Quantification of underwater calling and foraging activities in the African clawed frog *Xenopus laevis*

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Abstract. Aquatic anuran species are difficult to detect and observe and this is a major limit to the study of their behaviour and ecology. This habit limits the direct monitoring of sexual and foraging activity, and the investigation of how environmental factors influence their expression as well as how individuals allocate time between competing activities. We investigated this issue in *Xenopus laevis*, a mostly aquatic frog that forages and emits calls underwater. This model species in biology has been extensively studied in the lab but its behaviour in nature remains poorly described. We carried out a study in a pond during the breeding season in the French invasive range. We recorded underwater vocal activity as a proxy for sexual activity using a hydrophone, set food-baited traps to quantify foraging activity, and recorded environmental conditions (moonlight intensity, temperature and rainfall) over two lunar cycles. We found that individuals engage in these two activities during the breeding season. At the peak of the breeding period, vocal activity was expressed during the day. The investment in reproduction (calling activity) may reduce the time allocated to foraging on a circadian scale. The two activities seem to be partitioned depending on moonlight intensity, with a stronger effect on males. Foraging activity decreased and vocal activity increased when moonlight intensity increased. We also observed a negative effect of temperature and a positive effect of rainfall on vocal activity only. Our method is promising to monitor the activity of other aquatic anurans.

Keywords: activity pattern, amphibian, moonlight, sexual communication, time partitioning.

Introduction

Amphibians species are dependent on aquatic and terrestrial habitats at different stages of their life cycle. However, some species are exclusively aquatic or are considered as semi-aquatic when they stay in water most of their lifetime (Wells, 2007). For the most aquatic species, monitoring activities for ecological surveys or behavioural studies is challenging because of the difficulty to detect and observe individuals. In particular, aquatic anuran species emit call underwater during reproduction (Narins and Feng, 2006) while many species use aerial transmission of sound by calling from the terrestrial environment or at the water surface, which signals are more easily detected by a human observer (De Solla et al., 2006). Hence, the ecology and behaviour of such species in natural conditions is usually poorly known due to the difficulty of recording behaviour and the subsequent lack of knowledge about the environmental factors that influence the expression pattern of activities like breeding and foraging.

This is the case for pipid frogs, which are aquatic, call underwater (Yager, 1992; Tobias et al., 2010), feed within the water column (Carreño and Nishikawa, 2010), and move overland only to reach the next water body (Measey,

2016). *Xenopus laevis* is a particularly prominent example of the difficulty of studying aquatic anurans. This species has been intensively studied in the laboratory to the extent that it is considered as a biological model in developmental biology (Gurdon and Hopwood, 2003; Measey et al., 2012; van Sittert and Measey, 2016). It has also been extensively used for human pregnancy testing (Elkan, 1938; Gurdon and Hopwood, 2003). Yet, few studies have studied its behaviour in its natural environment (but see Tobias et al., 2004; Ringeis et al., 2017; Elepfandt et al., 2022). Adults stay and mate at the pond bottom (Archard, 2013; Ringeis et al., 2017) but they move across the water column up to the surface when foraging (Measey, 1998). Vocal activity is related to reproduction as calling precedes and elicits amplexus (Tobias, Viswanathan and Kelley, 1998; Ringeis et al., 2017). Calls are emitted underwater (Picker, 1980) by males and females (Picker, 1980; Kelley, 1982; Tobias, Viswanathan and Kelley, 1998; Tobias et al., 2004). The fact that individuals are commonly captured using food-baited trap throughout the breeding season (Courant et al., 2019a), suggests that they engage both in reproduction and foraging activities during this period. However, because calls are emitted underwater their detection from the terrestrial environment is very difficult. The species is so secretive that the invasive population in western France was discovered about 20 years after its introduction (Fouquet, 2001; Fouquet and Measey, 2006). Other populations have been introduced in several continents and the species is now considered as a major global invasive amphibian (Measey et al., 2016). Thus, there is a need to improve our capacity to study aquatic amphibians for a better understanding of their ecology and behaviour, and in the case of *X. laevis* for gaining insight into the biological invasions it generates.

