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Temperature dependence of locomotor performance in the invasive frog, *Xenopus laevis*

Graduation Thesis

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This graduation thesis was made in the Natural History Museum in Paris, under the mentorship of dr. sc. Anthony Herrel and assistant supervisor Prof. Zoran Tadić, PhD, Department of animal physiology, Division of Biology, Faculty of Science. The thesis is delivered to the Division of Biology, Faculty of Science, University of Zagreb for the evaluation, with the aim of acquiring a title of Master of Environmental Science.

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TEMPERATURNA OVISNOST LOKOMOTORNE IZVEDBE INVAZIVNE VRSTE ŽABE, XENOPUS LAEVIS

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Invazivne vrste ugrožavaju autohtone, te je njihov negativni utjecaj istaknut kao velika prijetnja globalnoj biološkoj raznolikosti. Invazivne vrste vodozemaca, ektotermnih organizama čija je tjelesna temperatura uvjetovana okolinom, ekstremno su osjetljive na promjene abiotičkih čimbenika u okolišu koji uvelike utječu na uspješnost kolonizacije područja invazivnom vrstom. U ovom radu proučavana je lokomotorna izvedba invazivne vrste žabe, afričke pandžašice *Xenopus laevis.* Istraživanje je provedeno na jedinkama vrste koloniziranog teritorija sjeverozapadne Francuske 2016. godine. Lokomotorno kretanje jedinki populacija s rubnog i centralnog dijela koloniziranog staništa testirano je u različitim temperaturnim uvjetima. Opažena je značajna razlika u lokomotornoj izvedbi dvaju populacija samo pri visokoj temperaturi što ukazuje na prilagodbu populacija vrste *Xenopus laevis* hladnijim temperaturnim uvjetima u Francuskoj gdje se nalaze već generacijama. Lokomotorna izvedba se razlikovala i s obzirom na spol jedinki, što je u skladu s dosadašnjim istraživanjima vrste gdje se mužjaci generalno uspješnije kreću. Dobiveni rezultati ukazuju na kompleksnost temperaturnih učinaka na fiziološke procese ektotermnih životinja, te da je vrsta vjerojatno sposobna kolonizirati šira područja.

Ključne riječi: žaba, kolonizacija, lokomocija, izdržljivost

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TEMPERATURE DEPENDENCE OF LOCOMOTOR PERFORMANCE IN THE INVASIVE FROG, XENOPUS LAEVIS

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Native species are frequently endangered by invasive species whose negative impact is widely recognized as a threat to global biodiversity. Amphibian invasive species are extremely sensitive to temperature variations, as they are ectothermic organisms whose body temperature is dependent on the temperature of the environment which greatly affects their capability to colonize new habitats. Locomotor performance of the invasive frog *Xenopus laevis* was studied in this research. The study was conducted in 2016 on individuals taken from the invaded northwestern territory of France. Populations from the periphery and the center of their invasive range were tested for locomotion at different temperature conditions. Significant dfference between populations in locomotor performance was noticed only at higher temperature conditions, implicating that populations have adjusted to colder temperature conditions in France where they have been introduced generations ago. Locomotor performance differed according to sex of the individuals, in accordance with other research on this species with males being generally better performers. Given results demonstrate the complexity of how temperature affects the physiological processes in ectotherms and indicate even more successful colonization of this invasive species.

Keywords: frog, colonisation, locomotion, stamina

(32 pages, 3 figures, 4 plates, 43 references, original in: English)

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Contents

1. Introduction

Biological diversity is the variety of life on Earth including all organisms, species, and ecosystems. The importance of biodiversity manifests itself in the interdependence of all living organisms and their balanced activity as the key to the health of the whole planet (cbd.int). Besides habitat loss, over-exploitation and pollution, one of the main causes of biodiversity loss are invasive species (also known as alien species) who replace numerous local species and often cause their extinction (Heinrichs et al., 2016; Paul & Kar, 2016; Dias et al., 2017). An invasive species of frog, *Xenopus laevis* which originates from southern Africa has been successfully colonizing North America, South America, Asia, and Europe in the past few decades (Measey et al., 2012; Ihlow et al., 2016). It is recognized as a major threat to local faunas (Measey et al., 2012). Whether the species will manage to colonize novel habitat largely depends on their locomotor traits, which are highly dependent on temperature of the environment when it comes to ectothermic amphibians (Angiletta et al., 2002a). Since it is expected that global temperature fluctuations will have a negative impact on the ecosystems in the next few decades (Beaumont et al., 2011), it is necessary to determine the impacts of temperature change on physiological traits such as locomotor performance of this invasive species in order to predict species potential for further colonization and spreading.

