SYMPOSIUM

Rapid Shifts in the Temperature Dependence of Locomotor Performance in an Invasive Frog, Xenopus laevis, Implications for Conservation

Laurie Araspin,[*,†] Anna Serra Martinez,[*] Carla Wagener,[†] Julien Courant,[*] Vivien Louppe,[‡] Pablo Padilla,[*,§] John Measey[†] and Anthony Herrel 🅾 [1,*]

*Bâtiment d'Anatomie Comparée, UMR 7179-CNRS, Département Adaptations du Vivant, Muséum National d'Histoire Naturelle-Sorbonne Universités (MNHN), 55 rue Buffon, 75005 Paris, France; †Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch 7602, South Africa; ‡Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National, d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP 51, 75231 Paris, France; §Behavioural Biology Group, Laboratory of Fish and Amphibian Ethology, Freshwater and OCeanic Science Unit of reSearch (FOCUS), University of Liège, 4020 Liège, Belgium

The last two authors contributed equally to this work.

1E-mail: anthony.herrel@mnhn.fr

Synopsis Temperature is a critical abiotic factor impacting all aspects of the biology of organisms, especially in ectotherms. As such, it is an important determinant of the potential invasive ability of organisms and may limit population expansion unless organisms can physiologically respond to changes in temperature either through plasticity or by adapting to their novel environment. Here, we studied the African clawed frog, Xenopus laevis, which has become invasive on a global scale. We compared adults from an invasive population of western France with individuals from two populations in the native range in South Africa. We measured the thermal dependence of locomotor performance in adults given its relevance to dispersal, predator escape, and prey capture. Our results show significant differences in the limits of the 80% performance breadth interval for endurance with the French population showing a left shift in its limits congruent with the colder climate experienced in France. The French invasive population was introduced only about 40 years ago suggesting a rapid shift in the thermal physiology. Given that all individuals were acclimated under laboratory conditions at 23°C for 2 months this suggests that the invasive frogs have adapted to their new environment. These data may allow the refinement of physiologically informed species distribution models permitting better estimates of future ranges at risk of invasion.

Introduction

Biological invasions have increased dramatically over the past two centuries (Seebens et al. 2017). These invasions are due to anthropogenic causes (Liendo et al. 2015) and have changed patterns of biodiversity at a global scale (Simberloff et al. 2013). However, most introductions do not lead to invasions and a species can be invasive in one locality but not another (Mack et al. 2000). Indeed, in many cases intraspecific variation in invasion success has

been demonstrated, raising the question of its drivers (Zenni and Nuñez 2013). Species are often introduced in regions that differ dramatically in climate or habitat from their native ranges (Lodge 1993; Facon et al. 2006). Consequently, introduced species will face novel environments, stressors, and a host of additional selective pressures that are different from those encountered in their native range (Novak 2007). Subsequently, these introduced populations tend to evolve different traits in their introduced

compared with their native ranges (Maron et al. 2004). Many organisms that have established in novel environments have shown the potential for rapid adaptation (Richardson and Pyšek 2006; Lavergne and Molofsky 2007; Urban et al. 2007), which can occur within 20 generations or less (Prentis et al. 2008). For example, invasive cane toads have been shown to rapidly evolve dispersal phenotypes due to spatial sorting (Shine et al. 2011). Whereas certain life history and phenotypic traits of invading species may facilitate expansion by enabling them to outcompete indigenous species (Catford et al. 2009; Cortes et al. 2016), others may prove to be disadvantageous to the invader when environmental conditions change (Simberloff and Gibbons 2004). This suggests that a high degree of plasticity or adaptability would be beneficial for invasive species.

Selection on dispersal capacity, particularly locomotor traits (Stevens et al. 2010), can be expected to occur in expanding invasive populations once established. However, the dispersal ability of an individual depends on many features, including temperature (Bestion et al. 2015). Understanding how temperature impacts locomotion and dispersal is thus critical to predict future range expansions. Temperature is a characteristic of an animal's habitat and one of the dimensions of the ecologic niche (Magnuson et al. 1979). Cellular responses to temperature are linked to the metabolism supplying ATP for cellular maintenance, membrane and protein synthesis (Hulbert and Else 2000), and play a role in growth, reproduction, and locomotor performance. Thus, these processes have direct fitness consequences (Johnston and Temple 2002; Guderly 2004). Temperature performance curves describe the physiological capacity of an organism to respond to variation in temperature (Angilletta 2006; Sinclair et al. 2016) and are a useful tool to quantify the potential for a species to thrive under varying thermal conditions. Locomotor performance is particularly relevant as it is fitness-relevant (Arnold 1983), impacting survival and prey capture (i.e., burst performance traits), and dispersal (endurance capacity). In ectotherms, locomotor performance is directly dependent on temperature and as such variation in the temperature range in a novel area may determine the success of establishment and spread of an invasive species. However, the thermal environment often varies seasonally and daily, resulting in an intrinsic plasticity in the response of most animals to temperature (Osborn and Briffa 2006). Consequently, a greater plasticity in the dependence of locomotor performance on temperature may predispose certain organisms to become successful invaders.

