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Presence of an alien turtle accelerates hatching of common frog (Rana temporaria) tadpoles

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Introduction

The impacts of invasive species on native communities are still difficult to generalise due to the limited number of species and environments researched (Griesemer et al. 2018; Ramírez Albores et al. 2019; Rolim et al. 2015; Tricarico et al. 2016). However, inappropriate responses of individuals to invasive predators can strongly affect native populations of their prey (Mooney and Cleland 2001). In amphibians, predation can account for a significant proportion of the total mortality of all their developmental stages (Gunzburger and Travis 2005; Chivers et al. 2001; Laurila et al. 2002; Nyström et al. 1997). The ability to detect, recognise, and respond to potential predators is, therefore, an important part of antipredatory behaviour (Bennett et al. 2013; Polo-Cavia and Gomez-Mestre 2014), and native populations can have especially serious problems facing the presence of new alien predators (Gomez-Mestre and Díaz-Paniagua 2011; Nunes et al. 2019; Polo-Cavia et al. 2010). In general, embryonic and early larval stages are the most vulnerable to predation (Laurila et al. 2002; Wells 2007), and the ability to respond to the presence of a predator can therefore significantly increase the fitness of an individual and thus the viability of the entire population (Vonesh and Bolker 2005; Warkentin 1995).

Whether intentionally or unintentionally introduced, the recent wide occurrence of the red-eared slider (*Trachemys scripta elegans*) in Europe (GISD 2021) presents a new opportunity to investigate the responses of naive native amphibian populations to a new predator. Although red-eared slider (hereafter referred to as slider) is not reproductively successful throughout Europe (Cadi et al. 2004; Ficetola et al. 2009; Mikátová and Šandera 2015; Standfuss et al. 2016), even the mere presence of adults may pose a certain risk to native

species. In previous studies, we found that the presence of the slider affects several life history parameters of common frog (*Rana temporaria*) tadpoles, such as movement activity, trajectory of movement (Berec et al. 2016), time to metamorphosis, or size at metamorphosis (Vodrážková et al. 2020). Although sliders are usually still hibernating at the time of common frog breeding (Gibbons et al. 1990; Speybroeck et al. 2016), which eliminates the risk of direct predation, kairomones released by sliders into the aquatic environment provide amphibians with information about their presence. Since the slider is an opportunistic predator and can consume frog eggs (Ernst and Lovich 2009), some response of common frog embryos is to be expected.

For frog embryos, there are two basic strategies for avoiding predation or significantly reducing its effects: the development of egg unpalatability and hatching plasticity (Wells 2007). The unpalatability of eggs is a passive strategy in which the embryo relies on the predator's inability or unwillingness to consume eggs, which imposes costs on its host even if the host never comes in contact with the predator; environmentally cued hatching is characterised by an embryo's active capability to alter the time of hatching according to the conditions it encounters during embryonic development. Hatching plasticity has been documented many times in amphibian embryos, and predator presence has been shown to trigger early hatching from eggs incubated in both air and water (Chivers et al. 2001; Warkentin 2011). In terrestrially laid eggs, hatching can be stimulated by vibrational cues during the direct physical attacks of predators, such as snakes (Jung et al. 2019; Warkentin 1995), frogs (Vonesh and Bolker 2005), katydids (Poo and Bickford 2014), wasps (Warkentin 2000), or egg-eating fly larvae (Vonesh and Bolker 2005). In aquatic environments, these responses are induced mainly by chemical cues from predators (kairomones) or by chemical cues that are released from injured prey during predation events (Dodson 1988; Laurila et al. 2002; Nicieza 1999; 2000; Petranka et al. 1987; Smith and Fortune 2009; Tollrian 1994).

This study aimed to shift our previous focus (Berec et al. 2016; Vodrážková et al. 2020; in review) to a different developmental stage, namely, embryos in eggs. We investigated whether the presence of a slider can alter the hatching time of common frog embryos. We hypothesised that the presence of a slider would accelerate the hatching time, so the ontogenetic stage and body size at hatching were also measured. The uniqueness of this study lies in the use of a stage-nonspecific predator, which is virtually absent in the literature. At the same time, it is an alien predator from a taxonomic group to which the prey has no common history.

