

Management in Practice**Effects of conspecific lures, call playbacks, and moonlight on the capture rate of *Xenopus laevis*, a major invasive amphibian**Léa Lorrain-Soligon¹, Théo Cavin¹, Avelyne S. Villain², Emilie C. Perez², Darcy B. Kelley² and Jean Secondi^{1,3,*}¹Faculté des Sciences, Université d'Angers, 49000 Angers, France²Department of Biological Sciences, Columbia University, New York, N.Y. 10027 USA³Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR5023 LEHNA, F-69622, Villeurbanne, FranceAuthor e-mails: jean.secondi@univ-angers.fr (JS), lea_lorrain-soligon@outlook.fr (LLS), cavintheo@gmail.com (TC), avelyne.sylvie.villain@gmail.com (ASV), perezemilie@gmail.com (ECP), dbk3@columbia.edu (DBK)

*Corresponding author

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OPEN ACCESS**Abstract**

Given the status of the African clawed frog *Xenopus laevis* as a global amphibian invader, and the potential spread of its invasive populations in Europe and other continents, it is essential to identify the environmental factors and methods that maximize the trapping output of control actions. Cost-effective methods should maximize the number of trapped individuals, and preferably the number of females. We tested five types of attractants in traps, split into two categories: playbacks and conspecific lures, and compared their efficiency in terms of number of trapped individuals (total, females, and males) against the control method currently in use in France (use of food bait). We also estimated the influence of moonlight, an environmental factor known to affect amphibian activity. Playback methods did not increase the capture probability for either sex. In contrast, using a female as a lure allowed us to trap both more individuals (224% compared to the control), more females (186%) and more males (190%), whereas using a male only allowed us to trap more males (167%). These effects were stronger under low moonlight intensity, and at the end of the breeding season. Using female lures appeared to be the best method, both due to a higher number of trapped individuals and a higher number of trapped females. Our study also emphasizes the need for considering the influence of the lunar cycle when planning fieldwork to optimize the cost-efficiency of control actions. We recommend to preferentially set traps under low moonlight intensities.

Key words: control method, trapping, attractant, playback, lunar cycle, African clawed frog

Introduction

Aquatic ecosystems, which are among the most diverse on Earth (Dudgeon et al. 2006), are particularly sensitive to biological invasions (Cox and Lima 2006). The African clawed frog (*Xenopus laevis*) is considered to be one of the three most harmful amphibian species impacting these ecosystems (Measey et al. 2016). Developing efficient capture techniques is an important conservation issue to protect native communities in colonized areas and avoid the further spread of invasive populations. Native to southern Africa, the frog has been exported worldwide (Sittert and Measey 2016) and

introduced in France where the expanding population now covers about 4000 km² (Vimercati et al. 2020) and its range is expected to extend (Ihlow et al. 2016). The species is a major predator of the pond ecosystem and affects particularly amphibian and invertebrate communities (Courant et al. 2017b). Control strategies should thus be implemented to manage its invasive populations to reduce their ecological impacts, but this has proven to be difficult where the species is well established (Mora et al. 2019). In France, control actions have been undertaken and, as in other countries (see Mora et al. 2019), these control actions could not achieve eradication. In fact, eradication remains difficult for widespread populations (Shine and Doody 2011), like those of *X. laevis*. Some methods such as seine netting were found to be effective (De Villiers et al. 2016) but are not widely applicable to all contexts and may cause damages to the ponds. Therefore, improving capture methods for this species remains an issue, particularly in areas of high ecological value. Technical solutions should maximize the number of captured individuals for a given capture effort (Yeager et al. 2014; Muller and Schwarzkopf 2017). Trapping with food baits is the standard method in use in France. However, the number of captured individuals is not constant over time which suggest that unidentified environmental factors influence capture rates. Moreover, and as far as we know, interactions between males and females have never been considered in the design of control methods for this species. Studies conducted with other amphibian invaders, such as *Rhinella marina* (Yeager et al. 2014; Tingley et al. 2017) and *Lithobates catesbeianus* (Snow and Witmer 2011), suggested that equipping a trap with a live conspecific may increase the probability of capture. For *Rhinella marina*, it was also proved that an acoustic lure improved trapping efficiency (Schwarzkopf and Alford 2007; Muller and Schwarzkopf 2017; Tingley et al. 2017; Muller et al. 2018). In *X. laevis*, the two sexes are actively involved in mating and emit calls (Picker 1980; Tobias et al. 1998). A phonotactic response to calls can be triggered, either with natural or synthesized calls (Picker 1980; Wang et al. 2010). We thus hypothesized that the use of conspecific individuals or call playbacks would improve capture efficiency. Maximizing the number of trapped females is a desirable characteristic of any trapping method designed to reduce the reproductive output of a population (Yeager et al. 2014; Tingley et al. 2017). Therefore, identifying such methods is a priority for the control of invasive populations.