Here we study endurance capacity in *Xenopus laevis* at two different temperatures to quantify how locomotor capacity is impacted by temperature. Endurance is particularly relevant in the context of this invasive species as its ability to spread and colonize new areas will be impacted by its endurance. Furthermore, we test whether differences between sexes and populations from the center and the periphery of the invasive range can be detected. Previous studies on closely related species (Herrel et al., 2014) have shown that male individuals are typically more performant than female individuals for a given body size. As such this may also be the case in *X. laevis* which is known to be sexually dimorphic in body size. Finally, as individuals on the invasion front are considered locomotor specialists we could expect for them to show narrower temperature~performance breadths than individuals from the center of the invasion area.

1.1. Biological diversity

1.1.1. Totality of biological diversity

By Convention on Biological Diversity (cdb.int) biological diversity is the variability among living organisms from all sources including *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. Diversity within species is commonly defined as the diversity between alleles, genes and organisms, while diversity between species refers to complete amount of all different species. Biodiversity is heterogeneously distributed over the planet, with some regions being more rich with different organisms (Gaston, 2000; Tittensor et al., 2010). In broader sense than biodiversity, natural heritage includes even geology and geomorphology. It is estimated that there are over 10 million species on planet Earth and in the oceans, with 1,4 million catalogued to date (Mora et al., 2011), with decrease in their number (Dirzo et al., 2014; Pimm et al., 2014). Besides contributing to the global ecological balance, organisms worldwide are used for food and contribute to the well-being of human race. Consequently, a global reduction in the number and abundance of plant and animal species is an undesirable phenomenon.

1.1.2. Invasive species as a threat to biological diversity

Threats to biological diversity are numerous and include habitat loss and destruction, over-exploitation of species, pollution or contamination of the environment, global climate change, alterations in ecosystem composition and invasive alien species (Dirzo et al., 2014; Pimm et al., 2014; Heinrichs et al., 2016; Paul & Kar, 2016). Human fluctuations together with transport of animals and plants in the recent century have resulted in the introduction of non-indigenous species in nearly every country, either with purpose or by accident. By direct predation on native species or through competing with them, invasive organisms significantly influence other animals' survival rates (Ihlow et al., 2016) unquestionably creating new interspecies interactions which may lead to extinctions. In order to prevent further invasions, the import of non-native species is illegal in many countries. On the other hand, eradication of invasive species usually has many types of negative and unwanted consequences on native species and ecosystems (Zavaleta et al., 2001) and removing one species can lead to significant increase in abundance of other species (Cole & Litton, 2013) causing ecological imbalance.

1.2. *Xenopus laevis*

1.2.1. Characteristics of the species

"Amphibian" comes from the Greek language (*amphi*-of both kinds, *bios*-life), referring to the life history of animals generally undergoing metamorphosis from an aquatic larval form called tadpoles to a terrestrial air-breathing adult with lungs. Amphibians are ectothermic organisms, regulating their body temperature with behavior as they rely on the conditions of the environment (Angilletta et al., 2002a; Angilletta et al., 2002b; Herrel & Bonneaud, 2012).