Materials and methods

Five freshly laid clutches of common frogs were collected in pools around Holubov and Vrábče, South Bohemia, the Czech Republic, on 2 April 2021. Pools were monitored daily to collect egg clutches laid during the night before. Neither the eggs nor their parents encountered the slider or any other turtle species at the collection locality. The experiment was performed in six glass tanks (size: $100 \times 55 \times 50$ cm) filled with 20 cm of tap water. Glass tanks were equipped with a Claro 300 filter pump (300 L.h–1) and rinsed three times a week. The experiment was carried out in a temperature-controlled laboratory room. The room temperature was 14.8 ± 0.4 °C (mean \pm S.D.) during the experiment. Fluorescent tubes (2 x 36 W) with a light regime of 12 h/12 h were used. During the dark phase of the day, the glass tanks were illuminated with red light to allow permanent monitoring of egg hatching.

Three adult sliders (carapace length: 18 cm, 20 cm, and 21 cm) were used as predators. A turtle was placed in each of three glass tanks three days before the experiment was initiated and fed three times a week with ReptoMin Tetra turtle gammarus. To prevent physical but not chemical contact between a turtle and frog eggs, a glass barrier was placed inside each glass tank with a 6 cm gap at both ends so that water could flow freely throughout the tank. On the

other side of this barrier, five perforated opaque boxes ($20 \times 14 \, \text{cm}$) with holes 1 mm in diameter were glued to the bottom of the glass tanks.

Approximately 150 eggs were taken from each clutch and placed randomly into five boxes in individual glass tanks, so there were eggs from all five clutches in each glass tank. Each glass tank was continuously monitored using a camera (Niceboy Stream Pro). Hatched tadpoles were counted every 24 h. Hatching was defined as the point at which the whole of the hatchling had left the jelly. To maintain a good resolution of the camera recording, hatched tadpoles were transferred every six hours to a depot tank. At the time when half of the eggs in each box had hatched, two tadpoles were taken from the group of tadpoles hatched in the last six hours. These tadpoles were photographed under a stereomicroscope (Olympus SZX 7) and measured (to the nearest 0.01 mm) using QuickPHOTO MICRO 3.2 software. Their developmental phase was determined according to Gosner (1960).

The experiment involved a balanced three-way full factorial design (turtle presence/absence, glass tank, and clutch). As a nonnormal distribution was found for all three sets of our data (hatching time, developmental stage, and size at hatching), strategies other than classic inferential methods based on means such as factorial ANOVA had to be used (Field and Wilcox 2017). A robust three-way alternative based on trimmed means with χ 2-distributed test statistics and adjusted critical values was suggested to resolve such data (Mair and Wilcox 2020). For statistical analysis of our data, the *t3way* function from the WRS2 package ver. 1.1-3 (Mair et al. 2021) in R software (Torfs and Brauer 2014) was used. The recommended 20% trimmed mean was used because it achieves nearly the same amount of power as the mean when sampling from a normal distribution (Mair et al. 2021). Given the number of eggs, statistical significance was assessed at the 99.9% level.

Results

The presence of a turtle affected all parameters studied. We found a significant difference in hatching time between the presence and absence of a turtle (Table 1). In the absence of a turtle, embryos hatched in 12 days (median; 10-13 days min-max). The presence of a turtle accelerated hatching by two days (median; 10 days; 8-11 days min-max) (Fig. 1). Hatching time differed significantly among glass tanks, but the effect of this factor was negligible in comparison to the effect of turtle presence (see Supplementary file: Fig. 2). The effect of clutches was marginally insignificant (Table 1). If we use the standard 5% significance level, this factor is also considered of relatively minor significance in comparison to the presence of turtles.

Similarly, significant differences were found between the developmental stage and size of freshly hatched embryos in the presence of a turtle and without it (Table 1). In the presence of a slider, embryos hatched at developmental stage 20 (median; 18-21 min-max) with a median size of 5.68 mm (median; 3.58-8.70 mm min-max), while in the control, freshly hatched embryos had developed to stage 23 (median; 22-24 min-max), with a median size of 10.43 mm (9.31-12.90 mm min-max) (Fig. 1).

Table 1.

Analysis of variance for the hatching time, developmental stage, and size at hatching of common frog embryos.