Environmental factors, such as moonlight intensity, which is known to influence the trapping of insects (Nowinszky et al. 1979; Nirmal et al. 2017), fishes (Jatmiko et al. 2016), amphibians (Deeming 2008), and their activity (Grant et al. 2013), could also modulate the activity of *X. laevis* and influence its capture probability. Moreover, because trapping usually occurs during the breeding season, date should be considered because individuals may be less active at the end and/or at the beginning of the breeding period

Table 1. Six trapping method treatment groups for *Xenopus laevis* and number of trapping nights (n).

Attractant	Treatment	n	Description
Food	Control	42	Dog food as bait
Conspecific lures	Female lure	42	one live female as a lure
	Male lure	42	one live male as a lure
Conspecific calls	Male calls	15	playbacks of male calls
	Female calls	16	playbacks of female calls
	Chorus calls	15	playbacks of a mix of male and female calls

than at its peak. These parameters should thus be considered when scheduling capture sessions to target the optimal periods for trapping.

In this study, we trapped at a single high-density site of *X. laevis* for two months during the breeding season and compared several trapping methods, namely playbacks of conspecific males and females and live adult lures of either sex, to the current standard method which use food baited traps. We also estimated the effect of date, as the study encompassed the peak of breeding in *Xenopus laevis* (Courant et al. 2017a), and moonlight intensity on trapping efficiency, estimated as the number of trapped individuals and with a particular focus on the number of captured females. Methods that remove a higher number of females are considered more desirable because of their stronger effect on population vital rates.

Materials and methods

The study was conducted between 4 May 2018 and 6 July 2018 in the French invasive range in the Deux-Sèvres department in Saint Martin de Sanzay (47.0808735, -0.2003814, WGS84), where *X. laevis* is now established. Earlier investigation revealed that the study site hosts a large population of several thousand individuals. We trapped two wastewater treatment unit ponds, 2250 m² each and situated 10 meters apart. The ponds had been fenced with wire mesh on 4 April 2018 to prevent emigration or immigration. The experiment lasted 64 days and yielded data for 46 days of capture. Capture was performed using standard submerged funnel traps (60-cm length × 30-cm width × 6-mm mesh diameter) (Yves Roudier, Brie-sous Mortagne, France), with floats to avoid the drowning of individuals. Five treatments were tested in addition to the control. The control treatment was traps baited with dry dog food (Food bait, approx. 100 g, Frolic®, Mars, McLean (VA), USA), which is the standard trapping method in France for this species. The other treatments tested five types of attractants in traps. First, we placed one adult *X. laevis*, either a single female (Female lure treatment) or a single male (Male lure treatment), in individual traps. These two treatments were tested for 42 nights (see Table 1). Additionally, we tested three playback treatments by broadcasting conspecific calls underwater overnight. We either used male advertisement calls (Male calls treatment) which are intended to attract females and signal dominance (Picker 1980; Tobias et al. 2010), rapping calls (Female calls treatment)