The African clawed frog, Xenopus laevis, is a principally aquatic frog native to sub-Saharan Africa (Furman et al. 2015) and is widely used in laboratories worldwide. This species shows important phenotypic differentiation between populations in its native range (Du Preez et al. 2009) suggesting that it is particularly plastic in its physiology. The escape or voluntary release of individuals has led to the establishment of populations on four continents: Asia, Europe, South America, and North America (Measey et al. 2012). The invasive population from France is of particular interest due to its ongoing expansion and has been well studied in terms of its morphology and physiology (Louppe et al. 2018; Padilla et al. 2019a, 2019b), locomotor performance (Louppe et al. 2017), reproduction (Courant et al. 2017), behavior (Kruger et al. 2019), and genetic composition (De Busschere et al. 2016). Moreover, negative impacts on native biota have been demonstrated (Courant et al. 2018a, 2018b). Interestingly, the invasive population in France faces a different climate (oceanic temperate) compared with the native climate in South Africa (Rödder et al. 2017; Table 1). Given that the population has expanded rapidly over the past 40 years (Vimercati et al. 2019) this suggests that they either show broad thermal tolerance and plasticity or that they have adapted to the local climate.

Previous studies have suggested that future distribution scenarios for global invasions will be improved by the investigation of traits leading to invasiveness coupled to the dynamics of introduced species (Courchamp et al. 2017). Moreover, a comparison of suites of morphological or physiological traits from native and non-native populations may help to understand the relationship between adaptive responses and successful invasions (García et al. 2013). Studies of the thermal sensitivity of locomotor performance can provide a useful means to understand how physiological traits can limit species distributions and may help to identify and characterize future range expansions (Chown et al. 2010). The aim of the present study is to test whether the thermal sensitivity of locomotor performance differs in invasive and native populations (France and South Africa) of X. laevis. Specifically, we test whether performance breadths and optimal temperatures for stamina and burst performance in addition to critical thermal limits differ between populations. To do so we analyzed terrestrial endurance and jumping capacities for individuals from the invasive (France) and native (South Africa) ranges.

Table 1 Mean temperature, seasonal variability, extreme annual temperatures, and coldest and warmest month temperatures in France and in the east and west South Africa

Sites	Bouillé St-Paul (France, Deux-Sèvres)	Stellenbosh (South Africa, Western Cape)	St Lucia (South Africa, Eastern Africa)
Mean temperature (°C)	11.79	17.18	21.32
Seasonal variability	542.66	372.52	280.21
Maximal temperature (°C)	23.00	27.20	31.30
Minimal temperature (°C)	−0.50	6.60	10.70
Mean temperature of the warmest month (°C)	18.63	21.60	24.53
Mean temperature of the coldest month (°C)	5.42	12.57	17.68

Note: Data were derived from Worldclim2 (Fick and Hijmans 2017).

Materials and methods

Individuals used in this study were caught in two different areas in South Africa ($N=30$, 12 males and 18 females; KwaZulu-Natal $N=15$, 8 females and 7 males; and Western Cape $N=15$, 10 females and 5 males). Animals from the two regions in South Africa showed no differences in their thermal responses (Stamina: $F_{1,24}=0.16$; $P=0.69$; Burst: $F_{1,23}=1.02$; $P=0.322$) and as such the data were pooled for all subsequent analyses. Individuals from the invasive population originated from western France (Deux-Sèvres; $N=43$, 23 males and 20 females). Upon arrival in the laboratory in Paris each individual was pit-tagged allowing a unique identification. Animals were housed at the Function and Evolution Laboratory of the National Museum of Natural History in Paris, France. Specimens from the native population were maintained in 30 L aquaria, two per tank and those from the invasive population were housed in 65 L aquaria with 5–10 individuals per tank. Animals were fed thrice weekly with frozen heart beef or mosquito larvae. The temperature of water was maintained at 23°C and animals were acclimated at this temperature for 2 months before starting the experiments. All protocols were in accordance with the guidelines of institutional animal care and use committee at the MNHN.

Morphometrics

Body dimensions were measured following Herrel et al. (2012). The mass was measured with a digital scale (Ohaus, Brooklyn, NY, USA; precision ±0.1 g) and snout–vent-length (SVL) was measured using a pair of digital calipers (Mitutoyo; precision ± 0.01 mm).

Critical minimal and maximal temperatures

Individuals were placed in individual containers with some water (to prevent dehydration) and put in an incubator (Aqualytic-LIEBHERR, TC 256 G/256 L/2–40°C) where temperature was decreased or increased slowly (an average of 2°C each 45 min and 1°C each 45 min from 6°C downward for minimal temperature and from 28°C upward for maximal temperature). Animals were warmed up slowly as their thermal inertia was substantial and faster rates resulted in animals being cooler or warmer than the temperature set on the incubator. Animals were inspected regularly and checked for the lack of a righting response. As soon as animals were no longer able to turn over after having been placed on their back, we considered that temperature (measured with a thermocouple inserted into the cloaca) to be that animal's critical temperature.

Performance

Stamina tests were performed at 19°C, 23°C, 27°C, and 31°C. We were unable to measure stamina at 16°C as animals warmed up during the stamina tests often up to 2°C above their initial temperature of 16°C. The muscle contractions occurring during repeated jumping likely produce enough heat to warm up the animals over the course of a stamina trial which lasted often 5–6 min at these low temperatures. Individuals were placed in individual containers with some water (to prevent dehydration) for 3 h in an incubator set at the desired test temperature. For each trial, body temperature was recorded using a K-type thermocouple before and after performance. The room temperature was set as close as possible to the test temperature. Measures of stamina were performed by chasing animals individually until exhaustion (animals unable to right themselves when put on their back) across a 3 m long circular track with a humified cork substrate (Herrel and Bonneaud 2012; Louppe et al. 2017). The total distance and time to exhaustion at the end of the trial were recorded. After each trial animals were returned to their tank, fed and left to rest for at least 2 days. Trials were repeated twice per individual and the

maximal time and distance were retained for further analyses.