Effects	Hatching time		Developmental stage		Size at hatching	
	Chi-square	p	Chi-square	p	Chi-square	p
Turtle presence (T)	11605.05	0.0001	24.14	0.0001	249.03	0.0001
Glass tank (G)	25.39	0.0001	0.07	0.9700	7.98	0.0600
Clutch (C)	32.35	0.0010	4.97	0.5050	6.57	0.3690
TxG	7.80	0.0220	0.23	0.9040	11.33	0.0250
TxC	10.79	0.0330	1.77	0.8540	0.68	0.9680
GxC	35.59	0.0010	24.66	0.2070	22.59	0.2310
$T \times G \times C$	20.96	0.0110	6.66	0.8550	13.03	0.5360

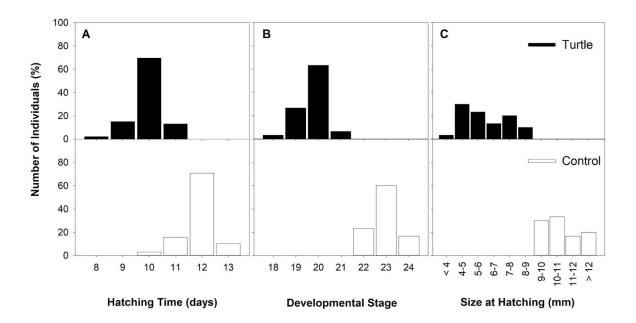
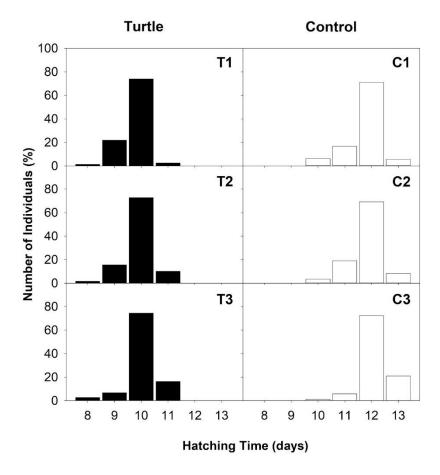


Figure 1.Histogram of **A** hatching time, **B** Gosner (developmental) stage, and **C** size at hatching of the embryos of common frogs in the presence of a red-eared slider (turtle) and control.

Supplementary file 1



Supplementary file: Figure 2.

Hatching time of the embryos of common frogs in individual glass tanks (T1-T3 and C1-C3) in both treatments (with the presence of a slider (T) or without (C)).

Discussion

Developmental plasticity is an adaptive response of anuran embryos and larvae to the risk of predation (Altig and McDiarmid 1999; Benard 2004; Warkentin 2011). Here, we present evidence for the developmental plasticity of common frog embryos in the presence of a redeared slider and, together with a previous study (Vodrážková et al. 2020), provide a comprehensive picture of the influence of this alien predator on the early phases of the common frog life cycle. We have previously shown (Vodrážková et al. 2020) that tadpoles of common frogs respond to turtle presence by shortening larval development. In the present study, we

confirmed a similar response in common frog embryos, which hatched earlier in the presence of a slider. At the same time, the embryos were smaller and less developed when exposed to the chemical signals of a predator. We also found an effect of a glass tank on hatching time, which was nevertheless negligible in comparison with the effect of predator presence, and which could be related to the slight temperature stratification in the experimental room (the glass tank in which the difference was detected was closest to the door).

