Walker, Saveliev & Smith (2009), and used General Additive Modelling (GAM) to explore the relationship between activity and temperature and humidity. We initially applied a simple linear model which was then modified to include variance structure e.g., room was added as a random variable (see Edwards [2019] for full GAM methodology). We then further developed a maximal model fitted with Maximum Likelihood (ML) and non-significant terms were removed stepwise (Zuur et al. 2009). We compared the fit of models using Akaike's Information Criterion (AIC), and then refitted and validated the final model with Restricted Maximum Likelihood (REML) (Zuur et al. 2009). Residuals from the final model were found to display heterogeneity (a non-random pattern) which meant there was a strong chance of there being a relationship between the variables (Zuur et al. 2009). GAM was therefore deemed appropriate because it allows for non-linear relationships between the response variable and multiple explanatory variables to be modelled (Zuur et al. 2009).

Results

Activity patterns and microhabitat use

Under both warm and cool conditions golden mantellas showed a bimodal pattern of activity during the day with little activity during night hours (Figure 2). The first peak in activity occurred around or approximately one hour after the larger 150w metal halide lamps were activated.

On average, more mantellas were active outside the leaves in the warmer room than in the cooler room (Median number active in the warm room = 2.90; Median number active in the cool room = 0.75; $T = 0$, $n = 24$, $p \leq 0.01$). Humidity was not significantly different between chambers in the warm and cool rooms (Warm room median = 88.69%; cool room median = 90.70%; $T = 99.5$, $n = 24$, $p = 0.25$). Activity levels peaked in the morning between 06:15 and 10:00 hrs under both temperature regimes. A later, second peak in activity was also observed, but this occurred earlier under warmer conditions (13:00-15:00 hrs) than it did under cooler conditions (17:00-18:00 hrs). The total number of frogs active between 06:30 and 18:00 hrs increased with an increase in temperature, with most activity occurring between temperatures 21°C – 22°C (Figure 3a). Activity was also at its highest when humidity levels were around 85% (Figure 3b). However, even under warm conditions and during the activity peaks, less than half of the frogs were usually active outside leaf microhabitats in the open areas of the enclosures.

Relationship between activity and temperature and humidity

General Additive Modelling (GAM) showed temperature and humidity both affected activity levels. Fitting LOESS smoothers to the temperature and humidity data strongly suggested both relationships were non-linear (Figure 3). From here we developed GAMs with smoothing terms on temperature, which was significant ($F = 33.81$, $df = 7.346$, $p < 0.001$), and humidity which was also shown to be significant ($F = 8.86$, $df = 3.945$, $p < 0.001$).

Discussion

The regulation of daily activity rhythms in amphibians has been poorly studied, and the phasing and amplitude of activity can vary ontogenetically, seasonally, and spatially, as well as between species (e.g.

Rusak 1981; Oishi et al. 2004). Although mantellas are generally regarded as day-active on account of their aposematic colouration and unpalatability to diurnal predators (Vences & Glaw, 2003), there can be exceptions to this rule (Andreone, 2002). Our continuous monitoring showed that golden mantellas were largely diurnal, but with a bimodal behavioral rhythm that has probably evolved to avoid the warmest and driest part of the day in the forest. Nevertheless, even during the peak activity periods when golden mantellas were active on the surface, individuals continued to shuttle in and out of leaf litter so that only up to half of the individuals were observable at any point in time.

There was a difference in activity levels at different temperatures, with frogs in the warmer enclosures (20-25 °C) being more active in the open areas outside the cover of the leaves than those in the cooler enclosures (16-19 °C). Several studies involving ectotherms have shown that both the amplitude and phasing of activity can shift with extreme changes in temperature (Heckrotte 1975; Griffiths 1983; Ellis, Firth & Belan, 2009). In golden mantellas the phasing of the second peak was slightly later under cooler conditions and had a lower amplitude than the first peak.

The difference in intensity of activity between temperatures may be explained by general amphibian physiology and subsequent responses to temperature and humidity levels. Amphibian metabolic rates increase exponentially with an increase in temperature until their body temperature reaches its thermal optimum, above this point metabolic rate then falls until it reaches a critical thermal maximum (Duellman and Trueb, 1994). Although critical thermal minima and maxima for the golden mantella are unknown, the temperatures used here were based on those at which activity has been observed in the field so they probably lie near the centre of the thermal range. As with other amphibians then, golden mantellas are most likely thermoconformers (e.g. Rasolonjatovo et al., 2020), avoiding extremes of temperature near critical thermal minima and maxima.