The African clawed frog, *Xenopus laevis* (Daudin, 1802) is an aquatic frog of the Pipidae family, order Anura (Figure 1). The name *Xenopus laevis* (*xeno*-strange, *pous*-foot, *laevis*-smooth) is derived from its very smooth skin and three black claws on their feet. Adult individuals are around 10 cm long and have generation time of 2 years. Eggs and embryos of this species are key *in vitro* systems for studies of fundamental aspects of developmental, cell and molecular biology today because they are big and simple for manipulation (Gurdon, 1996; Collart et al., 2017; Ratzan et al., 2017; Wuest et al., 2017). Although recently much has been published on *Xenopus laevis* (Measey et al., 2012; Ihlow et al., 2016; Collart et al., 2017; Wuest et al., 2017), its ecology remains largely unknown partially due to animals' dependence on aquatic environment which makes them hard to study. This is predator species which feeds with variety of invertebrates, zoobenthic and zooplankton, as well as with small fish (Gurdon 1996; Measey, 1998) making it a major threat to indigenous species.

Figure 1. *Xenopus laevis* (flickr.com)

1.2.2. Invasion process

This predator and scavenger is native to Southern Africa, but has become invasive world-wide and succeeded to inhabit rivers, lakes and swamps all over the world (Measey et al., 2012). *Xenopus laevis* has been exported from South Africa when discovered by Europeans and eventually became one of the most used and studied laboratory animal today.

At the beginning of 20^{th} century *Xenopus* was brought to Europe to be studied as every newly found species, soon to be used in medical purposes and later on, their usage has spread through numerous scientific areas. Only one injection of urine containing human chorionic gonadotropin (pregnancy hormone) induces the laying of eggs in frogs which was the quickest and simplest pregnancy test for many years. Consequently, this species had been wastly exported to numerous laboratories, first in Europe and North America and later worldwide (Gurdon & Hopwood, 2000). Colonies of this species were initially established for pregnancy testing but were later used for studies in experimental medicine and many fields of biology including embryology, neurobiology, and genetics (Horn, 2004). Over the years, individuals have escaped from laboratories and with the development of new pregnancy tests many were deliberately released (Measey & Tinsley, 1998). Since then this species has become an invasive and can be considered a threat to other species in an ecosystem (Mack et al., 2000).

1.3. Impact of temperature on animals' physiological traits

Predicted increases in global temperature, as well as direct anthropogenic impacts such as deforestation, will most probably increase the vulnerability of ecoregions in the next decades (Beaumont et al., 2011). Thus, it is relevant to determine the effect of temperature on animal's locomotor capacity. Moreover, the thermal characteristics of environment determine thermal performance breadth; temperature range within an individual can perform 80% or more of their maximal performance. Depending on whether they perform at narrow or wide temperature ranges, organisms may be classified as thermal specialists or generalists (Huey & Herz, 1984; Angilletta et al., 2002b). Species that are not often confronted with temperature fluctuations have most often evolved narrow thermal performance breadths, as a wide thermal range of performance demands a greater amount of energy due to the production of multiple enzymes included at different temperatures (Van Damme et al., 1991; Angilletta et al., 2003). Otherwise, widening the temperature range where an organism maintains its one function at maximum is often accompanied by trade-offs with other physiological traits (Starostova et al., 2003).

All physiological processes in amphibians are highly dependent on environmental temperature (Huey et Hertz, 1984; Navas et al., 2008; Angilletta et al., 2002a; Angiletta et al., 2012). The introduction of species to new environments thus confronts them with novel climatic conditions. However, the spread of an introduced population depends highly on locomotion possibilities which are influenced by temperature (Navas et al., 2008; Herrel et al., 2012). Probably invasive species introduced into novel environments could be able to either rapidly adapt to new temperature regimes or show significant phenotypic plasticity allowing them to perform well over a wide range of temperatures.

On the other hand, phenotypic plasticity is induced by both biotic and abiotic factors. For example, presence of predators in frog tadpoles (Miner et al., 2005) result with growth of longer tails and smaller body sizes. The result is slower growth rate as they invest less in foraging (Miner et al., 2005). Phenotypic plasticity can also be induced by variation in temperature through impact on organisms in early stages of development, and can be divided into two categories: developmental plasticity that occurs during the gametic or embryonic development, and reversible plasticity, also called acclimation, induced in juvenile or mature organisms. Both are linked, however, as acclimation capacity may be altered by conditions which occur during early development (Beaman et al., 2016).

