



May future climate change promote the invasion of the marsh frog? An integrative thermo-physiological study

Pablo Padilla^{1,2} · Anthony Herrel^{2,3} · Mathieu Denoël¹

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Abstract

Climate change and invasive species are two major drivers of biodiversity loss and their interaction may lead to unprecedented further loss. Invasive ectotherms can be expected to tolerate temperature variation because of a broad thermal tolerance and may even benefit from warmer temperatures in their new ranges that better match their thermal preference. Multi-trait studies provide a valuable approach to elucidate the influence of temperature on the invasion process and offer insights into how climatic factors may facilitate or hinder the spread of invasive ectotherms. We here used marsh frogs, *Pelophylax ridibundus*, a species that is invading large areas of Western Europe but whose invasive potential has been underestimated. We measured the maximal and minimal temperatures to sustain physical activity, the preferred temperature, and the thermal dependence of their stamina and jumping performance in relation to the environmental temperatures observed in their invasive range. Our results showed that marsh frogs can withstand body temperatures that cover 100% of the annual temperature variation in the pond they live in and 77% of the observed current annual air temperature variation. Their preferred body temperature and performance optima were higher than the average temperature in their pond and the average air temperature experienced under the shade. These data suggest that invasive marsh frogs may benefit from a warmer climate. Broad thermal tolerances, combined with high thermal preferences and traits maximised at high temperatures, may allow this species to expand their activity period and colonise underexploited shaded habitat, thereby promoting their invasion success.

Keywords Invasive species · Ectotherm · Temperature · Thermal tolerance · Performance curve

Introduction

Human-induced climate change (Cattiaux et al. 2015; Simmons et al. 2017; IPCC 2022) puts pressure on living organisms, pushing them to their physiological limits (Parmesan and Yohe 2003; Warren et al. 2018). Indeed, temperature affects the rates of chemical reactions within an organism and consequently their physiology (Tattersall et al. 2012). Their response to temperature is described by reaction norms that typically have a parabolic shape (Cossins and Bowler 1987; Angilletta 2009) (Fig. 1). Amongst Metazoa, ectothermy is the most common thermoregulatory mechanism, and because ectotherms rely mostly on environmental temperature, many species are expected to be impacted by climate change (Deutsch et al. 2008; Sinclair et al. 2016; Lotze et al. 2019; Sánchez-Bayo and Wyckhuys 2019). Regardless of their geographical origin, both tropical and temperate species are at risk from global warming (Deutsch et al. 2008) and of the predicted stronger temperature variations (Paaijmans et al. 2013; Vasseur et al. 2014; Dillon

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Highlighted student paper through the study of an overlooked invasive frog species, we show that multi-traits methods improve our understanding of how an invasive ectotherm may benefit from climate change.

✉ Pablo Padilla
pablo.padilla@uliege.be

¹ Laboratory of Ecology and Conservation of Amphibians (LECA), Freshwater and Oceanic science Unit of reSearch (FOCUS), University of Liège, Liège, Belgium

² Département Adaptations du Vivant, UMR 7179 C.N.R.S/M.N.H.N., Paris, France

³ Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium

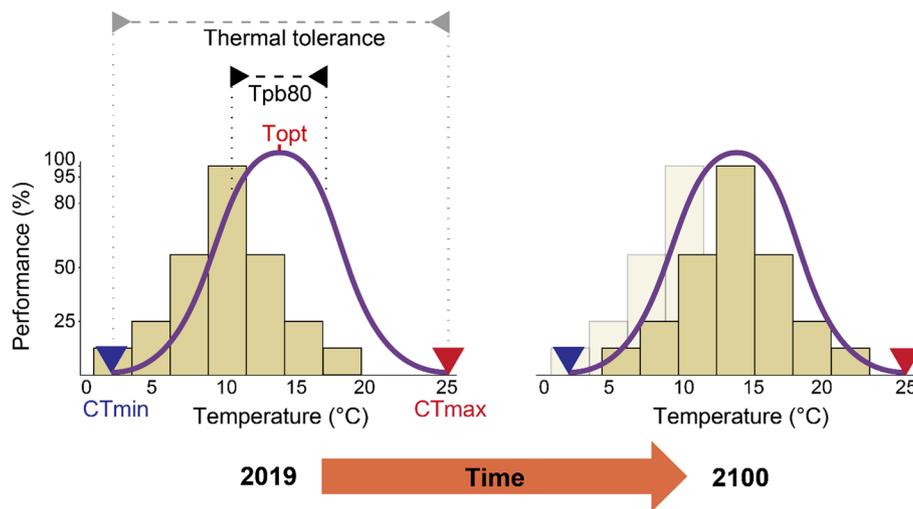


Fig. 1 Theoretical representation of a shift of annual temperature distribution (histogram) that better fits a performance curve of an invasive ectotherm. The curve, in purple, is bounded by the critical thermal minimum (CT_{min} , blue triangle), and the critical thermal maximum (CT_{max} , red triangle). The range of temperature between these bounds defines the thermal

tolerance where the organism can maintain activity (horizontal grey dashed lines). The temperature associated with the maximum value of performance defines the thermal optimum (T_{opt} , red). Finally, the range of temperatures where performance is greater or equal to a desired level (commonly 80% or 95%) defines a performance breadth (T_{pb} , horizontal black dashed line; Angilletta et al. 2002)

et al. 2016). This is especially the case for amphibians which are already amongst the most threatened vertebrates (Stuart et al. 2004; IUCN 2022) and for which climatic change has been invoked as a direct driver of population extinction (Araújo et al. 2006; Wake and Vredenburg 2008; Blaustein et al. 2010). Other drivers of population decline such as invasive species may interact with climate change and precipitate the extinction of threatened populations (Pounds et al. 2006; McMenamin et al. 2008).