Most activity was observed at temperatures of approximately 21°C to 22°C in the warm room, which may be indicative of the thermal optimum for this species and corresponds to surface body temperatures observed in the field (unpublished data). Temperatures cooler than 18°C result in lower activity levels even if humidity is above 80%. Rija et al. (2014) obtained similar results in Kihansi spray toads (*Nectophrynoides asperginis*) after they compared activity levels at different times of day, temperatures and relative humidity. Equally, a study by Köhler et al. (2011) concentrated on activity levels and optimal body temperatures for common frogs (*Rana temporaria*) and found that jump lengths peaked at an optimal temperature and shortened with a decrease in temperature. Recent research by Edmonds et al. (2020) focussing on seasonal behaviour in captive frogs found that golden mantellas maintained higher nearest neighbor distances in the warmer months during summer. The same study found that more mantellas were observed outside shelters during warmer months. Several other studies focussing on amphibians have also recorded temperature-dependent activity levels and behavior (Putnam & Bennet, 1981; Samajova & Gvozdik, 2009; Sanabria, Quiroga, Gonzalez, Moreno & Cataldo, 2013).

Our results suggest the optimum time to encounter golden mantellas is about four hours after first light at 10:00 hrs. Under warmer conditions (20°C – 25°C) a second peak in activity occurs between 13:00 and 17:00 hrs. This information will be useful to in situ conservation managers for determining the best time of day to survey mantellas, or catch individuals in order to translocate them to other areas to mitigate the potential impacts of forest loss. However, the results also showed that even under optimum conditions, usually less than half of the frogs present in the enclosures are active and visible at any one time outside the leaf litter refuges. Low levels of detectability in the field remains a challenge for cryptic species such as amphibians (Schmidt 2003; Sewell, Beebee & Griffiths, 2010; Barata, Griffiths & Ridout, 2017). Ex situ studies in which the actual number of frogs present in an enclosure is known may therefore inform the design and analyses of such field surveys. For example, if counts of mantellas in the field represent under half the frogs actually present, this has implications for estimating detectability, population sizes, and sustainable harvesting rates.

Our results demonstrate how experimental manipulation of environmental conditions in replicated enclosures can provide information on activity and microhabitat use that would be intractable to obtain in the field (Lawton, 1996). Integrating such ex situ data with that obtained in situ may provide a more holistic evidence base for conservation decision-making. The golden mantella has a very restricted range of 2,110 km^2, and modelling the potential future distribution under different climate change scenarios predicts a shift and reduction in suitable habitat to less than 7% of this area by the end of the century (Edwards, 2019). The long-term future of the species may therefore hinge on further surveys and habitat assessments identifying areas for habitat creation and management for the species, as well as the potential for assisted colonization. Understanding how golden mantellas respond to potential changes in rainfall, humidity and temperature may therefore inform the design of such future management interventions.

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Figure legends

Figure 1: Design of the Froggotron. Top, Leaves were set out to cover approximately 50% of the floor area as indicated by the shaded squares. The clear squares represent coconut matting areas on the tank floor without leaves. Bottom, two Froggotrons viewed from the public viewing gallery (leaves are in a different arrangement for a pilot study).

Figure 2: The mean 24-hour activity rhythm of *M. aurantiaca* plotted at 30 min intervals (with standard error bars) held at two temperatures and averaged over ten consecutive days. Daylight hours are between 06:15-18:15 hrs; lights are turned out fully and the tanks are in darkness at all times before and after this period and are represented by light-dark bars above each plot.

Figure 3: The total number of frogs observed outside leaves combined across all tanks over ten consecutive days in relation to a) temperature (cooler enclosures 16-19°C; warmer enclosures 20-25°C) and b) % humidity over the same time period. Data points (black dots) are fitted with a LOESS smoother (blue line) to most closely model the relationship between temperature and the total number of frogs seen. The shaded area represents a 95% confidence interval.

Conflict of interest statement.

We can confirm that there is no conflict of interest.

Data Availability Statement

We can confirm that the data that supports the findings of this study are available from the corresponding author upon reasonable request.

Figure 1: Design of the Froggotron.