1.4. Aims

The aims of this research are:

1. Compare locomotor performance of *Xenopus laevis* generally at 18 and 23 °C.

2. Determine the effect of population origin (center and periphery of invaded area), body mass and sex on performance at lower temperature (average 18 °C).

3. Determine the effect of population origin (center and periphery of invaded area), body mass and sex on performance at higher temperature (average 23 °C).

2. Study area

This research was conducted on individuals from the territory in northwestern France (Figure 2). Part of the invaded territory belongs to regional natural park Loire-Anjou-Touraine, protected by UNESCO since 2000 and characterized by extremely rich natural heritage such as forest, grasslands, limestone steppes, agricultural fields and finally river Loire and its affluents. Invaded territory includes urban areas of Doue-la-Fontaine, Saumur and Thouars, so as rivers Loire, Layon, Argenton, Thouet and Dive, all inhabited by numerous flora and fauna.

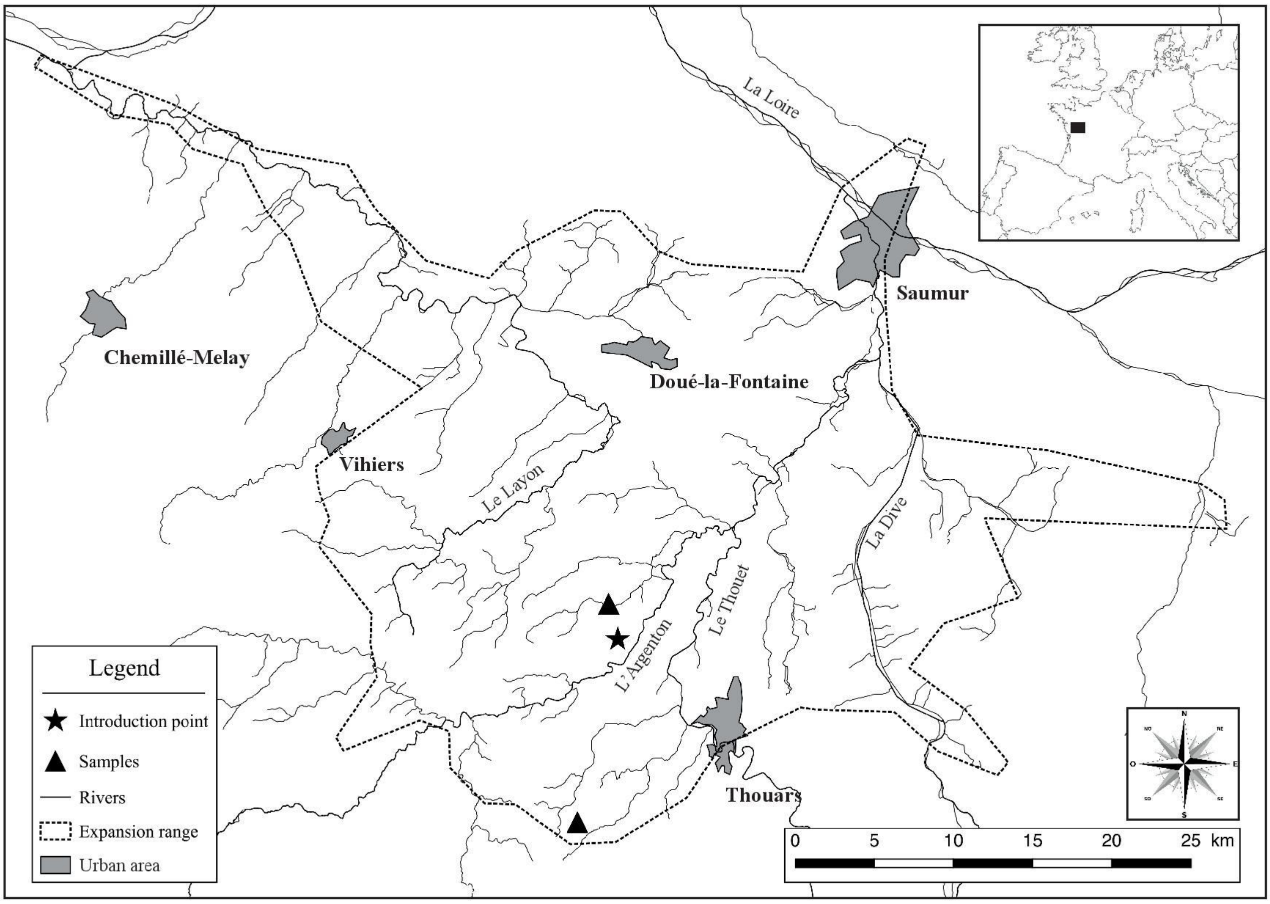

Figure 2. Map showing the localities of the populations of *Xenopus laevis* in the northwest of France that were used in the present study.

3. Materials and methods

3.1. Experimental set up

Xenopus laevis individuals studied in this research project were captured in France in 2015 in ponds and bodies of standing water within their current range using fykes. Individuals were taken from the center of their invasive range, as well as from the periphery in order to study characteristics and potential divergence of two populations living in different environmental conditions.