expressed by receptive females (Tobias et al. 1998), or a chorus constituted of male and female calls (Chorus calls treatment) (see Supplementary material Appendix 1). We used an underwater speaker AQUA 25 (Bandwidth: 80–20000 Hz; Power: 30 W; Nominal sound power: 105 dB; Fase, Aix-les-Mille, France) powered by an amplifier BST NOMAD12UHF (Bandwidth: 30–20000 Hz; Power RMS: Max 200 W / 400 W; Lotronic, Saintes, Belgium). This speaker was placed underwater 30 centimeter away from the traps and 20 centimeter above the pond bottom. A single playback type was played on a given night, and another playback type was randomly selected to be played on the next night during the duration of the experiment (female calls $n = 16$; male calls $n = 15$; chorus calls $n = 15$) (see Table 1).

Four evenings a week, between 20:00 and 21:00, four pairs of traps were placed 12 meters apart in a pond, each pair corresponding to one stimulus type (food bait, female lure, male lure, or either female calls/male calls/chorus calls). The spatial arrangement of stimuli was changed each evening so that the order would have no influence on the results. On the next evening, the position of the traps was shifted 48 meters to trap a new part of the pond. This way, the whole perimeter of the pond was trapped in a week (Appendix 2). The traps were then placed in the other pond. The traps were collected every morning between 09:00 and 10:00, the captured individuals were sexed and counted. All individuals were then released, but two males and two females were kept as live lures stimulus for the next evening. Moonlight intensity was estimated according to Nowinszky et al. (1979), who estimated relative moon brightness as a function of the phase angle of the moon.

We analyzed the number of trapped individuals (total, females, or males) using generalized linear models with negative binomial distribution of errors. Model diagnostics were carried out by checking overdispersion of residuals. Trapping method, moonlight intensity, and date (coded as the number of days since 1 January) were considered as fixed effects. The full models included all main effects and two-way interactions. We included interactions with date because the study period encompasses the breeding period during which activity levels of individuals may change in opposite ways, and because moonlight intensity is not linearly related to date. Interactions between moonlight intensity and the trapping methods is expected as moonlight influences different activities (breeding, foraging) in amphibians and our methods target different activities (food or sexual calls). Predictors showed a moderate level of correlation (Pearson correlation test, $p < 0.236$) avoiding severe collinearity issues (Quinn and Keough 2002). The best model was selected using a backward selection procedure using likelihood-ratio tests. To test planned comparisons between the control method and each treatment, we applied a Dunnett test using the *multcomp* R package (Bretz et al. 2011). For each method, we also tested if number of trapped individuals differed from the number of captures obtained with

Table 2. Mean trap capture rates of *Xenopus laevis* for the total number of trapped individuals, females, and males, with standard error, for six trap treatment types with number of trapping nights (n).

Method	n	Trapped individuals \pm SE	Trapped females \pm SE	Trapped males \pm SE
Food bait	42	6.81 \pm 3.17	4.41 \pm 2.10	4.53 \pm 2.37
Male calls	15	6.93 \pm 5.14	4.64 \pm 4.13	4.82 \pm 2.89
Female calls	16	9.50 \pm 9.22	6.63 \pm 6.06	7.18 \pm 7.62
Chorus calls	15	10.67 \pm 12.55	7.69 \pm 8.48	4.62 \pm 6.16
Male lure	42	10.05 \pm 3.21	3.81 \pm 1.74	7.59 \pm 2.54
Female lure	42	15.26 \pm 5.74	8.24 \pm 4.50	8.63 \pm 2.99

the control method (food baited traps), using the *jtools* R package, allowing us to calculate confidence intervals. A difference was considered to be significant when 95% confidence intervals of two groups did not overlap. Data analysis were performed using R 3.5.1 (R Core Team 2020) and RStudio v1.1.419.