In many cases, invasive species can maintain an activity over a broad range of temperatures and as such may be less impacted or even benefit from the ongoing climatic crisis (Huang et al. 2011; Zerebecki and Sorte 2011; Kelley 2014). Bennett (1987) hypothesised that warmer temperatures maximise locomotor capacity which may benefit dispersal in invasive species. Consequently, the interaction between invasive species and climate change may result in unprecedented risks to native ecosystems (Rahel and Olden 2008; Mainka and Howard 2010). Despite the general vulnerability of amphibians to temperature change, some introduced amphibians are able to withstand and quickly adapt to new environmental conditions (Vimercati et al. 2018; Mittan and Zamudio 2019; Araspin et al. 2020). African clawed frogs (*Xenopus laevis*) and bullfrogs (*Lithobates catesbeianus*), for example, are two species that have been introduced worldwide (IUCN 2015, 2020). Andersen et al. (2021) recently predicted suitable niches on all continents except Antarctica for both species. Johovic et al. (2020) also showed that climate change would benefit the spread of bullfrogs. However, most of

the model predictions for invasive species are based on occurrence data only. Empirical measurements of not only the thermal limits but also thermal preferences and physiological response to temperature of invasive species need to be gathered and then used to improve these predictions (Ginal et al. 2023).

Some traits have been recognised to be associated with the invasive potential of a species (Sakai et al. 2001; Allen et al. 2017). Range expansion, for example, is a stage during invasion that benefits from greater dispersal capacity and survival. Stamina may play an important role during dispersal and is driven by the capacity to maintain prolonged muscular effort and an efficient metabolism. On the other hand, a quick reaction time and explosive locomotor performance may allow a better escape from predators and increase prey capture success. To establish and disperse, invaders also need to overcome abiotic ecological filters, such as temperature (Olyarnik et al. 2009). Indeed, global surface temperature is continuously increasing and a global warming of 2 °C will be exceeded in the twenty-first century (IPCC 2022). A broad thermal performance breadth would then help invaders to maintain their performance and potentially fitness. By consequence, global warming will result in a shift in environmental temperature that may maximise locomotor performance (Fig. 1). These two adaptations (i.e. large thermal tolerance range and broad thermal performance breadth) combined may allow activity and habitat use of invasive species to be less constrained by daily and annual variations in environmental temperature in addition to increasing their dispersal efficiency and invasive potential.

In the present paper, we performed a multi-trait study using, as our model species, marsh frogs. The *Pelophylax* genus is widely distributed in the Palearctic (Lymberakis et al. 2007; Dufresnes and Mazepa 2020), with multiple introductions out of their native range particularly in Western Europe, such as Belgium (Holsbeek and Jooris 2010), Switzerland (Dubey et al. 2014) or France (Doniol-Valcroze et al. 2021). These have resulted in the establishment of invasive populations (Dufresnes et al. 2017b). The major threats reported from their invasion are their potential hybridization with native species of the genus (Holsbeek and Jooris 2010) as well as predation on native species (Pille et al. 2021). The invasive range of these animals has increased over the last decades with new areas being rapidly colonised such as the Larzac plateau in southern France where *Pelophylax* frogs were introduced after being historically absent (Dufresnes et al. 2017a; Denoël et al. 2022; Duret et al. 2022). It has been suggested that recent warmer conditions may have enhanced their invasion (Dufresnes et al. 2017a), but this remains untested to date. The Larzac plateau has seen its temperature increased over the last years (Ali et al. 2022). Climate models predict that warming will be more rapid in the region compared to the global average (Kjellström et al. 2018). If this increase in temperature does indeed benefit the invasive capacity of these frogs, then this may have major consequences to the native ecosystem.

Specifically, the goals of this study were to evaluate whether warm temperatures such as those arising due to climate change could favour invasive marsh frogs. We expect marsh frogs to show: (i) a broad thermal tolerance providing them with a large period of activity; (ii) a preference for high environmental temperatures that may be higher than the current environmental temperatures; (iii) locomotor capacities that are maximised at high temperatures, i.e. higher than the current environmental temperatures. Lastly, sex differences in thermal traits are not often investigated, whereas they may be expected due to the inherent differences in physiology and behaviour between males and females (Bodensteiner et al. 2021). We therefore took the opportunity of this study to test for an effect of sex in each thermal trait previously mentioned.

Materials and methods

Study organisms

Adult marsh frogs (*Pelophylax ridibundus*) were caught in August 2020 (Critical thermal limits: $n=40$, 20 for critical minimum and 20 for critical maximum with 10 females and 10 males in each; Stamina: $n=21$, 8 females and 13 males; Jump force: $n=25$, 11 females and 14 males) and April 2022 (Preferred temperature: $n=29$, 11 females and 18 males) at

the border of ponds in Larzac (43°51'N–3°21'E, Hérault, France). Previous molecular analysis confirmed the taxonomic assignment and the invasive status of the marsh frogs in the studied population (Dufresnes et al. 2017a; M. Pabijan, pers. comm.). All individuals were PIT-tagged (Biolog-ID, 134.2 kHz) to allow individual identification. The tag was inserted dorsally under the skin (Christy 1996). The snout–vent length (SVL; from the tip of the snout to the end of cloaca) was measured with callipers after gently laying each frog on a flat surface (mean \pm SE = 68.23 \pm 1.91 mm). Each frog was weighed (mean \pm SE = 30.97 \pm 2.61 g) using a digital scale (Ohaus, Brooklyn, NY, USA; precision 0.1 g). Sex was identified by the presence of a vocal sac and nuptial pads on the males' thumbs and later verified through dissection and inspection of the reproductive organs.