Investigating the activities individuals are engaged into during the breeding season is of particular interest because the breeding period is time and energy consuming and many organisms need to partition time between foraging and reproduction, which includes searching for a mate, mating and laying eggs (MacWhirter, 1991; Abrahams, 1993). Some environmental parameters influence the expression of these behaviours and regulate time allocation between activities. Moonlight affects time partitioning of activity in amphibians (Vignoli et al., 2014; Onorati and Vignoli, 2017; Bissattini, Buono and Vignoli, 2020). Several studies reported more reproduction events (Vignoli and Luiselli, 2013; Onorati and Vignoli, 2017), more intense calling activity (Lima et al., 2021), increased mobility (FitzGerald and Bider, 1974; Henrique and Grant, 2019), or higher general activity (Muller, Cade and Schwarzkopf, 2018) at lower moonlight intensities. However, the effect of moonlight on amphibian activity is conflicting, with an even number of studies where activity increased or decreased during full moon, suggesting that the response depend on the species (Grant, Halliday and Chadwick, 2013). Multiple pressures such as the need for reproductive synchronization, the detection of visual signals, predation risk, efficient foraging or accurate orientation, generate species-specific trade-offs regarding the need to express them under optimal moonlight intensities (Lillywhite and Brischoux, 2012; Grant, Halliday and Chadwick, 2013; Vignoli and Luiselli, 2013). Other environmental parameters influence amphibian activities such as temperature (Oseen and Wassersug, 2002; Wells, 2007) or rainfall (Cayuela et al., 2012). Amphibians' performance, including calling activity, increases with temperature (Putnam and Bennett, 1981; Oseen and Wassersug, 2002; Navas, Gomes and Carvalho, 2008) while rainfall stimulates reproductive dynamics (Cayuela et al., 2012) and elicits vocal activity (Oseen and Wassersug, 2002; Pellet and Schmidt, 2005). Higher rainfall and temperature can allow a larger allocation of energy to breeding, and thus a reduced energy allocation to foraging. To estimate the

effects of the factors influencing energy allocation between foraging and reproduction during the breeding season, both activities need to be monitored, which requires determining in which activities individuals are engaged.

We conducted a field study to synchronously monitor the expression of vocal activity and foraging activity of *X. laevis* during the breeding season in the French invasive range. We monitored underwater calling activity as a proxy for sexual activity in the pond using hydrophones (Degregorio, Wolff and Rice, 2021). We used the number of trapped individuals in food-baited trap as a proxy of foraging behaviour, as already used in other species (Winne, 2005). We also recorded moonlight intensity, temperature and rainfall. Our objectives were to (1) describe the time patterns of vocal and foraging activities during the breeding period, (2) understand potential time partitioning between these two activities, and (3) estimate the effects of environmental parameters on the expression of these activities.

Metods

The study was carried out between 15 May 2018 and 6 July 2018 at one breeding site in Saint Martin de Sanzay (47.0808735, −0.2003814, datum WGS84). This study site lies within the core area of the invasive range in western France about 16 km away from where *X. laevis* has been introduced (Fouquet and Measey, 2006). It is a wastewater treatment unit made of three shallow ponds of 1 m deep on average. Two ponds about 10 meters apart were used to monitor vocal and foraging activity. They each cover an area of 2250 m^2 and host a dense aquatic vegetation and a high density of individuals. As a control action against the dispersal of this invasive species, the ponds were fenced with wire mesh on 4 April to prevent emigration or immigration of *X. laevis*. We set traps on 35 nights using submerged funnel traps (60-cm length × 30-cm width × 6-mm mesh diameter), with floats to avoid the drowning of individuals. We used baited traps with dry dog food so that the number of individuals caught reflect the intensity of foraging activity. Five evenings a week, two traps were set between 2000 h and 2100 h, just before sunset, and collected the next morning between 09:00 h and 10:00 h. Individuals were sexed and counted, the sex ratio computed (number of males/number of males and females), and then released. On the next evening, the traps were set 48 meters away from the location of the previous night, which allowed to trap another

part of the pond. Completing the perimeter of the pond took one week. Then, the traps were placed in the other pond.

To monitor calling activity, our proxy for sexual activity, we used a hydrophone (HTI-96-min/SSQ; sensitivity: –165 dB à 240 dB; frequency range: 2 Hz to 30 kHz, High Tech, Inc, Long Beach (MS), USA) connected to a recorder SM4 (Wildlife Acoustics, Maynard (MA), USA). The hydrophone was plunged in the water about 2 meters from the bank and rested about 20 cm above the pond bottom. Like for trapping, the location of the hydrophone was shifted by 48 meters every evening to sample the entire pond perimeter. The hydrophone was always placed in the pond not used for trapping, so that trapping would not interfere with the spontaneous vocal activity. We recorded vocal activity for 30 minutes every hour for 35 days. The audio files were scanned by hear for 5 seconds-periods at minutes 1, 9, 19, 29 of each hour, and the occurrence or absence of *X. laevis* call was noted for each of these four observation periods. We tallied the number of hours for which calls were detected during at least one period (vocal activity).