Results

Summaries of the total number of individuals, number of males, and number of females trapped using each method are presented in Table 2 and Figure 1. For the total number of trapped individuals, the best model included method and moonlight intensity (Table 3). Neither date nor its interaction with moonlight intensity were retained. Trapping efficiency differed significantly between methods (Table 2, Figure 1A). The method using a female as a lure trapped significantly more frogs than the control method (Dunnett post hoc test: estimate = 0.85 \pm 0.26, $z = 3.25$, $p < 0.01$) (Figure 2, Table 3). Overall, trapping with a female lure caught on average 15.26 individuals each night compared to 6.81 when using food baited traps (Figure 1A, Table 2), which is 224% of the control capture rate, or a factor of 2.24. For all other methods, we observed no differences from the control (all $p > 0.1$) (Figure 2). Moreover, the number of trapped individuals significantly decreased with moonlight intensity (estimate = -1.662 , SE = 0.360, $z = -4.611$, $p < 0.001$) (Figure 3).

Considering each sex separately, the number of trapped females was influenced by the method, moonlight intensity, and date (Table 3). We trapped more females than with the control method when using a female lure (Dunnett post hoc test: estimate = 0.64 \pm 0.27, $z = 2.67$, $p = 0.03$) (Figure 2). Overall, trapping with a female lure caught on average 8.24 females each night compared to 4.41 for the food baited traps (Figure 1B, Table 2), which is 186% of the control capture rate. We also trapped more males than with the control method when using a female lure (Dunnett post hoc test: estimate = 0.73 \pm 0.26, $z = 2.82$, $p = 0.01$) (Figure 2), capturing on average 8.63 males each night compared to 4.53 for the food baited traps (Figure 1C, Table 2), which is 190% of the control rate. Moreover, the method using a male as a lure also trapped significantly more males compared to the control (Dunnett post hoc test: estimate = 0.66 \pm 0.26, $z = 2.52$, $p = 0.03$) (Figure 2), capturing on average 7.59 males each night compared to 4.53