Individual specimens were housed at the Function and Evolution (FUNEVOL) laboratory at the Muséum National d'Histoire Naturelle in Paris, France. In the laboratory animals were kept in aquariums at temperature of 24 °C, a temperature similar to the water temperature in the animal's natural habitat. Frogs were housed up to 10 individuals in 50 litre aquariums and fed twice a week with beef heart and earthworms. Each individual was pit-tagged (Nonatec, Lutonic International, Rodange, Luxembourg) allowing them to be unambiguously identified. There were 82 individuals in total (Table 1) which variate in weight from 8 to 112 grams.

Table 1. Numeric distribution of center, periphery, male and female individuals tested.

		Number of individuals
Sex	f	39
	m	43
Origin	center	34
	periphery	48

3.2. Measurements

Before the onset of each trial, every individual was identified and placed in a box with water in an incubator set at the target temperature. Two conditions were chosen, 7 °C and 26 °C. Animals were left in the incubator for 2 to 3 hours in order for them to reach the target temperature. However, at the end of the performance trials the body temperature of the animals changed to 18 °C and 23 °C respectively. Animals were chased manually until fatigued in a 3 meter long circular track (Figure 3). Frogs were considered to be fatigued when unable to turn over after having been placed on their back. The total distance which they jumped and the time passed were then recorded as an estimate of the animal's maximal endurance capacity. We measured the body temperature and weight of each animal after each performance trial after which animals were returned to their aquarium and left to rest one week before another trial. For each temperature three trials were done for each individual. Room temperature was around 21 °C.