Transportation and housing

Frogs were brought inside large coolers filled with 3 cm of water to the Function and Evolution (FUNEVOL) laboratory at the Muséum National d'Histoire Naturelle of Paris, France. Frogs were maintained singly in 5 L tanks (21.4 \times 36.5 \times 16.5 cm; water depth: 5 cm) with holes in the lid. Tanks were inclined by placing a 10 cm wood block under one of the sides creating a dry area that occupied one third of the tank. Animals rested for the first week to allow them to acclimate to laboratory conditions. Water in the tanks was renewed weekly. Two adult crickets (*Acheta domesticus*) were given twice weekly and additionally after each trial. Night and day periods were set to 12 h each. The room temperature was set at 24 °C.

Field temperatures

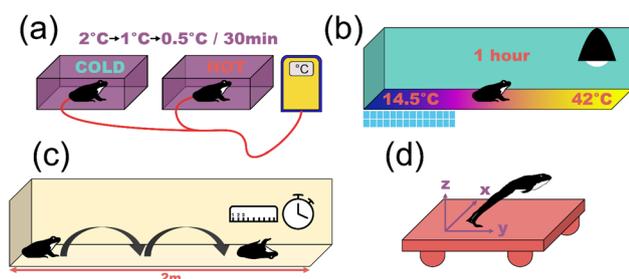
Air temperatures were recorded each 6 min and obtained from a meteorological station situated at 6 km from the site from January 2018 to January 2019 (Larvor et al. 2020; Table 1). Water frogs spend a large part of their time at the water–land interface and take shelters in the bottom of ponds. Therefore, we incorporated water temperatures with automatic measures each 30 min from March 2019 to March 2020 with a submersible temperature logger (HOBO U20L-01) placed at a depth of 1.5 m in a pond at the centre of the invaded area (Table 1).

Critical temperatures (CT)

Each frog was placed individually inside an incubator (Aqualytic-LIEBHERR, TC 256 G/256 L/2–40 °C) with light in a 5 L plastic box (21.4 \times 36.5 \times 16.5 cm), with 5 mm of water depth to prevent dehydration. Twenty animals (10 males, 10 females) were used to measure minimal critical temperatures, and twenty others (10 males, 10

Table 1 Environmental temperature annually and relative to marsh frog period of activity in Larzac, France

Temperature (°C)		Mean ± SE	Min	Max
Annual	Air	11.17 ± 0.02 °C	− 13.5 °C	33.2 °C
	Bottom of the pond	10.73 ± 0.03 °C	5.34 °C	21.37 °C
During period of activity (early spring to late summer)	Air	15.67 ± 0.03 °C	− 5.6 °C	33.2 °C
	Bottom of the pond	13.47 ± 0.04 °C	6.97 °C	21.37 °C

**Fig. 2** Graphical summary of each set of measurements made during the study on marsh frogs. **a** Critical thermal limits assessed with a thermocouple inserted inside the cloaca; **b** Preferred temperature estimated after one hour within a thermal gradient; **c** Stamina was estimated through the distance and the time travelled until exhaustion; **d** Jump force was measured using a force plate

females) were used for maximal critical temperatures to avoid too much stress on the same animals. To establish critical minimum temperature (CT_{min}), the incubator was set at 12 °C and the frogs were kept at that temperature for one hour. Next, the temperature was decreased at a rate of cooling of 2 °C each 30 min until reaching 6 °C when we switched to a rate of 1 °C each 30 min (Fig. 2a). For critical maximal temperature (CT_{max}), frogs were placed in a container placed inside a large cooler filled with water heated by a water heater. Experiments started at the acclimation temperature of 24 °C after which the temperature was increased with a rate of warming of 2 °C each 30 min until reaching 34 °C at which point we switched to a rate of 1 °C each 30 min (Fig. 2a). For both minimal and maximal critical temperatures, the temperature was increased or decreased by 0.5 °C every 30 min whenever animals showed slower righting response (Fig. 2a). Even if the onset of spasms has been considered by some researchers as a more precise measurement of thermal tolerance (Lutterschmidt and Hutchison 1997), we used the loss of righting response instead to avoid excessive stress (Taylor et al. 2021). The lack of a righting response was tested by giving the animal two seconds to recover a normal upright position after having been placed on their back. When the frog was no longer able to right itself during this short time period, its internal body temperature was measured using a thermocouple inserted inside the cloaca (APPA51 thermometer K-type, APPA Technology Corp, resolution 0.1 °C).