The study encompassed two lunar cycles (see supplementary fig. S1). We calculated moonlight intensity by adapting the formula given in Lozano and Zapata (2003). T × A × I where **T** is the proportion of night hours in which the moon is above the horizon, **A** is the maximum altitude reached by the moon each night as proportion of the maximum possible altitude and **I** is the proportion of full moon visible. However, we used an estimation of moonlight intensity (Nowinszky et al., 1979) rather than the initial variable A. The rationale is that the relationship between moon brightness and the proportion of full moon visible is not linear, especially during the moon surge that is the sharp increase in brightness at full moon (Nowinszky et al., 1979; Buratti, Hillier and Wang, 1996). This way we could consider both the extent of time moon is visible and its brightness. Data for computing T and A were retrieved from the Astrosurf website (http://www.astrosurf.com/c2a/). Cloud cover can be another important predictor of nocturnal activity in some amphibians (FitzGerald and Bider, 1974; Vignoli and Luiselli, 2013; Onorati and Vignoli, 2017). To better approximate how much light intensity reached the pond surface, we estimated cloud cover using data available on the Meteociel website (http://www.meteociel.fr/). On each date, we recorded nebulosity scores (in okta) for each night hour and computed mean nebulosity for each night. Because rainfall is expected to influence general activity in amphibians (Wells, 2007), we also recorded precipitations (mm). Finally, temperature is known to strongly affect activity patterns in amphibians (Wells, 2007; Muller, Cade and Schwarzkopf, 2018; Henrique and Grant, 2019) and warmer temperatures were suggested to favor reproduction in *X. laevis* (McCoid and Fritts, 1989). Throughout the study, we recorded water temperature every 30 min using data loggers (Hobo, Pendent Temp/Light 64 k, Onset) at 10 cm below the surface, and computed daily mean water temperature. Because temperature was strongly correlated with date, we used the residuals of the linear regression of temperature against date (supplementary fig. S2) to obtain the deviation from the expected value at a given date, hereafter referred as temperature deviation.

Data analysis

We analysed the circadian vocal activity of *X. laevis* during the whole study period by calculating for each hour of the day the probability of detecting calls, i.e., the number of days when call was detected over the total number of days of survey. We then tested the effects of moonlight intensity, lunar cycle as a factor (first, second), nebulosity, temperature deviation, and rainfall on foraging (number and sex ratio of trapped individuals) and calling activity (vocal activity). Correlation coefficients between predictors should be less than 0.7 (Quinn and Keough, 2002). We checked that this criterion was met (Pearson correlation: $r < 0.5$). For calling activity we used a quasibinomial linear model as the vocal activity dependent variables are bounded (between 0 and 24 h). For foraging activity, we used a negative binomial regression to account for the over-dispersion of our count data (Bolker et al., 2009; Zuur et al., 2009). These two types of regression were chosen after an analysis of dispersion, evaluated as the ratio of the residual deviance to the number of degrees of freedom, and by checking homoscedasticity of residuals. We also investigated the effect of environmental predictors on foraging activity of each sex. We computed a binomial GLM using the sex ratio of trapped individuals as response variable, and negative binomial GLMs on count data of males and females. In all our full models, we included the three interactions between lunar cycle and moonlight intensity, lunar cycle and nebulosity, and moonlight intensity and nebulosity. Temperature deviation and rainfall were included as main effects only as we did not expect a strong interaction with the cycle and to keep a reasonable number of predictors regarding our sample size. We carried out a backward model selection using F or Likelihood-ratio tests (Bolker et al., 2009; Zuur et al., 2009). We represented effects of the retained variables in the best models, using the ggeffects package. Because our study encompasses the peak of the breeding season (Courant et al., 2017a), and to visualize the raw data, we also represented vocal activity, foraging activity, and sex ratio of captures, against the date. Data analysis and representations were performed using R 3.5.1 (R Core Team, 2018) and Rstudio v1.1.419.