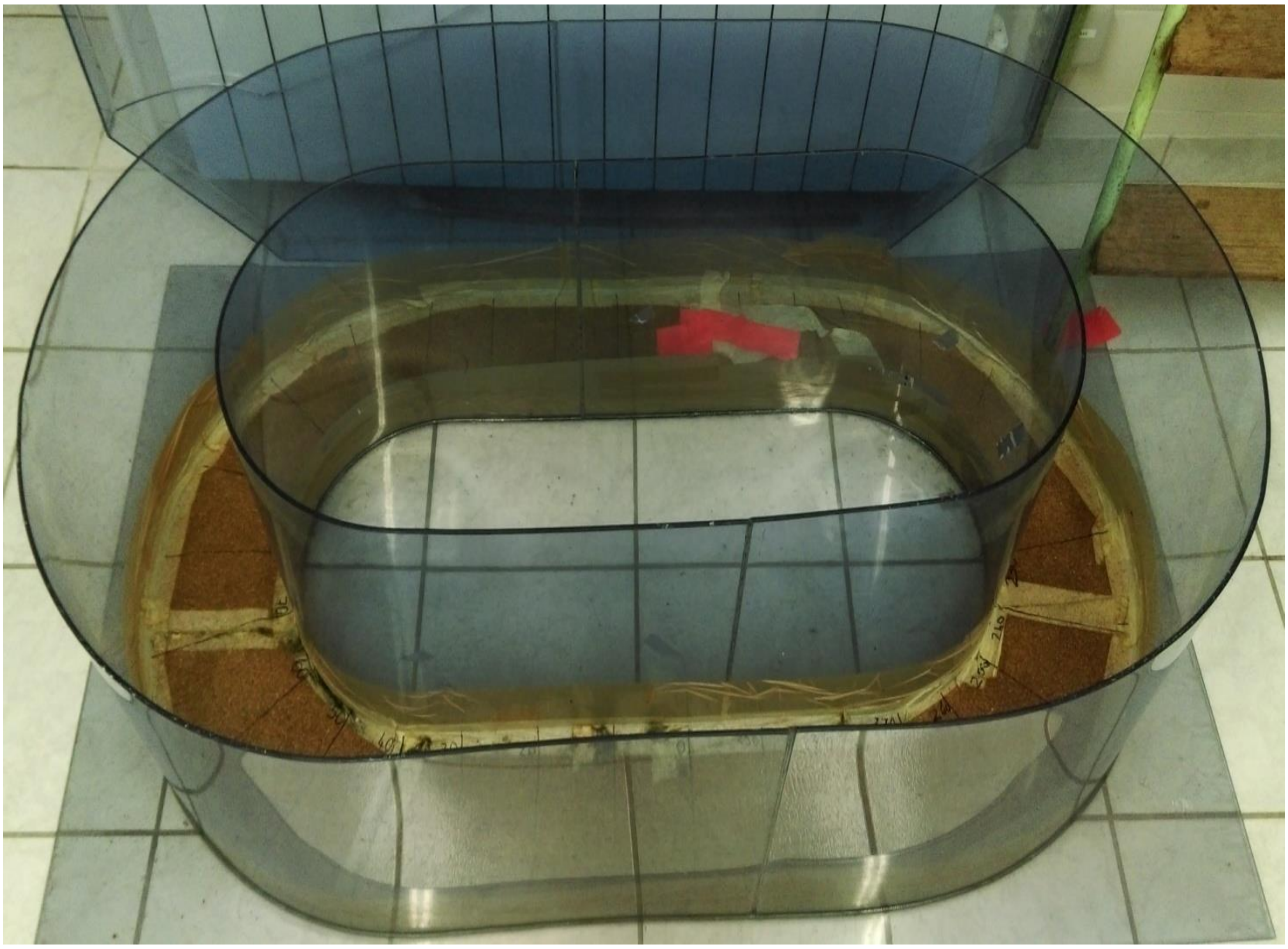

Figure 3. Circular track with distance marks used to measure stamina.

3.3. Data processing and analysis

We used $\log_{10}$-transformed data for all analyses. Data was first tested for correlation between time and distance using a Pearson correlation coefficient. Several outliers were detected based on the time versus distance plot and removed from the subsequent analysis. First, we ran a repeated measures ANOVA to compare performance at low and high (18 °C and 23 °C) body temperature. Given that the results were significant, they were then separately analysed for low and high temperature.

MANCOVAs were subsequently run to test for differences between sexes and populations in endurance capacity. For performance at low temperature we first ran full factorial models that included population and sex as factors and body weight and temperature as co-variables. Non-significant effects (population: Wilks' lambda = 0.99; $F_{2,76}$= 0.57; P = 0.57; population x sex: Wilks' lambda = 0,95, $F_{2,76}$ = 1.95, P = 0.15; temperature: Wilks' lambda = 0,96; $F_{2,75}$ =1,64; P = 0,20) and interactions were removed from the final model which retained only sex as main factor and body weight as a co-variable. For performance at high temperature we ran a similar model and detected a significant sex / population interaction effect (Wilks' lambda = 0.89, $F_{2,76}$ = 4,54, P = 0,014). Thus, analyses (MANCOVA) testing for differences between populations were run for both sexes separately. In each case subsequent ANCOVA's were run to test which variables differed between sexes and populations. All analyses were performed in SPSS v. 15. 0. (IBM, Armonk, NY, USA).