Preferred temperature (T_{pref})

The experimental setup consisted of five individual lanes (190 × 20 × 30 cm each) within a wood arena covered with cork. The gradient ranged from approximately 14.5 °C on the side cooled by ice packs to approximately 42 °C on the side heated by light bulbs (60 watts, Repti Basking Lamp Spot ZooMed, SL2-60) (Fig. 2b, Fig. S1). The room temperature was set to 24 °C and the average temperature in the lanes was 24 ± 1.73 (SE) °C. Each lane was humidified on its whole length before the trial with a spray bottle filled with tap water. Animals were not fed for three days before trials to avoid digestion effect on thermoregulation (Gatten 1974). One frog was set inside each lane and was left free to thermoregulate for one hour. After one hour, we measured the body temperature of each frog and calculated the mean across all individuals which we considered as an estimate of the population thermal preference. Each frog was recorded twice separated by three days. As we did not find significant difference between each recording (paired t -test: $t_{28} = -0.56$, $p = 0.57$, first recording: mean ± SE = 21.79 ± 0.68 °C, second recording: 22.27 ± 0.66 °C), we used the second recording to avoid potential bias coming from their initial discovery and exploration of the experimental setup. The temperature of the animals was assessed using a thermal camera (FLIR-E6xt 2.1L) and thermal image analysis software (FLIR Tools, version 6.4.18039.1003). Thermal pictures were taken with an incidence angle close to 0 °C and at a distance of one metre and an emissivity of 0.97 (Fig. S2). Temperature was also verified by a thermocouple (APPA51 thermometer K-type, APPA Technology Corp) inserted in the cloaca at the end of the trial. Since there were no significant differences of the methodology (i.e. thermal camera vs thermocouple measurements) on the measures of body temperatures (linear mixed model with method, sex and SVL as covariates on body temperature; methods: estimate = − 0.8, CI = − 1.62 to 0.03, $p = 0.06$; sex: estimate = 0.76, CI = − 1.59 to 3.11, $p = 0.52$; SVL: estimate = − 0.08, CI = − 0.29 to 0.12, $p = 0.42$), we decided to use the thermal camera values because of its instantaneity and to avoid delays created by the cloacal measurements due to the capturing and handling of the animals.

Terrestrial exertion

Frogs were stimulated by hand to move back and forth across a linear track (200 × 40 × 50 cm; graduated each 10 cm) with a humidified cork bottom providing grip. The time and the distance that frogs were able to continuously move until exhaustion were measured (Herrel and Bonneaud 2012a, b) (Fig. 2c). Time was measured using a stopwatch and distance was based on the number of graduations crossed by the frogs during movement. From these variables, we calculated a composite variable referred to henceforth as mean speed. Exhaustion was defined by the lack of a righting response determined by giving the animal two seconds to recover a normal position after having been placed on its back. After the trial, body temperature was verified using a thermocouple. Frogs were then placed back in their maintenance boxes, given food, and not used for other observations for one week. Trials were repeated twice at each temperature, and the maximum time and distance at each temperature were retained for each individual. To evaluate how exertion changes as a function of temperature (Angilletta 2009), our observations were repeated in random order. Because the thermal optimum for exertion was not clear after testing animals at four temperatures (9, 14, 19 and 24 °C), we ran additional exertion tests at two additional temperatures (4 and 29 °C) providing a better fit of our models.

Jump forces

Maximal jump forces were measured using a piezo-electric force platform (20 × 10 cm, Kistler Squirrel force plate, ±0.1 N; see Herrel et al. 2014) (Fig. 2d). The platform was connected to a charge amplifier (Kistler–Charge Amplifier type, 9865) and forces were recorded for 60 s at 500 Hz using the BioWare software (Kistler). A cork surface was glued to the force plate to provide a better grip. Frogs were placed individually on the force plate, allowed to rest a few seconds and then induced to jump by approaching them. Peak force data were extracted using the Kistler BioWare software, and the total resultant force (vector sum of the X-, Y- and Z-forces) was calculated. Three sessions of at least 3 jumps within each session were recorded and only the single best jump was retained and used in the analyses. Tests at four temperatures (14, 24, 28 and 33 °C) were enough to determine the thermal optimum. Prior to each test, frogs were placed individually for 3 h at the desired temperature in an incubator in a box with some water to prevent dehydration.

Statistical analyses

For both one-way analyses of co-variance (ANCOVAs) and generalised additive mixed model (GAMM), model

validation was performed by visualising the residuals which had a homogeneous, normal distribution and by plotting the response variable on fitted values. All analyses were done using R version 4.1.2 (R Core Team 2021).

Mass and snout–vent length (SVL) were significantly correlated ($t_{19} = 12.01$, $R = 0.94$; $p < 0.01$). We therefore used snout–vent length as our covariate in the analyses because mass is dependent on the daily food intake and excretion. Snout–vent length did not differ between males and females ($t_{19} = 0.64$, $p = 0.52$).

ANCOVAs were run for CT_{\min} and CT_{\max} to determine the effect of sex on body temperature after controlling for SVL. Another ANCOVA was run with the effect of sex on the preferred temperature with SVL as covariate.

Because temperature often has a non-linear effect on biological processes (Huey and Kingsolver 1989; Bulté and Blouin-Demers 2006), we fitted a GAMM (Wood 2011) for each performance trait. GAMM can fit complex non-linear relationships using a smoother function on sections of the data (Wood 2006). They are therefore good tools to estimate thermal performance curves (TPC) and were previously used in the study of reptiles (Vickers et al. 2017; Cecchetto et al. 2020). Effective degrees of freedom (edf) were used to quantify the strength of non-linearity: an edf of one being a linear effect, an edf between one and two was considered as a weak non-linear effect and an edf greater than two was a highly non-linear relationship (Zuur et al. 2009). In each model, SVL was used as covariate; temperature as a fixed effect dependent on a smooth function and sex was added as a fixed factor. Because the same frogs were measured at each temperature, we added individual identity as a random term (Wood 2006). For temperature, we used a smoothing parameter (k) that avoids both over smoothing and overfitting biologically incoherent variation. This was based on the models having the highest R -squared values and verifications from the function of the “mgcv” R package (v1.8–35; Wood 2011). F-statistics were reported with the model degrees of freedom (mdf), calculated by adding up the degrees of freedom of each term, and the residual degrees of freedom (rdf) calculated as the difference between the number of observations (n) and the mdf. To create the thermal performance curves, we used the predictions from the statistical models. The thermal optimum and the thermal performance breadth, i.e. the range of temperatures over which an animal can maintain 95, 80 and 50% of its maximal performance, were extracted from the model predictions (Taylor et al. 2021). Note that positive and negative predicted values at 2.8 °C and 38.4 °C can seem biologically impossible from our values observed at each CT. However, these predictions only indicate predicted CTs at colder/warmer temperature (Figs. 4, 5).