In the presence of stage-specific predators, amphibians can adapt the duration of the relevant developmental stage (Chivers et al. 2001; Ireland et al. 2007; Mitchell et al. 2017). In anuran embryos, specifically, the presence of egg predators has mostly been shown to induce early hatching of embryos (Chivers et al. 2001; Johnson et al. 2003; Laurila et al. 2001; Segev et al. 2015; Warkentin 1995; 2000), while tadpole predators induce delayed hatching (Laurila et al. 2002; Mitchell et al. 2017; Schalk et al. 2002; Sih and Moore 1993), thus increasing their chance of survival by escaping possible attacks. In such cases, a change in hatching time was typically associated with a change in size (Capellán and Nicieza 2007; Ireland et al. 2007; Johnson et al. 2003) or even a developmental stage (Capellán and Nicieza 2007; Chivers et al. 2001; Ireland et al. 2007; Moore et al. 1996), which is in full agreement with our results. However, the slider is not a stage-specific predator, as it is capable of consuming both amphibian eggs and larvae (Brown et al. 1995; Ernst and Lovich 2009; Chen 2006); thus, the allocation of risk between developmental stages of the frog may be more complex in this case (Warkentin 2011). Studies examining predator effects on the developmental rates of both eggs and larvae are rare because few predators consume both eggs and larvae simultaneously. Muraro et al. (2021) used a stage-nonspecific predator (Procambarus clarkii) and found, in concordance with our results, a reduction in hatching time in *Rana latastei* embryos. However, they did not study larval development. Ireland et al. (2007) solved the problem of predator stage specificity by simultaneously exposing frog eggs to stage-specific predators of eggs (leech: Nephelopsis obscura) and larvae (dragonfly: Aeshna canadensis nymphs), which resulted in no change in hatching time, whereas tests with separately acting predators produced the expected response of a reduction in hatching time in the egg predator treatment and an increase in hatching time in the larval predator treatment. In this study with embryos and a study with tadpoles (Vodrážková et al. 2020), the embryos/tadpoles responded to the presence of a predator by shortening the stage of development during which the embryo/tadpole would be exposed to the predator. It would be interesting to see how common frog tadpoles react to the presence of a slider if the entire development from eggs to metamorphosis was taking place with this predator present.

However, some studies have shown that frog embryos, including the common frog, do not always respond specifically to stage-specific predators by shortening hatching time (Capellán and Nicieza 2010; Laurila et al. 2001; Laurila et al. 2002; Saglio and Mandrillon 2006; Schalk et al. 2002; Touchon et al. 2006; Touchon and Wojdak 2014). The published differences in embryo responses may correspond to different signal intensities of the presence of a specific predator, and thus, the responses to indirect waterborne cues might be weaker than those to the direct, mechanical cues of a predator attack (Warkentin 2011). An evident response to water-borne cues of sliders may be related to a markedly stronger signal of a much largersized predator in our experiment compared to commonly tested invertebrate predators. The ability to scale predator danger and adjust hatching time accordingly has been found, for example, in embryos of southern leopard frogs (Lithobates sphenocephalus) (Johnson et al. 2003). Moreover, a possible absence of a change in hatching time does not necessarily imply a complete lack of response to the presence of a predator. It may be manifested by other types of responses, such as changes in the body shape of tadpoles (Laurila et al. 2001; Mandrillon and Saglio 2007; Saglio and Mandrillon 2006; Touchon and Wojdak 2014) or their behaviour (Saglio and Mandrillon 2006; Touchon and Wojdak 2014).

Native and naive prey may fail to detect the novel predator adequately as a dangerous threat, resulting in no (Cox and Lima 2006; Sih et al. 2010) or inefficient antipredator responses to counter the predator's attack strategies (Sih et al. 2010; Strauss et al. 2006). However, when responses in hatching time in naive prey are detected, they are often explained by the presence of syntopic, taxonomically related predators (Melotto et al. 2021; Muraro et al. 2021; Sih et al. 2010), although the time since invasion may also play an important role (Gomez-Mestre and Díaz-Paniagua 2011; Nunes et al. 2013). Our results suggested that a common evolutionary history is not necessary for a detectable response. Such a result has already been published for tadpole development time (Stav et al. 2007; Vodrážková et al. 2020), but as far as we know, it has not yet been published for hatching time in frog embryos. An explanation for embryo response to an alien slider may be in the ability of embryos to detect a kind of general "smell of fear" that is elicited by most predators, regardless of taxonomic classification (Sih et al. 2010).

Our work added a slider as an additional predator inducing changes in the embryonic developmental rate in ranid frogs. Since the impact of earlier embryo hatching (lower body size and lower stage of development) on fitness has been confirmed in several frog species (Laurila et al. 2002; Touchon et al. 2013; Vonesh and Bolker 2005; Warkentin 1995), the same impact can be expected for the common frog. The existence of defensive responses in slider-exposed embryos may reduce the threat that poses the spreading of this invasive species in Europe. On the other hand, the reduced size at hatching and developmental stage of common frog hatchlings represents additional risks of negative fitness impacts, and at the very least, the presence of sliders in non-native areas should receive increased attention.

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All methods were carried out in accordance with relevant guidelines and regulations. All experimental protocols were approved by the Czech Ministry of Agriculture, Department of Animal Welfare according to article No. 15, section 2 of the act registered under number 9103/2009-17210.

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