4. Results

4.1. General comparison of 18 and 23 °C

Animals were chased manually until fatigued in a 3 meter long circular track. The mean time and mean distance jumped before exhaustion were higher and longer at low temperature (18 °C) than at high temperature (23 °C). Individuals of both origins (center versus periphery) and sexes have a better overall performance for time and distance at 18 °C than at 23 °C (Table 2).

Table 2. General comparison of frogs' jumping time and distance for lowest and highest trial temperatures.

Dependent variable	Mean value ± S.D.
Max. Time Lowest Temperature (s)	373.89 ± 69.37
Max. Time Highest Temperature (s)	218.43 ± 67.7
Max. Distance Lowest Temperature (cm)	3641.83 ± 764.63
Max. Distance Highest Temperature (cm)	3277.8 ± 786.02

4.2. Performance at lower temperature (average 18 °C)

Both sex and body mass impacted the performance of *X. laevis* at low temperature (Table 3). The effect of population was not significant, however.

The variable of animal body mass affects time that the individuals are capable of performing more than it affects the distance they manage to cover. In contrast, the sex of the individuals has a larger impact on the distance jumped compared to the time (Table 3). At 18 °C male individuals performed better than female individuals. (Table 3).

Table 3. Tests for lowest trial temperatures of *Xenopus laevis* jumping performance.

Multivariate tests for males and females at 18 °C.				
	Wilks' λ	F	d.f.	P
Weight	0.918	3.473	2,78	0.036
Sex	0.909	3.908	2,78	0.024
Tests of between-subject effects for males and females performing at 18 °C.				
	Dependent variable	F	d.f.	P
Weight	Time	5.488	1,79	0.022
	Distance	5.050	1,79	0.027
Sex	Time	5.711	1,79	0.019
	Distance	6.149	1,79	0.015
Comparison of males and females at 18 °C.				
Dependent variable		Sex	Mean value ± S.D.	
Time (s)		female	362.64 ± 70.38	
		male	384.09 ± 67.63	
Distance (cm)		female	3509.74 ± 849.68	
		male	3761.63 ± 665.93	

d.f.: degrees of freedom.

4.3. Performance at higher temperature (average 23 °C)

Sex and population origin (center or periphery) both affected individual performance and showed a significant interaction effect, as well as the variation in temperature during the measurement (Table 4). Effects of body size were, however not significant.

4.3.1. Male performance

For males, the only variable that affected performance was the variation in body temperature at the end of the run. This specifically impacted the distance jumped to exhaustion. (Table 4). No differences between center and periphery populations were observed, however (Table 4).

4.3.2. Female performance

Female *X. laevis* showed significant differences between center and periphery populations. Moreover, the temperature at the end of the measurement also significantly impacted performance. The origin of the population had the biggest impact on the endurance time. The effect of temperature, however, was only noticeable as a global effect (Table 4). Females from the periphery show better locomotor performance in terms of the time spent moving until exhaustion compared to individuals from the center of invaded area (Table 4).

Table 4. Tests for highest trial temperatures of *Xenopus laevis* jumping performance.

Multivariate tests for male and female populations at 23 °C.				
	Wilks' λ	F	d.f.	P
Highest Temperature	0.830	7.763	2,76	0.001
Sex*Origin	0.893	4.539	2,76	0.014
Sex	0.942	2.345	2,76	0.103
Origin	0.956	1.739	2,76	0.183
Multivariate tests for males performing at 23 °C.				
	Wilks' λ	F	d.f.	P
Temperature at end of experiment	0.856	3.282	2,39	0.048
Tests of between-subject effects for center and periphery male populations at 23 °C.				
	Dependent variable	F	d.f.	P
Highest Temperature	Distance (cm)	4.286	1,40	0.045
	Time (s)	0.006	1,40	0.940
Comparison of center and periphery male populations at 23°C; mean values for time and distance.				
	Origin		Mean value ± S.D.	
Distance (cm)	Center		3312.14 ± 807.48	
	Periphery		3416.2 ± 763.87	
Time (s)	Center		231.93 ± 64.41	
	Periphery		230.66 ± 70.26	