Results

Critical temperature

The studied marsh frogs showed a CT_{min} (mean \pm SE) of 2.80 ± 0.21 °C, a CT_{max} of 38.40 ± 0.09 °C, and an average thermal range ($CT_{max} - CT_{min}$) of 35.60 ± 0.23 °C (Fig. 3). There was no significant effect of sex (ANCOVA; $F_{1,17} = 0.13$, $p = 0.91$) or SVL ($F_{1,17} = 0.09$, $p = 0.76$) for CT_{min} . However, for CT_{max} , the effect of sex was

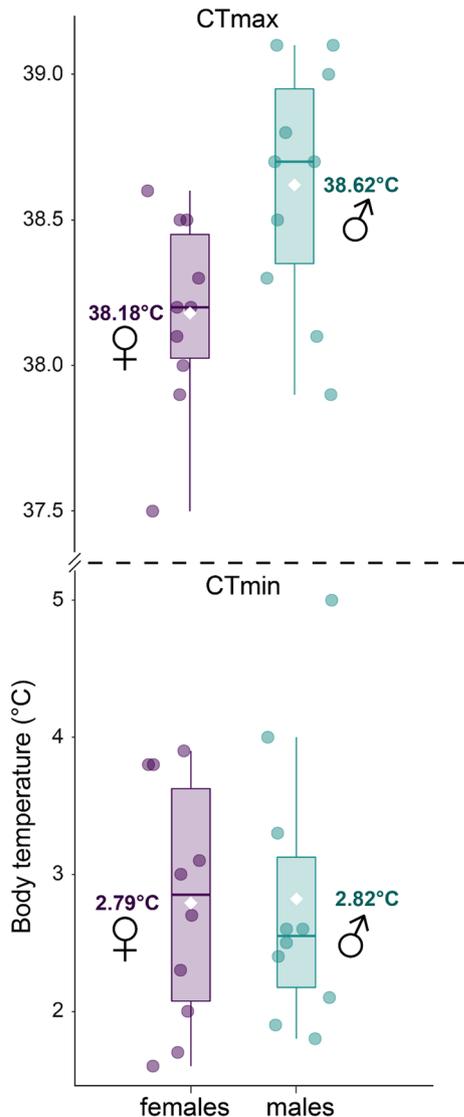


Fig. 3 Thermal tolerance in males and females of the invasive marsh frog. Critical thermal minimum (CT_{min}) is shown on the upper panel and the critical thermal maximum (CT_{max}) on the lower panel. A white diamond indicates the mean value and the middle line within the boxplot the median. Females are shown in purple and males in green. To allow a better visualisation of individuals, the Y-axis scale was rescaled for CT_{max}

significant ($F_{1,17} = 7.49$, $p = 0.01$) with males having a slight but significantly higher upper thermal tolerance (0.44 °C) than females (Fig. 3). Snout–vent length had no significant effect on CT_{max} ($F_{1,17} = 2.08$, $p = 0.16$).

Preferred temperature

After thermoregulating for an hour, marsh frogs showed an average body temperature of 21.8 ± 3.71 °C. There was no significant effect of either sex ($F_{1,26} = 0.12$, $p = 0.73$) or SVL ($F_{1,26} = 0.19$, $p = 0.67$).

Stamina

Based on the adjusted R -squared values (GAMM), temperature, SVL and sex together explained 82.8% of variation in the distance travelled by the frogs before exhaustion. Temperature had a significant highly non-linear effect on the distance travelled before exhaustion ($\text{edf} = 3.91$; $F_{20.27, 147.77} = 185.23$, $p < 0.01$; Fig. 4a). Predictions from the model fit estimated a thermal optimum (T_{opt}) at 24.32 °C and frogs were able to maintain more than 95, 80 and 50% of their performance over a range of, respectively, 11.58, 20.58 and 28.06 °C (Fig. 4a). Snout–vent length showed a significant highly non-linear effect on the distance travelled before exhaustion ($\text{edf} = 4.67$; $F_{20.27, 147.77} = 3.55$, $p < 0.01$). There was no significant effect of sex ($t_{21} = 1.32$, $p = 0.18$).

Based on the adjusted R -squared values (GAMM), temperature, SVL and sex together explained 66.4% of variation in time spent moving by the frogs before exhaustion. Temperature showed a significant highly non-linear effect on time spent moving before exhaustion ($\text{edf} = 3.92$; $F_{15.02, 152.98} = 78.10$, $p < 0.01$; Fig. 4b). Predictions from the model fit estimated a thermal optimum at 11.70 °C and frogs were able to maintain more than 95, 80 and 50% of their performance over a range of 4.82, 10.09 and 24.52 °C, respectively (Fig. 4b). There were no significant effects of SVL ($F_{15.02, 152.98} = 1.15$, $p = 0.28$) and sex ($t_{21} = -0.10$, $p = 0.91$).