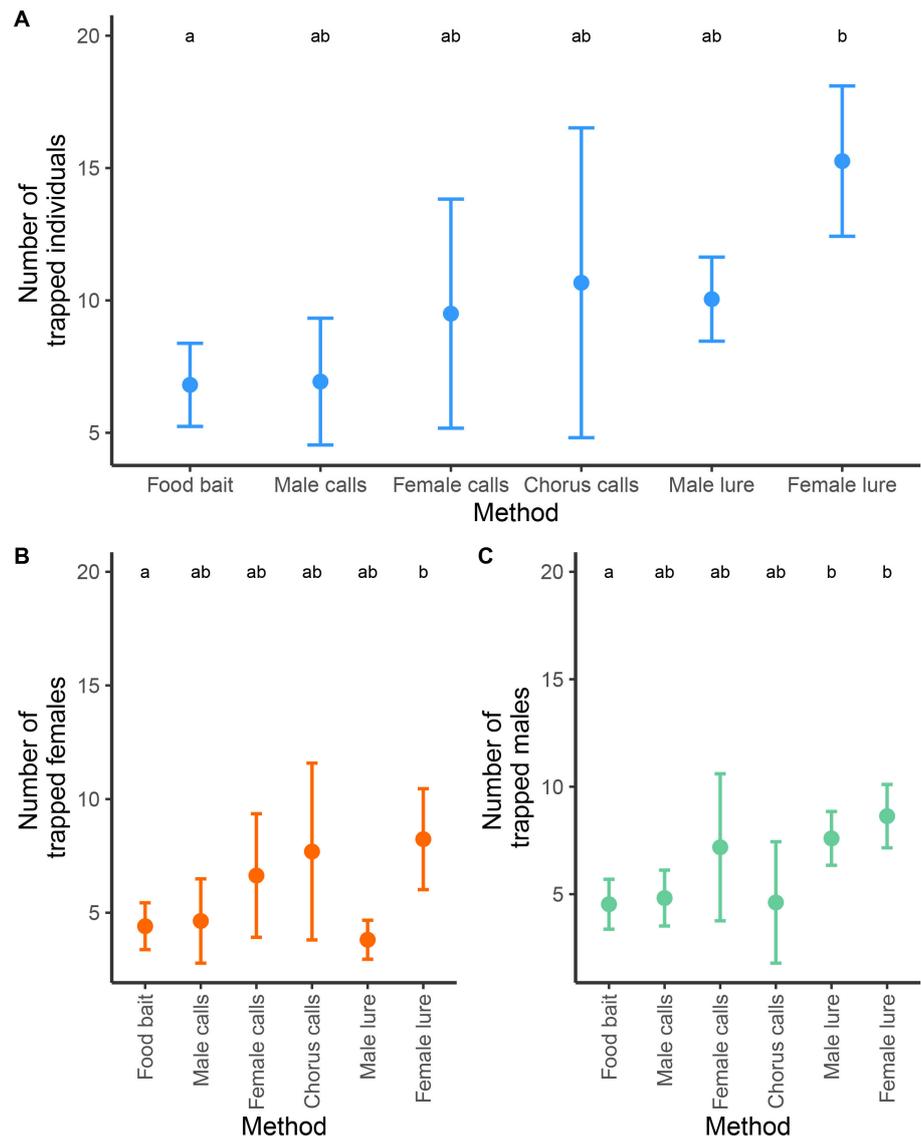


Figure 1. Influence of trapping method on (A) the total number, (B) the number of females, and (C) the number of males of *Xenopus laevis* trapped per night, mean \pm standard error. Different letters represent a significant difference between two groups at $\alpha = 0.05$ (see results). Note that raw data are represented and not the estimates for the partial effects of generalized linear models.

for the control method (Figure 1C, Table 2), or 167% of the control rate. However, this method did not increase either the total number of trapped individuals, or the number of trapped females (Figure 1C, Table 2).

Trapping efficiency for each sex also differed with environmental parameters. The number of females decreased when moonlight intensity increased (estimate = -0.904 , SE = 0.413 , $z = -2.190$, $p = 0.029$), the number of trapped females being higher at lower moonlight intensities (Appendix 3). Trapping numbers tended to increase with date also (estimate = 0.012 , SE = 0.005 , $z = 2.292$, $p = 0.022$). For males, the number of captures was influenced by the method and the interaction between moonlight intensity and date (Table 3). The number of trapped males increased when moonlight intensity decreased, but this effect was not observed after the peak of the

Table 3. Effect of method, moonlight intensity, and date on the capture of *Xenopus laevis* individuals in terms of total number of individuals, number of females, and number of males, as estimated by likelihood-ratio tests performed during backward model selection.

	Df	LRT	p
Number of trapped individuals			
Moonlight intensity	1	19.657	< 0.001
Method	5	13.729	0.017
Number of trapped females			
Moonlight intensity	1	4.884	0.027
Date	1	4.142	0.042
Method	5	14.640	0.012
Number of trapped males			
Moonlight intensity*date	1	5.864	0.015
Method	5	11.579	0.041