Results

Vocal activity was detected every day of the survey and lasted between 1 and 24 hours (mean $\pm$ SD = 10 h47 min $\pm$ 5 h44 min). Using these data, we estimated the diel calling activity of *X. laevis*. It followed a circadian rhythm with a higher probability of call detection during night hours, between 2100 h and 0500 h, and a peak around 0100 h (fig. 1). Calling was low in the afternoon and at its lowest around 15:00 h.

Raw vocal activity showed that the activity peak clearly matched the full moon of day 150 on May, 30 (fig. 2A, supplementary fig. S1), and vocal activity then decreased during the second lunar cycle (fig. 2A, supplementary fig. S1). The best model for vocal activity retained the interaction between lunar cycle and moonlight intensity ($F_{1,30} = 27.655$, $P < 0.001$), temperature deviation ($F_{1,30} = 5.491$, $P = 0.026$), and rainfall ($F_{1,30} = 7.328$, $P = 0.011$). Vocal activity increased with moonlight intensity during the first lunar cycle but showed a more complex pattern during the second cycle (fig. 3A, table 1). In fact, the effect of moonlight intensity on calling activity varied between cycle 1
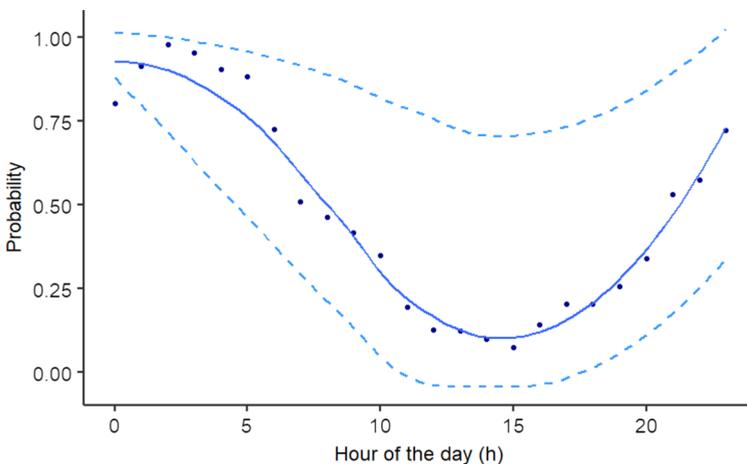

Figure 1. Circadian variation of the probability of call detection in *Xenopus laevis* (solid line). Standard errors of the mean are indicated as dotted lines. The lines highlighting the diel variation has been computed using a polynomial regression.
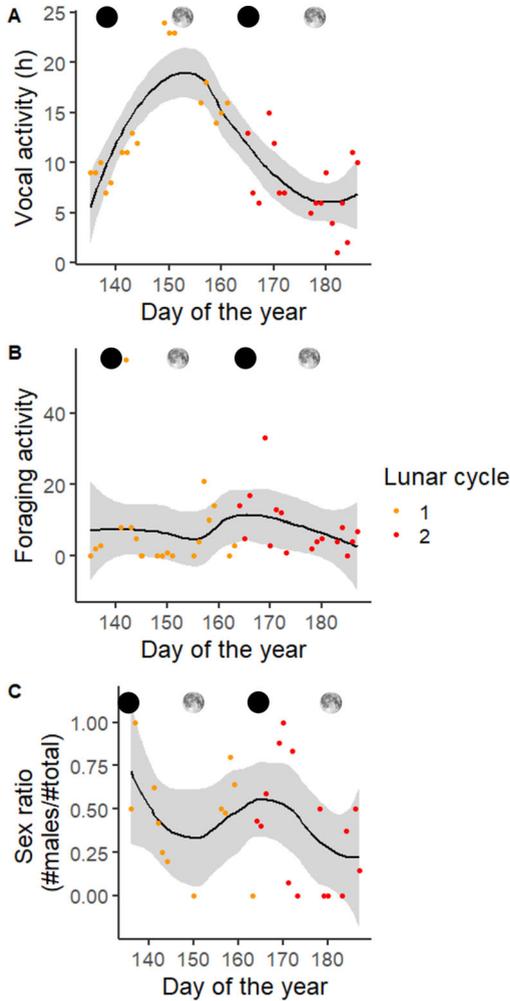
Figure 2. Variations of A) Vocal activity, B) Foraging activity as estimated as the number of animals captured in food baited traps and C) sex ratio of captures (number of males/ total number of individuals), during the study period, according to date and lunar cycle with points for observed values, and 95% confidence interval around the mean estimated from the best model.