Based on the adjusted R -squared values (GAMM), temperature, SVL and sex together explained 88.1% of the variation in average speed of the frogs. Temperature showed a significant highly non-linear effect on average speed during the endurance trial ($\text{edf} = 3.96$; $F_{16.23, 151.76} = 272.75$, $p < 0.01$; Fig. 4c). Predictions from the model fit estimated a thermal optimum at 27.20 °C and frogs were able to maintain more than 95, 80 and 50% of their performance over a range of 4.97, 10.58 and 21.88 °C, respectively (Fig. 4c). Snout–vent length showed a significant ($F_{16.23, 151.76} = 1.83$, $p = 0.17$) positive linear effect ($\text{edf} = 1$). There was no significant effect of sex ($t_{21} = 0.75$, $p = 0.45$).

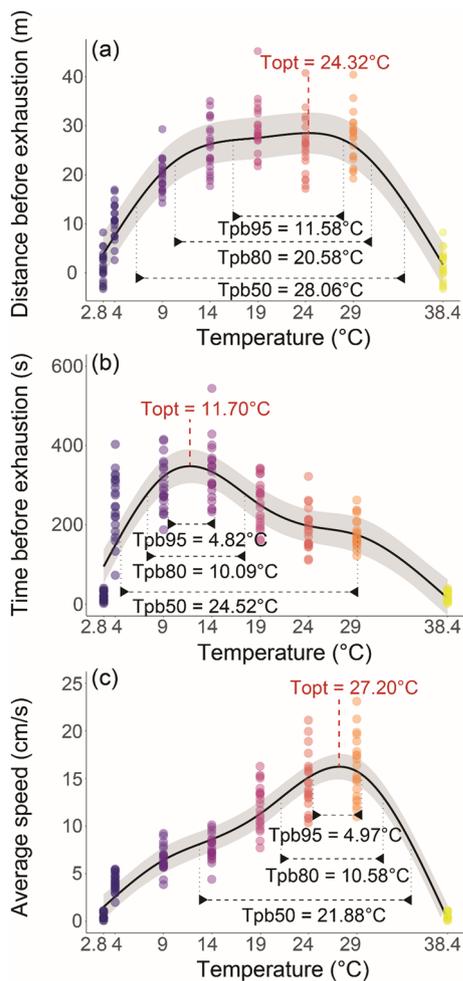


Fig. 4 Thermal performance curves predicted from GAMM models for **(a)** the distance travelled before exhaustion, **(b)** the time spent moving before exhaustion, and **(c)** the average “speed” (i.e. distance divided by time before exhaustion) in invasive marsh frogs. Thermal optimum (T_{opt}) and thermal performance breadths (T_{pb}) at 50, 80 and 95% of the maximal performance are displayed. The uncertainty of the estimate is displayed through a 95% grey confidence band. Data are shown as dots for each individual. Temperature is shown by the colour gradient

Jump force

Based on the adjusted R -squared values (GAMM), temperature, SVL and sex together explained 89.2% of variation in jump force of the frogs. Temperature showed a significant ($F_{21.73, 128.26} = 237.37$, $p < 0.01$; Fig. 5) highly non-linear relationship ($\text{edf} = 3.97$) with jump force. Predictions from the model fit estimated a thermal optimum at 29.77°C and frogs were able to maintain more than 95, 80 and 50% of their performance over a range of 4.53, 10.16 and 26.35 $^{\circ}\text{C}$, respectively (Fig. 5). Snout–vent length showed a significant effect ($F_{21.73, 128.26} = 5.94$, $p < 0.01$) that was highly non-linear ($\text{edf} = 2.67$). However,

no significant effects were detected for sex ($t_{25} = 1.08$, $p = 0.28$).

Discussion

Marsh frogs showed a thermal tolerance that covers the entire annual variation of bottom pond temperatures and 76.5% of the annual variation in air temperature, with colder temperature being the only limit (Fig. 6, Table 1). It is important to point out that air temperature is a representation of the environmental temperature in shaded area and that solar radiation can generate surface temperatures far exceeding observed air temperatures under the shade. These results suggest that warmer temperatures may allow invasive marsh frogs to have an increased margin of locomotor activity particularly in shaded conditions or during night time. Nonetheless, even if their upper thermal limit is 5.2°C greater than the current maximal air temperature recorded (Fig. 6), extreme thermal events may limit their fitness before reaching this critical limit. It is also interesting to note that under laboratory conditions, marsh frogs try to maintain a body temperature (T_{pref}) that is higher than the average temperature they can experience in shaded areas (Fig. 6, Table 1). The same applies for their thermal performance breadths on distance jumped before exhaustion, average speed and jump force (Fig. 6, Table 1). Our data suggest that warmer air temperature may allow them to better spread across shadier habitats and also to colonise previously unfavourable ponds whilst continuing to inhabit more exposed ponds (Denoël et al. 2022) due to their ability to bask or dive into the pond to thermoregulate. Lastly, regarding variation between males and females, a slight difference was observed in CT_{max} but not for other traits, suggesting a similar thermal biology for the two sexes.