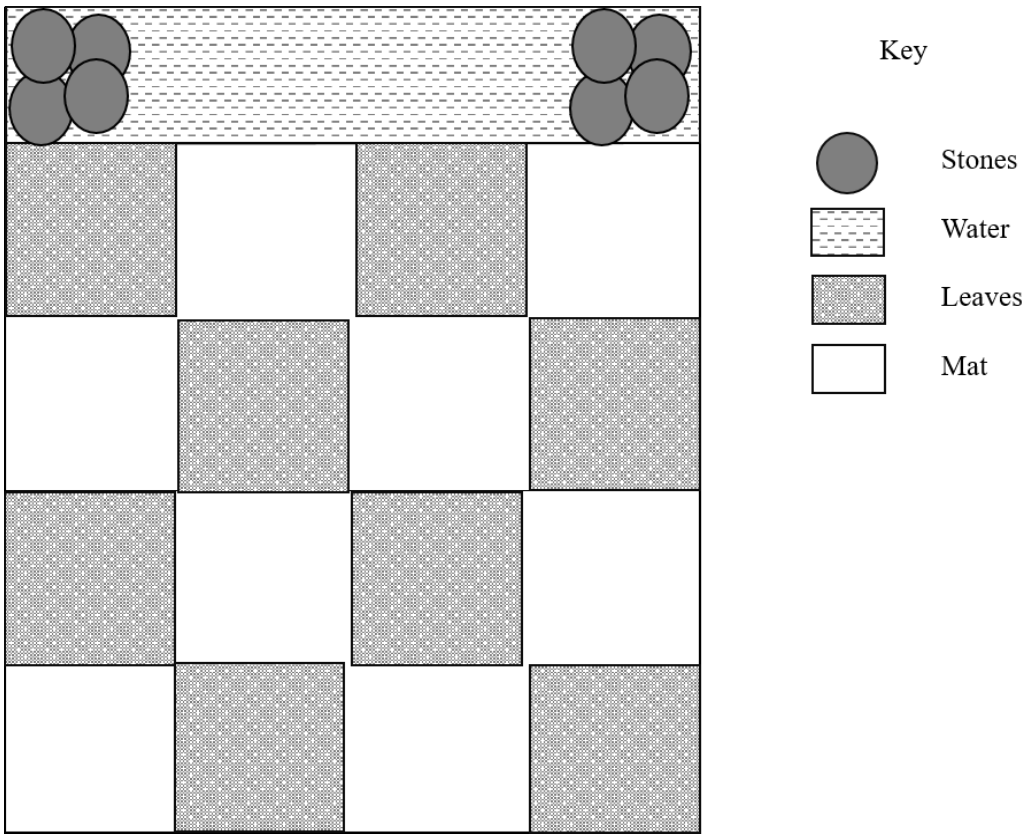
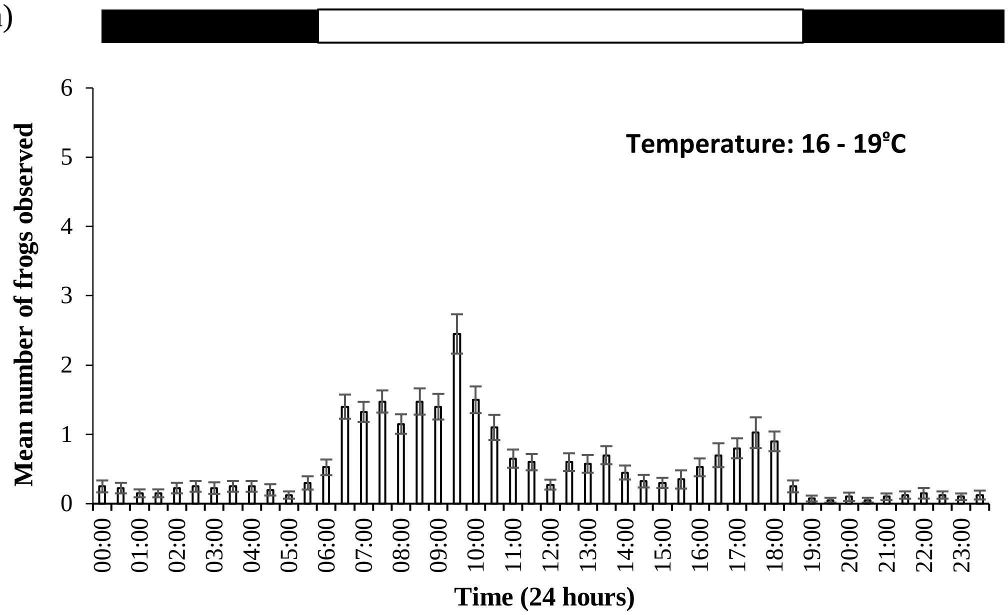


Figure 2a & b

a)