Figure 3. Effects of moonlight intensity, along with lunar cycle, on A) Vocal activity, B) Foraging activity as estimated as the number of animals captured in food baited traps and C) sex ratio of captures (number of males/ total number of individuals), with points for observed values, and 95% confidence interval around the mean estimated from the best model.

and cycle 2. If, in the first cycle, the effect was large, it was much reduced in the second one. Overall, moonlight intensity had a positive effect on vocal activity during the whole study period (table 1). Moreover, vocal activity decreased with increasing water temperature deviation, and increased with increasing precipitations (table 1).

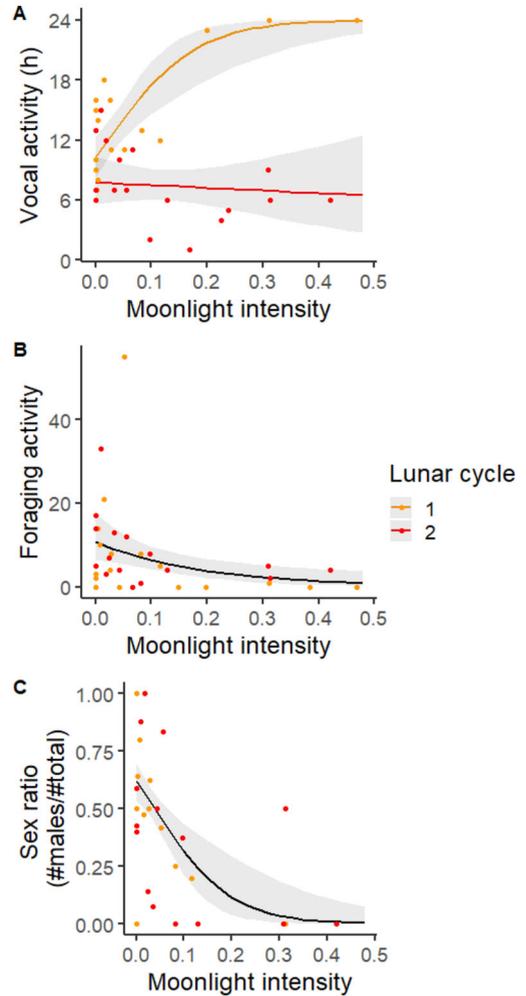Regarding foraging activity, we set baited traps on 35 nights and captured 266 individuals (132 males and 134 females) on 27 nights during the survey period (8 nights with no trapped individuals). The number of trapped individuals varied from 0 to 55 (mean ± SD = 7.80 ± 10.91) and reached maximal value during the new moon of each lunar cycle (fig. 2B). The best model for the number of trapped individuals included only moonlight intensity (LRT = 6.066, $P = 0.019$) (fig. 3B, table 1). Foraging activity, as indicated by the catch rate, decreased

Table 1. Effect of moonlight intensity, lunar cycle, nebulosity, temperature deviation and rainfall, on the vocal and foraging activity of *Xenopus laevis* as estimated from best generalized linear models after backward selection.

Response variable	Predictor	Coefficient	SE	t/Z	p
Vocal activity	*Lunar cycle*	−0.451	0.277	−1.631	0.114
	Moonlight intensity	39.306	9.780	4.019	<0.001
	Lunar cycle x Moonlight intensity	−13.281	3. 313	−4.009	<0.001
	Temperature deviation	−0.227	0.095	−2.395	0.024
	Rainfalls	0.050	0.018	2.716	0.011
Trapped individuals (#)	*Moonlight intensity*	−5.089	1.734	−2.936	0.003
Sex ratio	*Moonlight intensity*	−12.573	3.418	−3.678	<0.001
	Nebulosity	−0.25	0.124	−2.016	0.044
Trapped males (#)	*Moonlight intensity*	−10.86	3.508	−3.095	0.002
Trapped females (#)	*No minimal model*			−	

with moonlight intensity regardless of the lunar cycle considered. No effects of the cycle, cloud cover nor the interaction between cloud cover and cycle were detected. A similar result was observed for the sex ratio of captures. The best model retained moonlight intensity (LRT = 26.369, $P < 0.001$) and nebulosity (LRT = 4.232, $P = 0.040$). The sex ratio (number of males over the total number of individuals) of trapped individuals decreased with moonlight intensity and reached a minimum during the full moon of each cycle (figs 2C, 3C, table 1). This result is explained by the fact that the number of captured males was only dependent on moonlight intensity in the best model (LRT = 10.308, $P = 0.004$), and decreasing with moonlight intensity (supplementary fig. S3, table 1). In contrast, no predictor significantly affected the number of trapped females, and no minimal model was therefore retained (supplementary fig. S3, table 1). We also observed a marginal effect of nebulosity on sex ratio (LRT = 4.232, $P = 0.040$). However, this factor did not influence foraging activity of either sex (table 1).