Marsh frogs, an overlooked invasive species with a broad thermal tolerance

Despite the extent of their invasion over a large part of Western Europe, the invasive potential of the marsh frog is underestimated (Pille et al. 2021). Here we show that their thermal tolerance extends to over 35°C with an upper thermal limit beyond the maximum water and air temperatures (in shadow) in their natural environment. Similar tolerance ranges were found in the three most invasive amphibians: *Rhinella marina* (Johnson 1972), *Xenopus laevis* (Araspin et al. 2020) and *Lithobates catesbeianus* (Lotshaw 1977) (Suppl. Table S1). The first two species showed thermal tolerance ranges that are, respectively, 9% and 37% narrower than the marsh frogs (Suppl. Table S1). The thermal tolerance of *Lithobates catesbeianus* may, however, appear wider than that of marsh frogs

Fig. 5 Thermal performance curve predicted from GAMM models on jump force in invasive marsh frogs. Thermal optimum (T_{opt}) and thermal performance breadths (T_{pb}) at 50, 80 and 95% of the maximal performance are displayed. Uncertainty of the estimate is displayed through a 95% grey confidence band. Data is shown as dots for each individual. Temperature is shown by the colour gradient

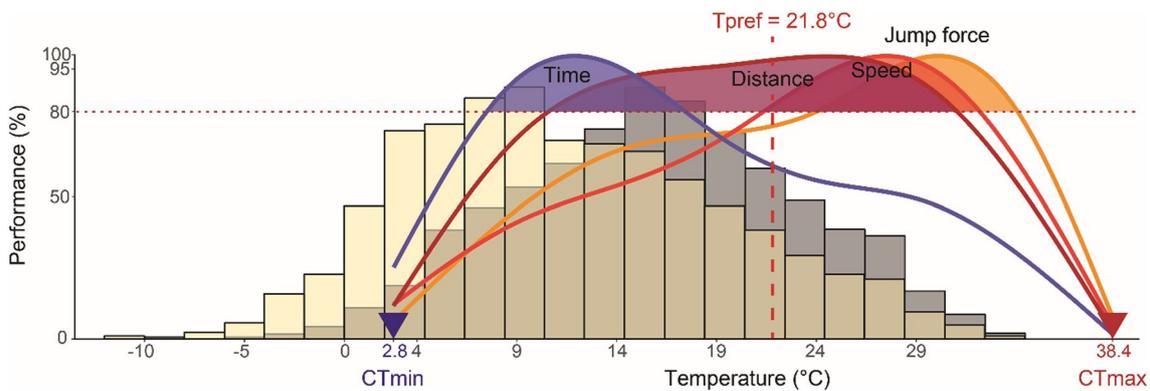
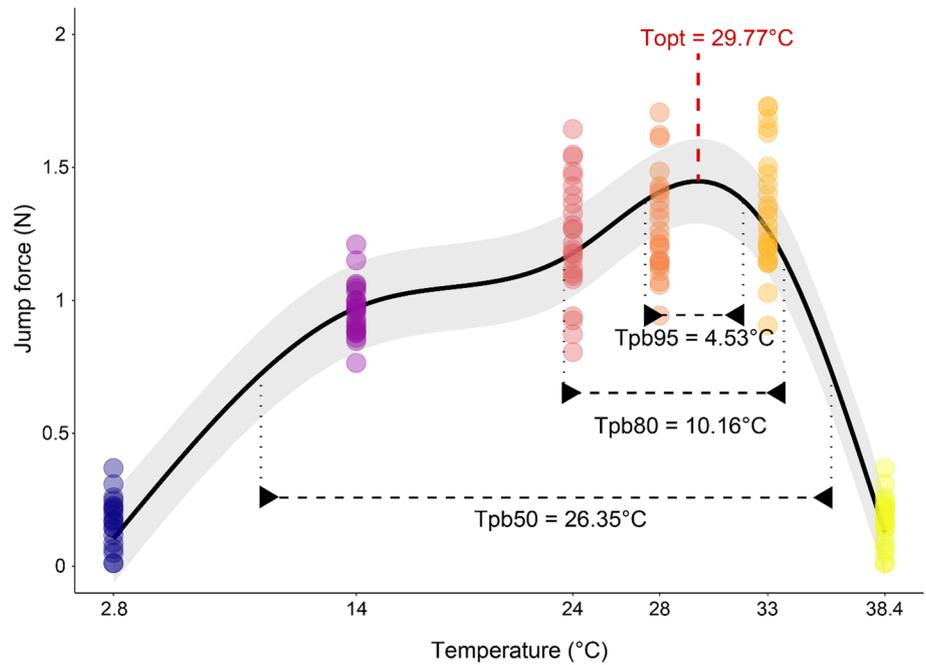


Fig. 6 Graphical summary of the thermal response of the invasive marsh frog (*Pelophylax ridibundus*), to the air temperature during their activity (grey) or during the annual variation (beige). The dotted

horizontal red line indicates the 80% thermal performance breadth. The dashed vertical red line indicates the preferred temperature (T_{pref})

(38.55 °C, Suppl. Table S1), yet was measured using the lower lethal temperature instead of the loss of righting response. Spellerberg (1972) evaluated both CT_{min} using the loss of righting response and the lethal minimal temperature on ten species of reptiles and the mean gap (\pm SD) between each measurement was 8.4 ± 2.5 °C. Overall, a broad thermal tolerance may allow invasive ectotherms to maintain a long period of activity year-round, in addition to being able to face daily variations in temperature as well as temperature extremes. We can expect from predicted warming that the environmental temperatures may remain within the thermal tolerance range of invasive ectotherms with a high upper thermal tolerance which may lead to

phenological changes (Sheridan et al. 2018). However, the lack of knowledge on the thermal tolerance of native amphibians is a limitation preventing a mechanistic understanding of their respective success. Some data on palmate newts from the studied area highlight that they will have a lower reproductive fitness in warmer temperatures (Galloy and Denoël 2010) and that droughts could impact population sizes in natural populations (Denoël 2006). Moreover, even in the scenario of thermal adaptation of some native species, the increased invasion of habitats due to the high thermal tolerance of marsh frogs would likely lead to multiple situations of habitat overlap with the native species and a consequent increase in predation risk (Pille et al. 2021).