Burst performance was measured at 16°C, 19°C, 23°C, 27°C, and 31°C. Individuals were placed in small containers with some water for 3 h in an incubator set at the desired test temperature. Jump force data were obtained via a force plate (Kistler Instruments AG, Type 5691A; see Herrel et al. 2014). Animals were placed on the force plate and were stimulated to jump five or six times within a 1-min recording session. Forces were recorded at 500 Hz and we used the Kistler Bioware software to extract peak X, Y, and Z forces (in Newtons). We then calculated the vector sum of the three forces and used the resultant force in all further analyses. Three trials per individual were recorded and the maximum jump force across all jumps and all trials was retained for further analyses.

Statistical analyses

In order to fulfill assumptions of normality and homoscedasticity, all data were $\log_{10}$ transformed before analyses. Analyses were performed using R (version i386 3.4.2; R Core Team 2019). To test for differences in locomotor performance (burst and stamina) between populations, univariate analyses of variance (ANOVAs) were run. Within populations (i.e., South Africa and France) we further tested for effects of temperature, mass, sex, SVL, and their interactions on locomotor performance using repeated measures multivariate analyses of variance (MANOVAs). Next, pairwise multiple comparisons tests (pairwise.t.test, "Stats" package version 3.4.2) with Bonferroni–Holm adjusted P-values were performed to test which temperatures differed from one another (temperature range: Stamina [19°C, 23°C, 27°C, and 31°C]; Burst [16°C, 19°C, 23°C, 27°C, and 31°C]). For each individual thermal performance curves (Angilletta 2009) were created using the minimum convex polygon method (Van Berkum, 1986). Optimal temperatures as well as temperature breadths T_{pb80} and T_{pb95} were analyzed using univariate ANOVAs to test for differences between populations and performance traits.

Results

Within the native population (South Africa) a significant difference in SVL ($F_{1,24} = 36.56$; $P < 0.001$) and mass ($F_{1,24} = 40.22$; $P < 0.001$) was observed with females being larger than males (Table 2). No differences in mass and SVL were observed between sexes in our sample of the invasive population (France).

Table 2 Morphometric measurements and sample size of invasive (France) and native (South Africa) populations

| Population		SVL (mm)	Mass (g)
France	Females ($N=20$)	73.54±2.84	53.27±5.30
	Males ($N=23$)	67.51±1.06	38.69±1.37
South Africa $N_{KZN}=15$ $N_{WC}=15$	Females ($N=18$)	75.96±1.75	46.87±2.67
	Males ($N=12$)	57.54±1.06	23.15±1.05

Note: Table entries are means±standard errors.

Stamina

Temperature significantly affected the maximal distance jumped until exhaustion in native ($F_{3,54} = 58.87$, $P < 0.001$;) and invasive *X. laevis* ($F_{1,32} = 42,68$; $P < 0.001$; Figure 1 and Table 3). SVL had a significant effect on the maximum distance jumped in native *X. laevis* ($F_{3,96} = 159.04$, $P < 0.001$). Temperature also had a significant impact on the time spent jumping until exhaustion for the native ($F_{3,54} = 113.52$, $P < 0.001$) and invasive populations ($F_{3,96} = 151.48$, $P < 0.001$). Moreover, the time spent jumping was dependent on the mass of the individuals ($F_{3,54} = 2.98$, $P = 0.04$). In the invasive population, a significant interaction between sex and temperature was observed ($F_{3,96} = 3.76$, $P = 0.013$). *Post hoc* tests showed that, in terms of distance, French frogs performed significantly different between each temperature ($P < 0.001$) in contrast to frogs from South Africa which differed for some but not all temperatures (Table 4). *Post hoc* tests on the time to exhaustion showed significant differences between all temperatures for both populations (invasive: $P < 0.001$; native: $P < 0.05$). Native frogs performed significantly better than invasive frogs at 23°C ($F_{1,64} = 47.91$, $P < 0.001$), 27°C ($F_{1,64} = 34.01$, $P < 0.001$), and 31°C ($F_{1,64} = 21.99$, $P < 0.001$), but not 19°C ($F_{1,64} = 0.448$, $P = 0.51$). The time to exertion further differed significantly between populations at all tested temperature ($P < 0.001$, for all temperatures) with invasive frogs becoming exhausted sooner.