Discussion

We synchronously monitored calling and foraging activities of *Xenopus laevis*. Our results suggest that the two activities are partitioned during the breeding period. Moreover, moonlight intensity had opposite effects on foraging and sexual signalling (vocal activity) as foraging activity decreased and vocal activity increased when moonlight intensity increased. The latter effect was not strongly consistent across the whole breeding season and may be restricted to the reproduction peak. We also observed a negative effect of increasing temperature, and a positive effect of rainfall, on reproduction only, as these factors did not influence foraging activity.

Vocal activity reached a peak on late May-early June consistent with the timing of reproductive organ growth in this population (Courant et al., 2017a). Field and lab studies have observed that *X. laevis* is mostly diurnal and that calling occurs at night. (Ringeis, 1997; Tobias, 2004). We found that calls were emitted throughout the day. To the best of our knowledge, we provide the first quantification of the circadian pattern of vocal expression in field conditions. Most amphibians species call primarily at night (Oseen and Wassersug, 2002) and the breeding activity of *X. laevis* is believed to occur from dusk to midnight in its native range in Southern Africa (Ringeis et al., 2017). Females are shown to be mainly active at night under laboratory conditions, searching for refugia during the day (Archard, 2013). But in western France, individuals can be very active during the day. Contrary to Ringeis et al. (2017),

we did not observe nights without calling activity. These discrepancies reveal a strong flexibility in the time budget allocated to sexual activity and may reflect an opportunistic calling behaviour (Elliott and Kelley, 2007; Xu et al., 2012), dependent on local conditions. The frog density in our site was much higher than in Ringeis et al. (2017) and sexual signalling behaviour may differ between the invasive and native range because of environmental factors such as temperature or predation risk. Foraging activity also varied with date and its peak lagged behind the vocal activity peak, which suggests some partitioning of activities even if both occurred during this period.

Moonlight intensity had a depressing effect on foraging and an enhancing effect on vocal activity. Frogs were more frequently trapped during darker nights (suggesting a higher foraging activity) and this effect depended on sex. The sex ratio of trapped individuals decreased with moonlight intensity, due to the lower number of trapped males, while the number of females remained constant. The difference between sexes was maximal at full moon and minimal at new moon. Because sex ratio is generally balanced in ponds (Elepfandt et al., 2022), we hypothesize that this was caused by the change in time budget of males which enhance calling activity under high light intensity. In contrast, females may need to feed more regularly as fasting reduces oocyte production (Holland and Dumont, 1975; Green, 2002). Unlike males that can stop feeding and spend more time in sexual signalling, fasting may not be used to increase fitness in females.

The positive effect of moonlight intensity on vocal activity was supported statistically but it was mainly found during the first lunar cycle of the study. This may be due to the fact that egg laying mostly occurred during the calling peak (Ringeis et al., 2017). Our results should be interpreted with caution, as one main shortcoming of our study is the duration of the monitoring period limited to one breeding season and

two lunar cycles. Extending the study over several years would ensure that the co-occurrence of full moon and the vocal activity peak is not coincidental. There is contrasting evidence of the effect of moonlight on activity budget in amphibians (Grant, Halliday and Chadwick, 2013). However, most studies have evaluated the effect of the lunar cycle on either reproductive activity (Vignoli and Luiselli, 2013; Onorati and Vignoli, 2017) or general activity (FitzGerald and Bider, 1974; Muller, Cade and Schwarzkopf, 2018; Henrique and Grant, 2019). Because we synchronously monitored these two activities, we provide preliminary evidence that the lunar cycle dynamically affects both activities in different ways, and may induce a time partitioning between breeding and foraging.

