



SYMPOSIUM

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

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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 (Garcia 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 humidified 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 <i>N_{kZN}</i> =15 <i>N_{wc}</i> =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

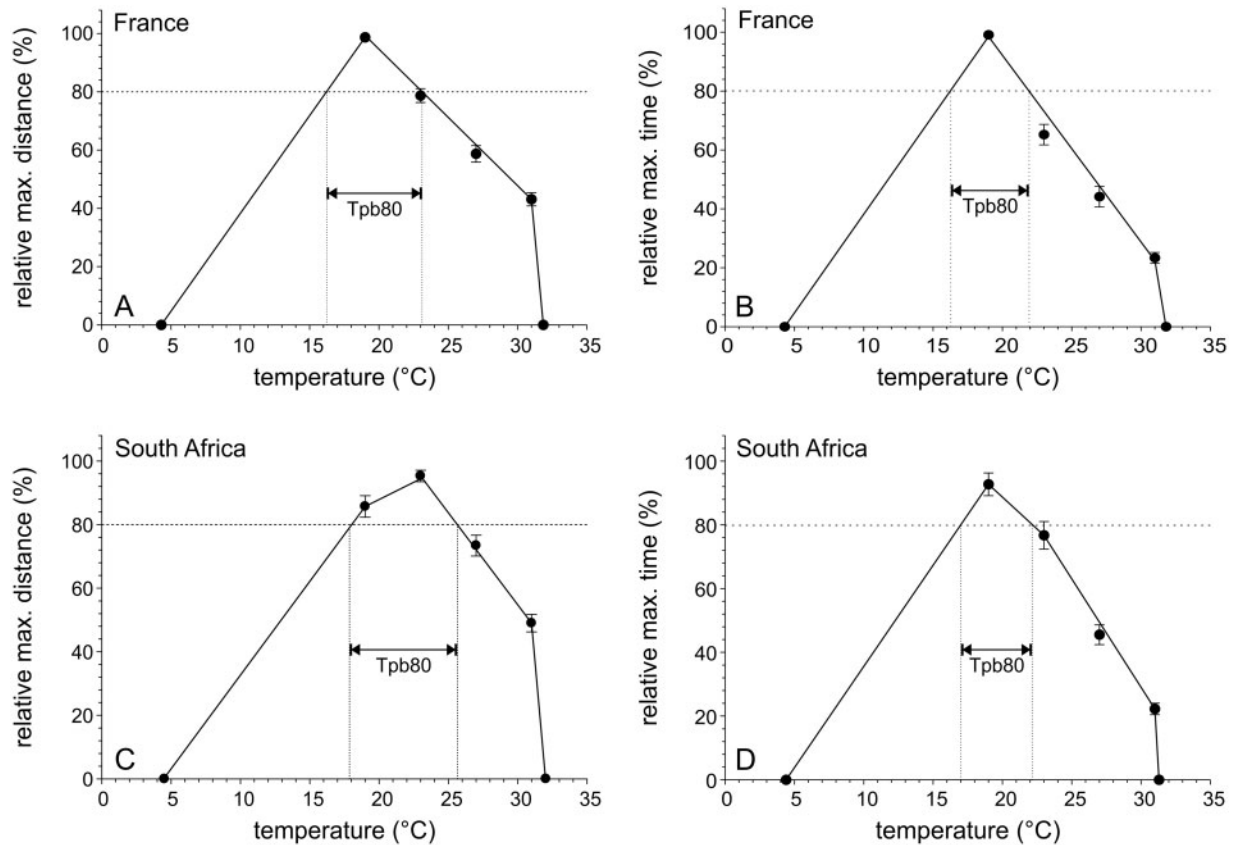


Fig. 1 Temperature performance curves illustrating the impact of temperature on endurance capacity in terms of distance (**A, C**) and time (**B, D**) for *X. laevis* from France (**A, B**) and South Africa (**C, D**). Indicated are the 80% thermal performance breadths for each trait and each population. Symbols represent means \pm standard errors of the mean.

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

Test temperature (°C)	Population	Distance (cm)	Time (s)
France $N=40$; South Africa $N=25$ ($N_{KZN} = 13$, $N_{WC}=12$)			
19	France	2664.75 \pm 141.65	258.58 \pm 20.85
	South Africa	2892.31 \pm 181.85	357.76 \pm 35.10
23	France	2028.25 \pm 83.77	161.67 \pm 14.10
	South Africa	3111.38 \pm 134.48	277.94 \pm 21.89
27	France	1456.50 \pm 68.90	99.49 \pm 7.09
	South Africa	2409.61 \pm 132.29	161.68 \pm 13.42
31	France	1074.25 \pm 45.40	56.83 \pm 6.32
	South Africa	1582.31 \pm 84.43	79.18 \pm 6.84

Note: Table entries are means \pm 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 ($Topt_{\text{France}}: 19.36^{\circ}\text{C}$; $Topt_{\text{South Africa}}: 21.56^{\circ}\text{C}$; $F_{1,56} = 28.3$, $P < 0.001$; Table 7). For burst performance no differences in optimal temperature were detected, however ($Topt_{\text{France}}: 23.94^{\circ}\text{C}$; $Topt_{\text{South Africa}}: 24.48^{\circ}\text{C}$;

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).