Burst performance

Temperature significantly affected burst performance in the native population ($F_{4,70} = 20.854$; $P < 0.001$; Figure 2 and Table 5). SVL and mass also significantly impacted jump force in these animals (SVL: $F_{1,17} = 10.77$, $P = 0.004$; mass: $F_{1,17} = 7.17$, $P = 0.015$). In the invasive population, temperature also significantly affected jump force ($F_{4,118} = 17.73$, $P < 0.001$; Figure 2 and Table 5). Jump force was further also dependent on SVL and
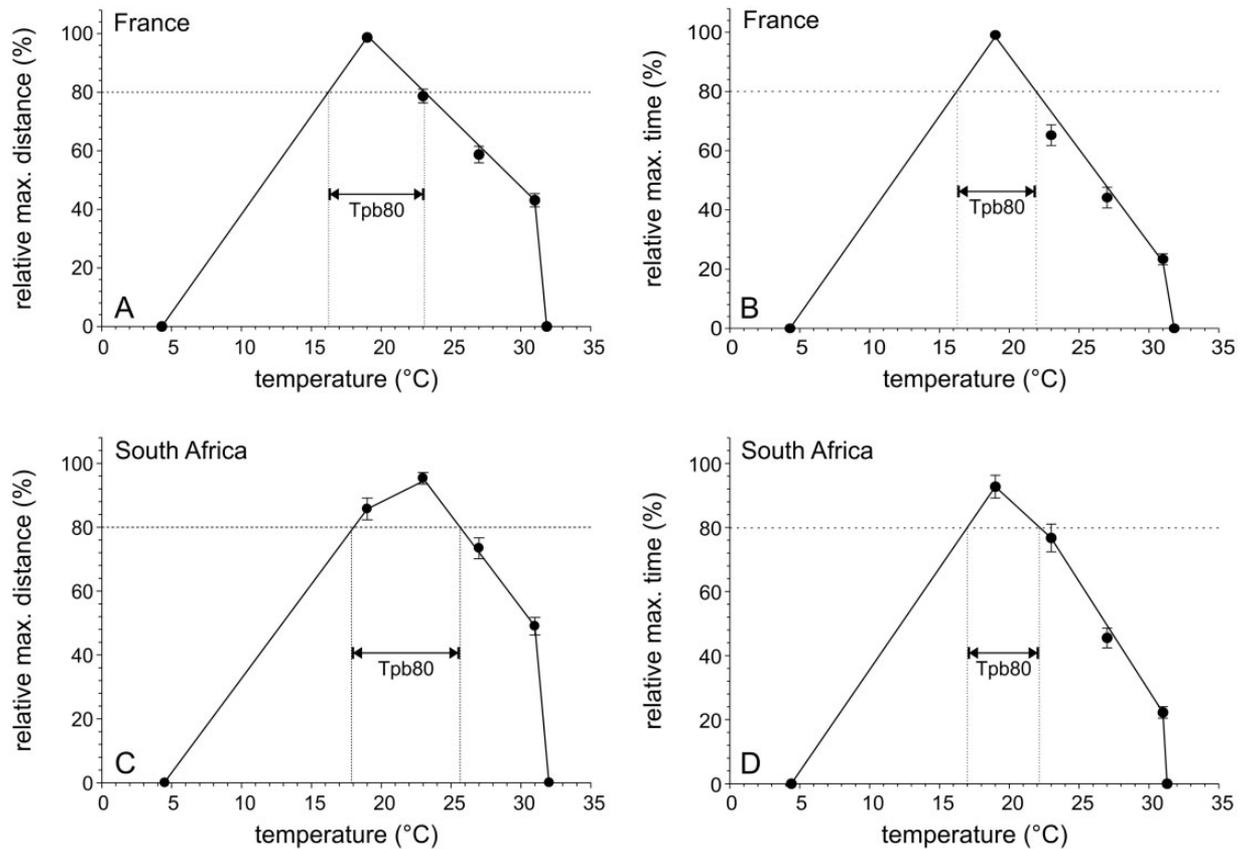
Fig. 1 Temperature performance curves illustrating the impact of temperature on endurance capacity in terms of distance (**A**, **C**) and time (**B**, **D**) for *X. laevis* from France (A, B) and South Africa (C, D). Indicated are the 80% thermal performance breadths for each trait and each population. Symbols represent means ± standard errors of the mean.

Table 3 Stamina of French and South Africa populations at different temperatures

Test temperature ($^\circ$C)	Population	Distance (cm)	Time (s)
France N=40; South Africa N=25 (N_{KZN} = 13, N_{WC}=12)			
19	France	2664.75±141.65	258.58±20.85
	South Africa	2892.31±181. 85	357.76±35.10
23	France	2028.25±83.77	161.67±14.10
	South Africa	3111.38±134.48	277.94±21.89
27	France	1456.50±68.90	99.49±7.09
	South Africa	2409.61±132.29	161.68±13.42
31	France	1074.25±45.40	56.83±6.32
	South Africa	1582.31±84.43	79.18±6.84

Note: Table entries are means±standard errors.

sex in the invasive population (SVL: $F_{4,118} = 2.94$, $P = 0.023$; sex: $F_{4,118} = 5.25$, $P < 0.001$). *Post hoc* tests demonstrated significant differences between some, but not all, temperatures irrespective of the population of origin (Table 6). No significant differences in burst performance were detected between populations at the different test temperatures ($P > 0.05$; Table 5).

Optimal temperature, critical temperatures, and performance breadths

Temperature optima varied significantly between populations for stamina ($Topt_{France}$: 19.36°C; $Topt_{South Africa}$: 21.56°C; $F_{1,56} = 28.3$, $P < 0.001$; Table 7). For burst performance no differences in optimal temperature were detected, however ($Topt_{France}$: 23.94°C; $Topt_{South Africa}$: 24.48°C;

Table 4 *Post hoc* tests testing for differences in stamina (max. distance) for South African ($N = 26$) and for French ($N = 40$) *X. laevis*

	19°C	23°C	27°C
South Africa			
23°C	NS	–	–
27°C	0.0024	0.00022	–
31°C	<0.001	<0.001	<0.001
France			
23°C	<0.001	–	–
27°C	<0.001	<0.001	–
31°C	<0.001	<0.001	<0.001