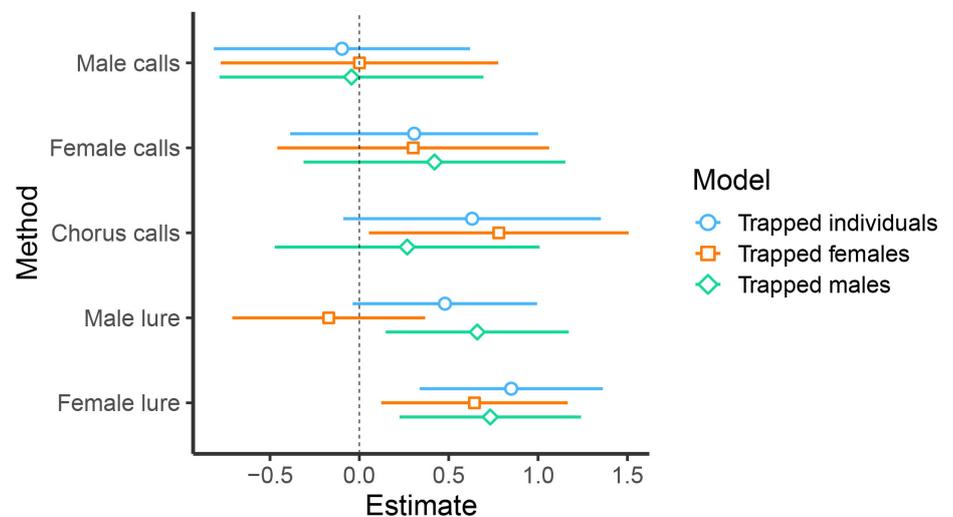


Figure 2. Increase in efficiency of trapping methods on the number of trapped individuals of *Xenopus laevis* (in blue), females (orange), and males (green), compared to the standard food-baited trapping method (dashed line). The figure represents the estimates of the partial effects of generalized linear models. Error bars represent 95% confidence intervals. Error bars crossing the dashed line indicate that the number of trapped individuals, or the number of trapped males or females, for the corresponding method and the control did not differ significantly at $\alpha = 0.05$.

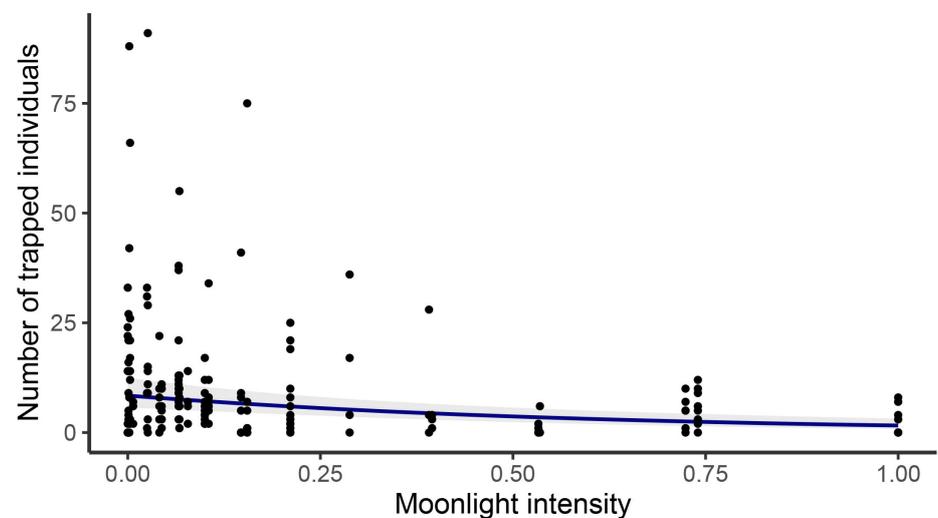


Figure 3. Effect of moonlight intensity on the number of trapped individuals of *Xenopus laevis* across methods. The line represents the predictions given by the best generalized linear model, the shaded area envelopes the 95% confidence intervals, and the points are observed values.

breeding period (interaction date \times moonlight intensity: estimate = -0.071 , SE = 0.030 , $z = -2.366$, $p = 0.018$). The main effects of moonlight intensity (estimate = 9.196 , SE = 4.941 , $z = 1.861$, $p = 0.063$) (Appendix 3) and date (estimate = 0.008 , SE = 0.006 , $z = 1.293$, $p = 0.196$) were not significant.

Discussion

We observed differences in trapping efficiency for *X. laevis* between methods in the total number of trapped individuals and for either sex. In the conditions of our study, adding a female as a lure in a trap yielded the greater number of captures of either sex compared to the control (standard food bait) method. We expected a higher trapping yield from playback methods, as they were shown to enhance trapping efficiency for other invasive species (Schwarzkopf and Alford 2007; Muller and Schwarzkopf 2017; Tingley et al. 2017; Muller et al. 2018), but none of the tested alternatives differed from the control. This result may be due to the broadcasting of only one type of call, or to a lower statistical power due to a smaller sample size than for the other methods. In other species, female attraction varies with call intensity or the type of calls (Lucas et al. 1996; Smith et al. 2003; Tingley et al. 2017). Difference in call intensity has already been noted in *X. laevis* by Ringeis et al. (2017), even within the same call type, and males are more sensitive to lower frequencies (Hall et al. 2016). Thus, a different outcome might be obtained when testing a broader range of intensities or a higher diversity of calls. We could not fit the loudspeaker inside the traps because it was too large; if we could, we might have expected more intense activity around the trap during the playback. However, such a solution is likely too costly for the resources of most control programs, especially if several playback systems must be acquired.