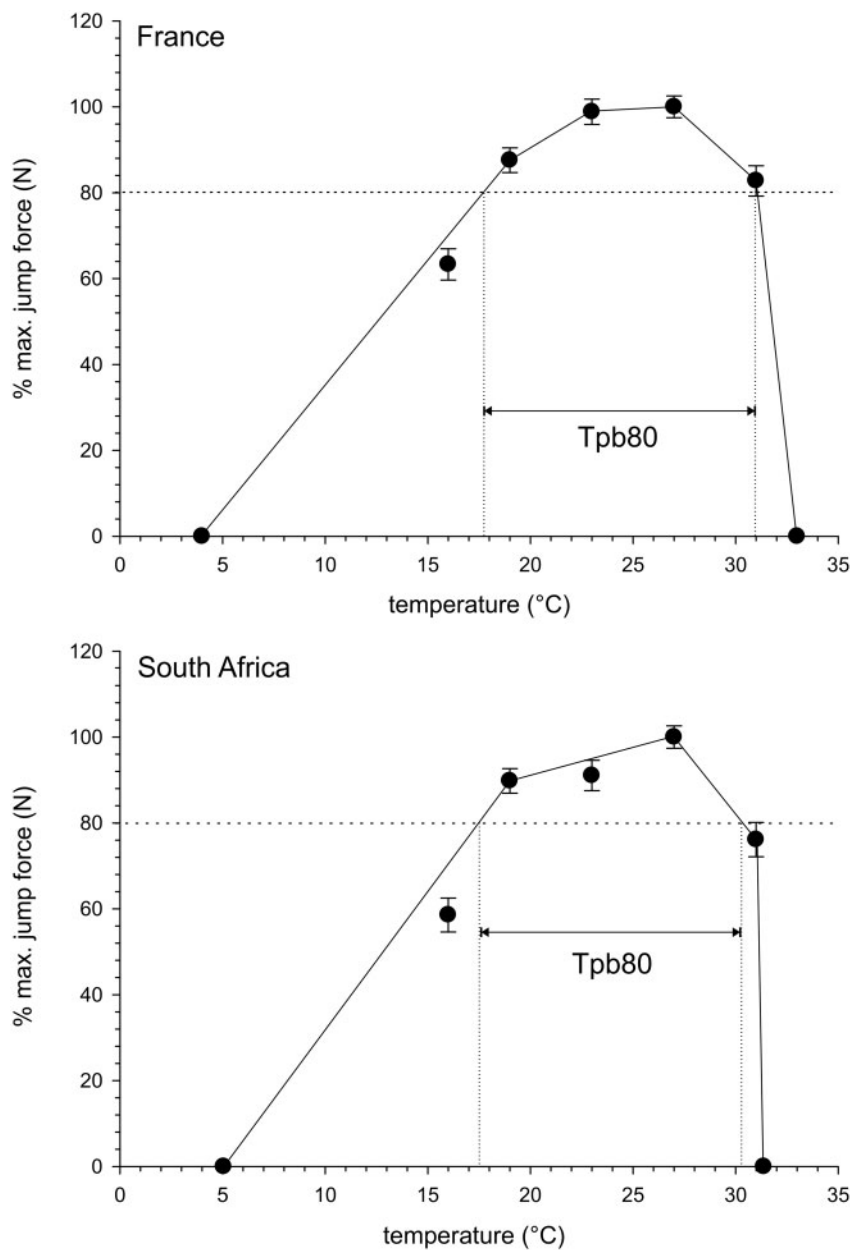


Fig. 2 Temperature performance curves illustrating the impact of temperature on jump force for *X. laevis* from France (top) and South Africa (bottom). Indicated are the 80% thermal performance breadths for each trait and each population. Symbols represent means \pm standard errors of the mean.

Discussion

Critical temperatures

When organisms are confronted with temperatures approaching their thermal tolerance limits, they can

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
	South Africa	8.08±0.52	18.02–26.1°C
T _{pb95} (°C)	France	3.05±0.22	18.21–21.27°C
	South Africa	3.24±0.32	20.34–23.58°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.

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 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 \pm 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.

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