$P > 0.05$). There were no significant differences between populations in their 80% and 95% thermal performance breadths (all $P > 0.05$). However, there are significant differences in the upper and lower limits of the performance breadth interval (80%: $F_{1,56} = 6.87$, $P < 0.01$; 95%: $F_{1,56} = 35.07$, $P < 0.005$; Table 7 and Figs. 1 and 2) indicating a left-shift of the temperature performance curve. Critical temperatures did not significantly differ between populations (CT_{min}: $F_{1,50} = 0.079$, $P = 0.78$; CT_{max} $F_{1,68} = 3.31$, $P = 0.07$; Table 8).
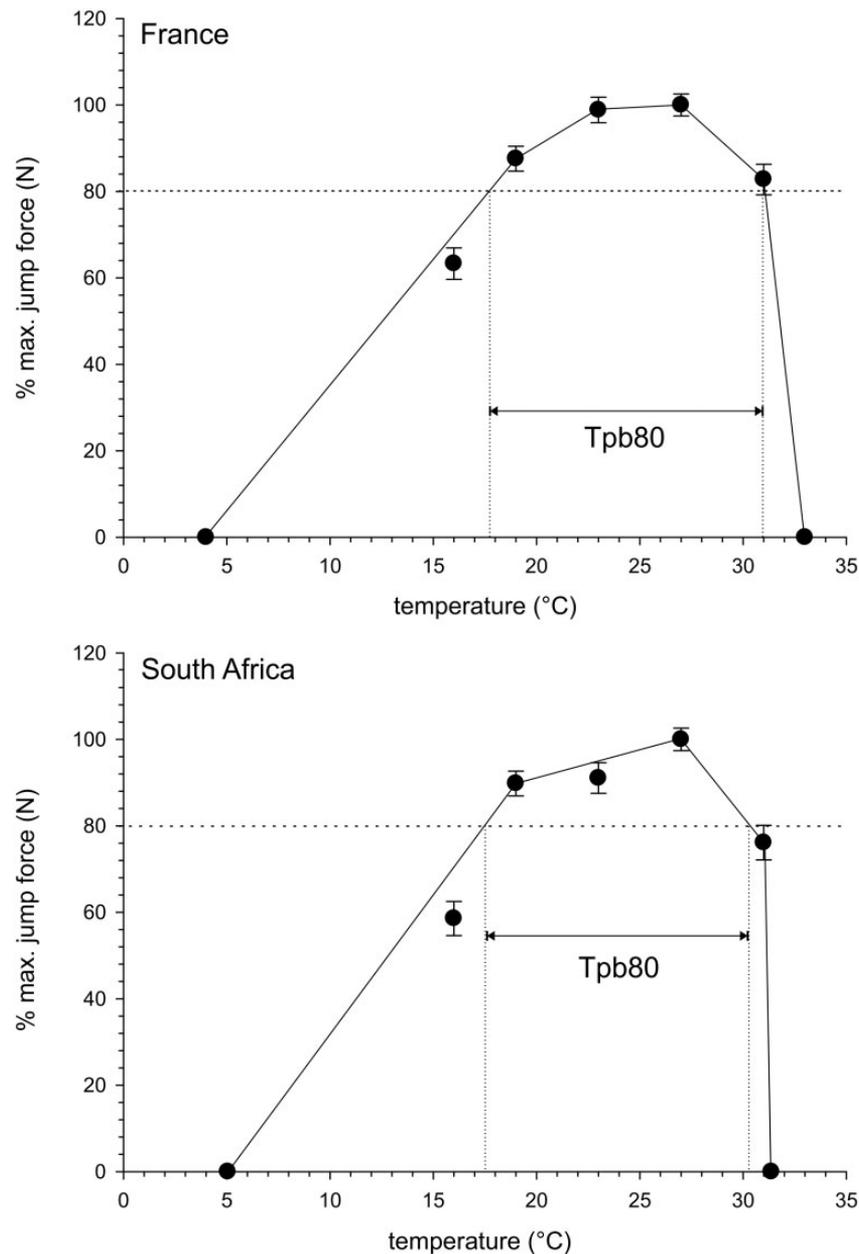
Fig. 2 Temperature performance curves illustrating the impact of temperature on jump force for *X. laevis* from France (top) and South Africa (bottom). Indicated are the 80% thermal performance breadths for each trait and each population. Symbols represent means ± standard errors of the mean.

Discussion

Critical temperatures

When organisms are confronted with temperatures approaching their thermal tolerance limits, they can often avoid these using behavioral strategies (Sinclair et al. 2016). Outside its physiological range an organism cannot maintain locomotor function and ultimately cannot survive (Angilletta 2009). This is a direct consequence of the thermal sensitivity of metabolic processes (Gillooly et al. 2001). Behavioral modulation may be less easy for principally aquatic animals like *X. laevis* and consequently the thermal tolerance limits can be expected to be broad. The thermal tolerance limits measured here were relatively broad. However, ectotherms from high latitudes often have even broader thermal breadths as thermal tolerance breadth increase with increasing latitude (Sunday et al. 2011). In our study thermal limits did not differ significantly between the native and invasive populations (France: 4.1–31.7°C; South Africa: 4.3–31.4°C) (Table 8). Thus, the invasive population has conserved the same physiological limits as the native population, in accordance with the idea that thermal ecology is conserved in many reptiles and amphibians (Sinervo et al. 2010). Moreover, if the limits in the native range are broad enough to cover the range of active temperatures in the invasive range, no changes would be expected.

Locomotor performance

Metabolism imposes strong constraints on resource allocation to fitness-relevant traits (Brown et al. 2004). Previous studies have suggested that thermal performance curves tend to have the same shape, with performance increasing with increasing temperature until a maximum is reached at the optimal temperature (T_{opt}) and then rapidly decreasing (Angilletta et al. 2002). Invasive and native populations in our study showed similar shapes of the thermal performance curve (Figs. 1 and 2). Interestingly, the temperature optima differed between the different performance traits with burst performance showing a higher optimal temperature than endurance

Table 5 Burst performance (jump force) in French and South-African populations at different temperatures

Test temperature (°C)	Population	Jump force (N)
France $N=31$; South Africa $N=25$ ($N_{KZN}=13$ and $N_{WC}=12$)		
16	France	0.62±0.06
	South Africa	0.67±0.06
19	France	0.92±0.09
	South Africa	0.99±0.06
23	France	1.01±0.12
	South Africa	1.03±0.09
27	France	1.01±0.09
	South Africa	1.13±0.08
31	France	0.77±0.09
	South Africa	0.86±0.07

Note: Table entries are means±standard errors.