Maximizing the number of trapped females is an important goal of many control programs. Most of the methods we tested caught as many females as males but only using a live female as a lure increased the number of trapped females. This method also increased the number of trapped males, and logically the total number of trapped individuals. Using a live male as a lure also increased the capture rate of males but it did not affect the number of trapped females nor the total number of trapped individuals. Thus, this method may only have a small additional impact on the reproductive output of a population. The sex dependent success of traps with male lures could be explained by the fact that *X. laevis* often feeds in the water column (Courant et al. 2018). A male staying close to the surface could be a cue to a potential food source for conspecifics. However, females may be less attracted to males than conspecific males to avoid the risk of male harassment. This hypothesis remains to be tested. Another possible explanation is that territorial males attempt to silence and repel

intruders when they compete for mates (Tobias et al. 2010) and get more frequently caught when performing these behaviors. Capture may be more likely when using a lure as opposed to broadcasting calls because the movements of trapped individuals may reinforce their detection and the motivation of the territory holder. Generally, males are often captured more frequently than females or juveniles (Yeager et al. 2014), which pattern could be explained in *X. laevis* by a greater mobility of males than females (Ringeis et al. 2017). According to these authors, no phonotactic approaches to calling males were observed. However, we often caught as many females as males, and more females than males for one method. Therefore, using a live female as an attractant could be preferred because this method captured more individuals and more females.

We found a significant negative relationship between relative moonlight intensity and the number of captures, which is consistent with the known effect of this environmental factor on the general activity of several amphibians (Grant et al. 2013). For the African clawed frog, reduced activity may be driven by a higher predation risk or lower prey activity at full moon (Nowinszky et al. 1979; Nirmal et al. 2017). These two hypotheses are not exclusive. Thus, it is preferable to avoid trapping on the brightest nights of the lunar cycle because the expected number of captures is the lowest, which may lower the output of control actions or underestimate population size, as already suggested for newts (Deeming 2008). This result is important to refine the optimal conditions for the capture of *X. laevis*. Trapping with live females as lures during the optimal phase of the lunar cycle and with a particular effort at the peak of the breeding season should reduce the local population size of *X. laevis* more than other tested alternatives.

One limit of this method is that traps with female lures can only be used for control and not for surveys investigating species presence because of possible accidental releases. Moreover, only individuals from the trapped pond or nearby sites should be used as lures to avoid the spread of pathogens like chytrids responsible for amphibian declines (Piotrowski et al. 2004). Whether or not the use of female lures is enough to achieve local eradication remains to be tested. Mora et al. (2019) already observed in Chile that trapping may not be enough to extirpate a *X. laevis* population, especially in strongly invaded areas. Some authors have suggested that attention should be paid to the conditions that promote coexistence between the invader and native species (Bucciarelli et al. 2014). Trapping alone may not be enough to achieve this goal and a mix of methods may be required. Nevertheless, trapping contributes to lower the stress on local ecosystems, and using a female as a lure seems to increase the capture probability. Our study highlights the fact that cost-efficiency gains could be further achieved by correctly timing trapping sessions with regard to the phase of the lunar cycle and the calendar date.

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Ethics and permits

This study has been carried out in compliance with ethical standards in France (Préfecture des Deux-Sèvres, Arrêté préfectoral R.1012017), and the authors are willing to share the original data and materials if so requested.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Procedure to create playback sound files of male and female *Xenopus laevis* calls.

Appendix 2. Experimental setup used on the two studied ponds.

Appendix 3. Effect of moonlight intensity on the number of trapped (A) females and (B) males across methods.

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