Is warmer better?

A recent study (Denoël et al. 2022) highlighted the invasiveness potential of this species and, more specifically, revealed that sun exposure was one of the pond features associated with their occurrence. Marsh frogs prefer habitats with a high sun exposition to bask under the current climatic conditions. Our data show that marsh frogs try to maintain a body temperature higher than the average air temperature found in a shaded environment. Niche shifts have already been observed at a larger scale in invasive amphibians (Rödger et al 2017; Tingley et al 2014), and our results suggest that warmer climates may facilitate the invasibility of habitats cooler than open landscapes, such as forests, and therefore increasing their overlap with native amphibians in these environments.

Each performance trait showed, similarly, a thermal optimum at a temperature that was higher than the mean air temperature in addition to showing broad thermal performance breadths. Warmer climatic conditions may shift the environmental temperature to conditions that will maximise most performance traits of this frog species and therefore its invasion potential. Furthermore, broad performance breadths indicate that this species is able to maintain performance despite daily variations in temperature. This is particularly the case for dispersal, as suggested by the distance moved before exhaustion, where 80% of its maximum capacity covers 58% of the frog's absolute thermal tolerance (Fig. 6). Araspin and co-authors (2020) similarly measured the thermal performance breadth at 80% for exertion (mean \pm SE = 8.25 ± 0.4 °C) in African clawed frogs, *Xenopus laevis*, a worldwide invasive species that was introduced in Western France and that shares the habitat with introduced populations of marsh frogs. Yet this range is 60% narrower, unveiling again the wide performance breadth and invasive potential of marsh frogs.

Thermal performance differs across traits

Given that an increase in temperature accelerates chemical reaction rates (Tattersall et al. 2012) which in turn drive the thermal dependence of muscle contraction (Bennett 1984), it is not surprising that all performance traits were significantly affected by temperature. Average speed during the endurance trial and jump force increases with temperature to reach their optimum at high temperatures and finally drops off near the critical maximal limit of the animal, typical for burst performance traits (Batty and Blaxter 1992; Pinch and Claussen 2003; Araspin et al. 2020). Both traits follow the response of chemical reaction rates to an increase in temperature predicting that locomotor capacity is optimised at high temperatures that are not often reached in a shaded environment (Fig. 6). These two traits are essential

for predator escape or prey capture, both relevant to the survival of invasive species.

Time and distance before exhaustion show, however, different thermal responses compared to one another, and also different from what was observed for burst performance. Because endurance capacity is dependent on oxygen uptake and the metabolic rate of the organism, we expected their thermal performance curves to follow the response observed for enzymatic reactions. James and co-authors (James et al. 2012) also showed that higher temperatures maximise the performance at the muscle level for both burst performance and endurance. Interestingly, time and distance before exhaustion were not maximised at high temperatures. This difference across traits needs to be quantified and used in the future predictions. Mechanistic models, for example, often use data on a single trait which does not reflect the overall thermal performance of an organism (van Damme et al. 1991; Kellermann et al. 2019). The time spent in movement is maximised at lower temperatures and declines towards the critical maximal limit. This trait being maximal at lower temperature may not reflect the dispersal of the frog, because longer time spent in movement does not mean more distance covered per se. This result seems mostly explained by slower responses and shorter jumps, but this requires further study. Lastly, the distance covered before exhaustion increases from low temperatures to quickly show a broad plateau. This low sensitivity to temperature is reflected through the shape of its thermal performance curve (Figs. 4a, 6), which is typically not observed in other studies on the thermal sensitivity of locomotion (Bennett 1990; Angilletta 2001; Araspin et al. 2020). This thermal response suggests that the distance covered before exhaustion, at least in invasive marsh frogs, is likely determined by a number of physiological factors that each cover different parts of the overall thermal range. In contrast to jump force which is mostly determined by muscle contractile properties, stamina is indeed also driven by the functioning of the cardiovascular and the respiratory systems.

Conclusions

Integrating multiple-trait measures with environmental variables enhances our understanding of the thermal dependence of invasive ectotherms (Ryan and Gunderson 2021; Young et al 2022). Broad thermal tolerance and thermal preferences with optima of performance at temperatures higher than the air temperature of their environment were observed for the invasive marsh frogs studied here. As previously suggested (Hellmann et al. 2008), all steps of the invasion process can benefit from an increase of temperature if it leads to more frequent temperatures within their thermal performance breadth and closer to

their thermal preference. Our results support this hypothesis with warmer temperatures favouring jumping capacity as well as the distance moved, and the average speed. This can allow animals to cover more distance which can facilitate their spread, including across shaded habitats. Dufresnes et al. (2017a) questioned whether the rapid warming of the last two decades may have helped invasive *Pelophylax* to successfully spread and establish in the region. Given that the annual mean air temperature in the region has been increasing by more than 0.05 °C each year since 1980 (field meteorological data), we suggest that climate change has indeed favoured the spread of this invasive species and will continue to do so given the current predictions of a mean warming in the range of 0.9 to 5.6 °C by the end of the twentieth century (Ali et al. 2022).

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability The code used for statistical analysis was written in R and is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

Consent to participate Not applicable.

Consent for publication All authors gave consent.

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