Table 6 *Post hoc* tests testing for differences in burst performance in *X. laevis*

	16°C	19°C	23°C	27°C
France ($N=31$)				
19°C	<0.001			
23°C	<0.001	NS		
27°C	<0.001	0.00753	NS	
31°C	NS	NS	0.043	0.0040
South Africa ($N=25$)				
19°C	<0.001			
23°C	<0.001	NS		
27°C	<0.001	NS	NS	
31°C	<0.001	0.01	0.0082	0.0082

Table 7 Temperature optima and performance breadths for locomotor performance in *X. laevis* from French and South-African populations

	Population	Stamina (m)		Jump force (N)	
France $N=33$; South Africa $N=25$ ($N_{KZN}=13$ and $N_{WC}=12$)					
T_{opt} (°C)	France	19.36±0.20		23.94±0.78	
	South Africa	21.56±0.39		24.48±0.74	
T_{pb80} (°C)	France	8.25±0.40	16.3–24.55°C	9.99±0.60	18.88–28.88°C
	South Africa	8.08±0.52	18.02–26.1°C	10.28±0.71	19.03–29.31°C
T_{pb95} (°C)	France	3.05±0.22	18.21–21.27°C	4.61±0.54	21.81–26.42°C
	South Africa	3.24±0.32	20.34–23.58°C	4.88±0.73	21.91–26.79°C

Notes: Table entries are the means of optimal temperature and the 80% performance breadth±standard errors. Next to the means of the performance breadths are indicated the limits of the performance breadth interval.

Table 8 Minimum and maximum critical temperatures (CT_{min} and CT_{max}) for *X. laevis* from France and South Africa

Population	CT_{min}	CT_{max}
France $N=27$; South Africa $N=24$ ($N_{KZN}=12$ and $N_{WC}=12$)		
France	4.32±0.19	31.77±0.19
South Africa	4.40±0.20	31.31±0.20

Note: Table entries are means±standard errors.

capacity. This is in accordance with previous studies showing that thermal optima and preferences can differ for different performance tasks (Huey and Stevenson 1979; Van Damme et al. 1991; Martin and Huey 2008; Herrel and Bonneaud 2012). Burst performance appears to be physiologically optimized at higher temperatures than endurance capacity. In many animals jump performance increases with increasing temperature (James et al. 2007, 2012) until a physiological limit threshold (Hirano and Rome 1984). Moreover, it has been shown that the power produced by the iliotibialis muscle in *Xenopus tropicalis* increases with temperature, suggesting that warmer is better for burst performance (Herrel and Bonneaud 2012; James et al. 2012), in accordance with our results.

Optimal temperatures for endurance capacity differed between native and invasive populations (South Africa: 21.56°C, France: 19.36°C). Moreover, the absolute endurance was significantly greater in frogs from the native population, except at 19°C. Thus, invasive frogs performed relatively better at cooler temperatures compared with the native South African frogs. In France, the climate is colder than in South Africa (Table 1), a significantly different climatic niche compared with that in the native range (Rödder et al. 2017). The observed differences in thermal optima appear correlated with differences in environmental temperatures (Table 1), in accordance with the prediction that the thermal optimum will be set at the temperature most encountered in the environment (Huey and Kingsolver 1993; Navas et al. 2008). Variation in muscle contraction kinetics can explain variation in locomotor speed (John-Alder et al. 1989) and oxygen transport relevant for endurance capacity. In amphibians, the maximal rate of oxygen consumption is strongly dependent on temperature (Seymour 1972). Indeed, even the resting or basal metabolism in amphibians increases with temperature (Whitford 1973). In contrast to endurance capacity, native and invasive populations performed equally well for burst performance. It has been demonstrated previously that force production is less temperature dependent compared with muscle

contractive velocity or metabolic rate (Herrel et al. 2007) and as such the lack of differences in the thermal dependence of jump force is not unexpected.

Performance breadths

In addition to the shift in the thermal optimum for endurance capacity, a shift in the 80% thermal performance limits for endurance capacity was observed between the native and invasive populations. Indeed, the thermal performance curve shows a left-shift toward cooler temperatures of about two degrees in the invasive population. Consequently, the invasive French population appears better adapted to lower temperatures for endurance. However, the absolute breadth of the performance curve did not differ between populations showing that the overall shape of the performance curve did not evolve. This may suggest a level of intrinsic constraint to the ability in *X. laevis* to broaden its temperature performance curve beyond certain physiological limits.

Plasticity has a clear and ubiquitous role in promoting phenotypic changes in response to climate variation (Pigliucci 2005; Urban et al. 2014). As temperature affects both locomotion and skeletal muscle performance, some ectotherms show acclimation under different thermal environments in order to maintain skeletal muscle and locomotor performance (Johnston and Temple 2002; Padilla et al. 2019a). However, other studies have shown that thermal physiology may evolve. For example, in *Limnodynastes peronii* differences appear among populations with populations from cooler environments tending to perform better at lower temperatures (Wilson 2001). As the invasive population expressed differences in the optimal temperature for endurance and shifts in the thermal limits despite being kept in a common environment for several months at identical temperatures, our results suggest that *X. laevis* has effectively adapted to the thermal environment of its invasive range in France. As French individuals are derived from two distinct genetic lineages from southern Africa (De Busschere et al. 2016), the genetic admixture could have facilitated the observed thermal adaptation.

Species distribution models (SDM) are commonly used in ecological and evolutionary studies and use geographic information on species presence and absence in different climatic zones (Brown 2014) to make predictions on future ranges under different scenarios of climate change (Ihlow et al. 2016). However, our data show rapid changes in the thermal performance of dispersal capacity (i.e., endurance) in the invasive population of *X. laevis* that

are not taken into account in these SDMs. Although the future distribution of *X. laevis* is likely to increase with climate change (Ihlow et al. 2016), these predictions do not include the ability of *X. laevis* to rapidly adapt to different climatic conditions and likely underestimate the future invasion potential of the species. Future modeling efforts should focus on incorporating physiological information on the thermal dependence of dispersal as well as potential for adaptation.