Four non-exclusive hypotheses may explain the opposite responses of vocal and foraging activity to moonlight. First, high moonlight intensity may facilitate sexual interactions so that individuals allocate more time mating if it is easier to locate and assess potential partners (see Byrne, 2002). Moonlight can also be used as a clock (Kronfeld-Schor et al., 2013) that maximizes the pool of adults reproducing at the same time (Onorati and Vignoli, 2017). The full moon synchronizes breeding in some fish and amphibian (Takemura et al., 2006; Ikegami et al., 2014). Indeed, in some anurans, it has been shown that moon phase influences parameters of sexual activity such as arrival to the breeding ponds, amplexus and spawning events are more frequent at full moon (Grant, Chadwick and Halliday, 2009). Second, high moonlight intensity may increase predation risk (Grant, Halliday and Chadwick, 2013). Adults move up the water column when foraging (Courant et al., 2018b) so that they are likely more exposed to predation when engaged in foraging than in sexual activity. Foraging on darker nights may reduce predation risk while sexual activity might be less constrained by predation risk due to the position of the frogs deeper in the pond. Invasive populations are often less exposed to predators (Colautti et al., 2004) but some native

mammals, amphibians or birds may prey on *X. laevis* (Lobos and Jaksic, 2005; Tinsley et al., 2015; Mora et al., 2016). Third, insects are a major component of *Xenopus laevis*' diet (Courant et al., 2017b, 2018b), and the activity of many insect species is related to the lunar cycle (Nowinszky et al., 1979; Nirmal et al., 2017) with a peak during the new moon, which is interpreted as an anti-predator strategy. Thus, frogs may spend more time foraging on darker nights when prey availability is likely higher. Lastly, as suggested above, the peak between maximal vocal activity and moonlight intensity could be coincidental, and the effect of moonlight intensity on both foraging and vocal activities need to be investigated across a longer study period.

Temperature was expected to influence vocal and foraging activity (e.g., Navas, Gomes and Carvalho, 2008). It was strongly correlated with date (supplementary fig. S3) and its seasonal variation may influence the timing of the breeding season. However, on a daily scale, individuals experience small variation in ambient temperature, and its effect may be higher across a longer time scale, i.e., when individuals experience higher temperature variations. Consistently, we found no effects of temperature deviation on foraging activity. However, breeding activity significantly decreased with water temperature deviation. Such a result suggests that the optimal temperature range is narrower for breeding, due to constraints on egg and larval development, than for foraging and that temperature was close to the optimal breeding temperature, and to the median thermal preferendum of the species (i.e., 22°C, see OECD, 2008; Casterlin and Reynolds, 1980). In addition, we found that rainfall positively influenced vocal activity, a logical finding as rainfall creates breeding habitats within the Mediterranean and semi-arid climates of its native range. Generally, rainfall stimulates activity (Wells, 2007) and influences reproductive dynamics (Cayuela et al., 2012) in amphibians. We have not measured light level at the pond surface, but we approached it

by including the interaction between moonlight intensity and cloud cover in our models. We found that neither cloud cover nor its interaction with moonlight intensity was a major predictor of activity. This result is consistent with those of a previous study (Courant et al., 2019), that also showed that cloud cover did not predict overland movements in *X. laevis* unlike moonlight intensity.

Very few studies have described the behaviour of *Xenopus laevis* in nature (but see Tobias et al., 2004; Ringeis et al., 2017; Elepfandt et al., 2022). We could monitor the vocal and foraging activity of this secretive amphibian. Our approach is useful for an aquatic species that can occur in turbid (Lobos et al., 2013), vegetated (Courant et al., 2018a), or deep ponds (Tinsley et al., 2015). It could also be used for other pipid species (Yager, 1992; Tobias et al., 2010), or other aquatic anurans (Narins and Feng, 2006). Our study provides insight into the influence of the lunar cycle on the regulation of time partitioning in these secretive amphibians, but should be taken with caution, as it was conducted on one single year at one breeding site. Further research is required to understand the interaction between sexual and foraging activities and how the moon cycle may alter it. This could be achieved by coupling the monitoring of activities in breeding sites over several years to an experimental approach. For instance, a mesocosm study could estimate the change in time partitioning of individuals exposed to predation risk and light intensities corresponding to different moonlight intensities under a tighter control of other environmental variables. This research has practical conservation interest too. *Xenopus laevis* is one of the most harmful amphibian invaders (Measey et al., 2016), and many invasive populations are expected to broadly expand (Ihlow et al., 2016; Ginal et al., 2021). A better understanding of how environmental factor affects the frog's behaviour may improve the efficiency of actions undertaken to control its invasive populations, for instance by setting traps when capturability is the highest.

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