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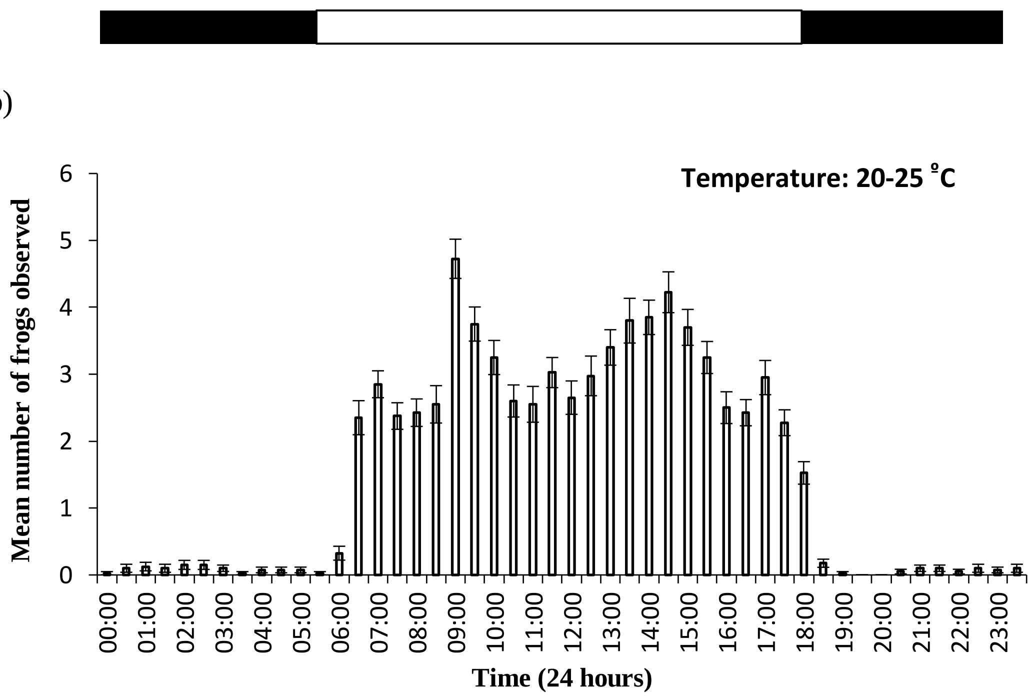
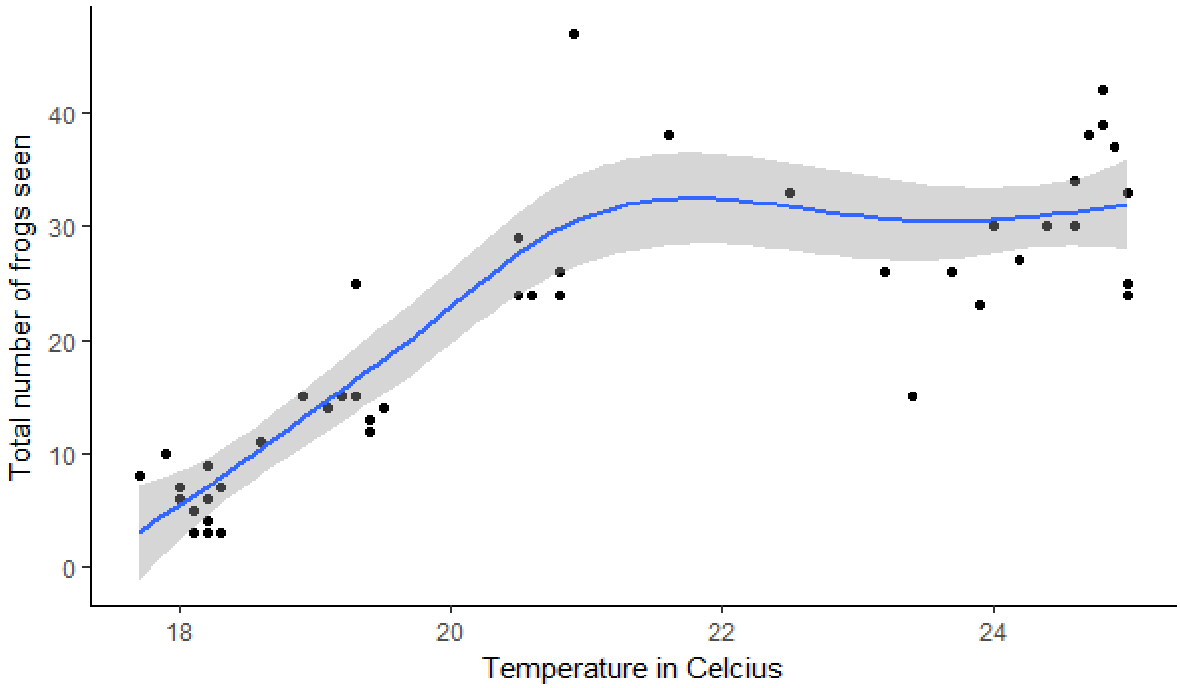


Figure 3a & b

a)



b)