Author contributions

A.H. and J.M. conceived the study. L.A., A.S.M., and P.P. collected the data. J.C., C.W., and J.M. collected the animals in the field. L.A., P.P., V.L. and A.H. analyzed the data. L.A. and A.H. wrote the article and all authors contributed to and approved the final version of the article.

Acknowledgments

Funding

References

Angilletta MJ. 2006. Estimating and comparing thermal performance curves. J Therm Biol 31:541–5.

Angilletta MJ. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford, UK: Oxford University Press.

Angilletta MJ, Niewiarowski PH, Navas CA. 2002. The evolution of thermal physiology in ectotherms. J Therm Biol 27:249–68.

Arnold SJ. 1983. Morphology, performance and fitness. Am Zool 23:347–61.

Bestion E, Clobert J, Cote J. 2015. Dispersal response to climate change: scaling down to intraspecific variation. Ecol Lett 18:1226–33.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–89.

Brown JL. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5:694–700.

Catford JA, Jansson R, Nilsson C. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15:22–40.

Chown S, Hoffmann A, Kristensen T, Angilletta M, Stenseth N, Pertoldi C. 2010. Adapting to climate change: a perspective from evolutionary physiology. Clim Res 43:3–15.

Cortes PA, Puschel H, Acuña P, Bartheld JL, Bozinovic F. 2016. Thermal ecological physiology of native and invasive frog species: do invaders perform better?. Conserv Physiol 4:cow056.

Courant J, Secondi J, Bereiziat V, Herrel A. 2017. Resources allocated to reproduction decrease at the range edge of an expanding population of an invasive amphibian. Biol J Linn Soc 122:157–65.

Courant J, Secondi J, Vollette J, Herrel A, Thirion J-M. 2018. Assessing impacts of the invasive *Xenopus laevis* on amphibians in western France. Amph Rept 39:219–27.

Courant J, Vollette E, Secondi J, Herrel A. 2018. Changes in the aquatic macro-invertebrate communities through the expanding range of an invasive anuran. Food Webs 17:e00098.

Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC. 2017. Invasion biology: specific problems and possible solutions. Trends Ecol Evol 32:13–22.

De Busschere C, Courant J, Herrel A, Rebelo R, Rödder D, Measey GJ, Backeljau T. 2016. Unequal contribution of native South African phylogeographic lineages to the invasion of the African clawed frog, *Xenopus laevis*, in Europe. PeerJ 4:e1659.

Du Preez LH, Kunene N, Hanner R, Giesy JP, Solomon KR, Hosmer A, Van Der Kraak GJ. 2009. Population-specific incidence of testicular ovarian follicles in *Xenopus laevis* from South Africa: a potential issue in endocrine testing. Aquat Toxicol 95:10–6.

Facon B, Genton B, Shykoff J, Jarne P, Estoup A, David P. 2006. A general eco-evolutionary framework for understanding bioinvasions. Trends Ecol Evol 21:130–5.

Fick SE, Hijmans RJ. 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–15.

Furman BLS, Bewick AJ, Harrison TL, Greenbaum E, Gvoždík V, Kusamba C, Evans BJ. 2015. Pan-African phylogeography of a model organism, the African clawed frog 'Xenopus laevis.' Mol Ecol 24:909–25.

Garcıa Y, Callaway RM, Diaconu A, Montesinos D. 2013. Invasive and non-invasive congeners show similar trait shifts between their same native and non-native ranges. PLoS ONE 8:6.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–51.

Guderly H. 2004. Metabolic responses to low temperature in fish muscle. Biol Rev 79:409–27.

Herrel A, Bonneaud C. 2012. Temperature dependence of locomotor performance in the tropical clawed frog, Xenopus tropicalis. J Exp Biol 215:2465–70.

Herrel A, James RS, Van Damme R. 2007. Fight versus flight: physiological basis for temperature dependent behavioral shifts in lizards. J Exp Biol 210:1762–7.

Herrel A, Gonwouo LN, Fokam EB, Ngundu WI, Bonneaud C. 2012. Intersexual differences in body shape and locomotor performance in the aquatic frog, Xenopus tropicalis. J Zool 287:311–6.

Herrel A, Vasilopoulou-Kampitsi M, Bonneaud C. 2014. Jumping performance in the highly aquatic frog, Xenopus tropicalis: sex-specific relationships between morphology and performance. PeerJ 2:e661.

Hirano M, Rome LC. 1984. Jumping performance of frogs (Rana pipiens) as a function of muscle temperature. J Exp Biol 108:429–39.

Huey RB, Kingsolver JG. 1993. Evolution of resistance to high temperature in ectotherms. Am Nat 142:S21–46.

Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am Zool 19:357–66.

Hulbert AJ, Else PL. 2000. Mechanisms underlying the cost of living in animals. Annu Rev Physiol 62:207–35.

Ihlow F, Courant J, Secondi J, Herrel A, Rebelo R, Measey GJ, Lillo F, De Villiers FA, Vogt S, De Busschere C, et al. 2016. Impacts of climate change on the global invasion potential of the African clawed frog Xenopus laevis. PLoS ONE 11:e0154869.

James RS, Navas CA, Herrel A. 2007. How important are skeletal muscle mechanics in setting limits on jumping performance?. J Exp Biol 210:923–33.

James RS, Tallis J, Herrel A, Bonneaud C. 2012. Warmer is better: thermal sensitivity of both maximal and sustained power output in the iliotibialis muscle isolated from adult Xenopus tropicalis. J Exp Biol 215:552–8.

John-Alder HB, Barnhart MC, Bennett AF. 1989. Thermal sensitivity of swimming performance and muscle contraction in northern and southern populations of tree frogs. J Exp Biol 142:357–72.

Johnston IA, Temple GK. 2002. Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. J Exp Biol 205:2305–22.

Kruger N, Measey J, Herrel A, Secondi J. 2019. Anti-predator strategies of the invasive African clawed frog, Xenopus

laevis, to native and invasive predators in western France. Aqua Invas 14:433–43.

Lavergne S, Molofsky J. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. Proc Natl Acad Sci U S A 104:3883–8.

Liendo D, Biurrun I, Campos JA, Herrera M, Loidi J, García-Mijangos I. 2015. Invasion patterns in riparian habitats: the role of anthropogenic pressure in temperate streams. Plant Biosyst 149:289–97.

Lodge DM. 1993. Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–7.

Louppe V, Courant J, Herrel A. 2017. Differences in mobility at the range edge of an expanding invasive population of Xenopus laevis in the west of France. J Exp Biol 220:278–83.

Louppe V, Courant J, Videlier M, Herrel A. 2018. Differences in standard metabolic rate at the range edge versus the center of an expanding invasive population of Xenopus laevis in the West of France. J Zool 305:163–72.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:22.

Magnuson JJ, Crowder LB, Medvick PA. 1979. Temperature as an ecological resource. Am Zool 19:331–43.

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P. 2004. Rapid evolution of an invasive plant. Ecol Monogr 74:261–80.

Martin TL, Huey RB. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. Am Nat 171:E102–18.

Measey GJ, Rödder D, Green SL, Kobayashi R, Lillo F, Lobos G, Rebelo R, Thirion J-M. 2012. Ongoing invasions of the African clawed frog, Xenopus laevis: a global review. Biol Invas 14:2255–70.

Navas CA, Gomes FR, Carvalho JE. 2008. Thermal relationships and exercise physiology in anuran amphibians: integration and evolutionary implications. Comp Biochem Physiol A 151:344–62.

Novak SJ. 2007. The role of evolution in the invasion process. Proc Natl Acad Sci U S A 104:3671–2.

Osborn TJ, Briffa KR. 2006. The spatial extent of 20th-century warmth in the context of the past 1200 years. Science 311:841–4.

Padilla P, Ducret V, Bonneaud C, Courant J, Herrel A. 2019a. Acclimation temperature effects on locomotor traits in adult aquatic anurans (X. tropicalis and X. laevis) from different latitudes: possible implications for climate change. Conserv Physiol 7:coz019.

Padilla P, Courant J, Herrel A. 2019b. Allocation trade-offs impact organ size and muscle architecture in an invasive population of Xenopus laevis in Western France. J Anat 235:1057–64.

Pigliucci M. 2005. Evolution of phenotypic plasticity: where are we going now?. Trends Ecol Evol 20:481–6.

Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ. 2008. Adaptive evolution in invasive species. Trends Plant Sci 13:288–94.

Rödder D, Ihlow F, Courant J, Secondi J, Herrel A, Rebelo R, Measey GJ, Lillo F, Villiers FAD, Busschere CD, et al. 2017. Global realized niche divergence in the African clawed frog Xenopus laevis. Ecol Evol 7:4044–58.

R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Richardson DM, Pyšek P. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr Earth Environ 30:409–31.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, et al. 2017. No saturation in the accumulation of alien species worldwide. Nat Commun 8:14435.

Seymour RS. 1972. Behavioral thermoregulation by juvenile green toads, *Bufo debilis*. Copeia 1972:572–5.

Shine R, Brown GP, Philllips BL. 2011. An evolutionary process that assembles phenotypes through space rather than through time. Proc Natl Acad Sci U S A 108:5708–11.

Simberloff D, Gibbons L. 2004. Now you see them, now you don't!—population crashes of established introduced species. Biol Inv 6:161–72.

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, et al. 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66.

Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CDG, Marshall DJ, Helmuth BS, et al. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?. Ecol Lett 19:1372–85.

Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagran-Santa Cruz M, Lara-Resendiz R, Martinez-Mendez N, Calderon-Espinosa ML, Meza-Lazaro RN, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–9.

Stevens VM, Pavoine S, Baguette M. 2010. Variation within and between closely related species uncovers high intraspecific variability in dispersal. PLoS ONE 5:e11123.

Sunday JM, Bates AE, Dulvy NK. 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proc R Soc B 278:1823–30.

Urban MC, Phillips BL, Skelly DK, Shine R. 2007. The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proc R Soc B 274:1413–9.

Urban MC, Richardson JL, Freidenfelds NA. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evol Appl 7:88–103.

Van Berkum FH. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. Evolution 40:594–604.

Van Damme R, Bauwens D, Verheyen RF. 1991. The thermal dependence of feeding behaviour, food consumption and gut-Passage time in the lizard *Lacerta vivipara*, Jacquin. Funct Ecol 5:507.

Vimercati G, Labadesse M, Dejean T, Secondi J. 2019. Assessing the effect of landscape features on pond colonisation by an elusive amphibian invader using environmental DNA. Freshw Biol published online (doi: 10.1111/fwb.13446).

Whitford WG. 1973. The effects of temperature on respiration in the amphibia. Am Zool 13:505–12.

Wilson RS. 2001. Geographic variation in thermal sensitivity of jumping performance in the frog *Limnodynastes peronii*. J Exp Biol 204:4227–36.

Zenni RD, Nuñez MA. 2013. The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122:801–15.