Multivariate tests for females at 23°C.				
	Wilks' λ	F	d.f.	P
Temperature at end of trial	0.704	7.368	2,35	0.002
Population origin	0.721	6.775	2,35	0.003
Tests of between-subject effects for center and periphery female populations performing at 23 °C.				
	Dependent variable	F	d.f.	P
Temperature at end of trial	Distance (cm)	0.778	1,36	0.384
	Time (s)	1.472	1,36	0.233
Origin	Distance (cm)	1.728	1,36	0.197
	Time (s)	8.624	1,36	0.006
Comparison of center and periphery female populations at 23°C; mean values for time and distance.				
	Origin		Mean value ± S.D.	
Distance (cm)	Center		3012 ± 718.85	
	Periphery		3321.05 ± 862.52	
Time (s)	Center		176.15 ± 41.3	
	Periphery		234.32 ± 74.25	

d.f.: degrees of freedom.

5. Discussion

The locomotor physiology of amphibians is highly sensitive to temperature (Huey & Hertz, 1984; Angiletta et al., 2002b). This is also the case for *Xenopus laevis* where temperature is an abiotic factor modifying an individual's endurance capacity. Despite the effect of temperature on performance, the strong correlations observed between measurements at the two temperatures (18 °C and 23 °C) indicate that performance is repeatable across temperatures. Indeed, an animal that is a good performer will generally perform well despite variation in temperature.

Although *Xenopus laevis* originates from South Africa which is characterized by a warm climate, its overall performance was higher at 18 °C compared to 23 °C for the invasive population of France. This suggests that individuals have been thermally adapted to colder environment in which they have been introduced. According to that, animals which have been living and breeding in France for over 30 years, are able to adapt to new environment over several generations (Measey et al., 2012).

Peterson et al. (1993) and Witters & Sievert (2001) reported 'the presence of multiple optima' in some ectotherms, implying that animals select certain temperatures for optimizing some function. For example, many species will choose higher body temperatures during digesting or gestating (Van Damme et al., 1991). Adjusting to novel temperature may involve a widening of performance breadth (Angiletta et al., 2002b). If so, then this may come at the cost of a reduction of absolute performance according to the 'jack of all trades master of none' hypothesis (Huey, 1984).

Interestingly, at 18 °C small variations in temperature do not affect the performance of the animals suggesting that animals may be performing close to the optimal body temperature for locomotion for this species. The wide distribution range of *Xenopus laevis* is certainly facilitated by phenotypic plasticity, but its possible extent remains unknown. In the beginning of the invasion, a reversible phenotypic plasticity most probably allows animals to establish and survive under new environmental conditions. After several generations long-term thermal adaptation might have occurred, resulting that new generations have better locomotor performance at lower temperatures, as suggested by our results.

Sexes were consistently different in locomotor performance. Previous studies have shown that this is the due to the relatively longer limbs in males (Herrel et al., 2014). Indeed, longer legs allow for a longer acceleration time and thus a higher take-off velocity and longer jump distance (Alexander, 2003; Toro et al., 2004; James et al., 2007). Our results match those from the study on the closely related species *Xenopus tropicalis* (Herrel et al., 2014). However, in *X. tropicalis* optimal performance for endurance was shifted towards slightly higher temperatures, what is consistent with the tropical nature and habitat of this species.

At 23 °C males outperformed females. When in undesirable conditions, females probably reduce certain performances as they generally have to invest more energy in reproductive output (Shine, 1979). Consequently, they pay the cost of keeping their reproduction level elevated. Interestingly and surprisingly, body mass impacted temperature only at higher temperature. This again suggests that at near-optimal temperature (18°C) animals are less susceptible to variation in body weight and in overall may be able to optimize their performance. These results demonstrate the complexity of how temperature affects the physiological processes in ectotherms.

Also, differences between animals from the center and the periphery populations were only observed at higher temperature. However, as the population from the center of the range has been maintained at the same temperature (23-24 °C) for over 1 year they may have acclimated to this temperature. However, in that case they would show higher, not lower performance at the acclimation temperature relative to animals from the periphery, which is not what was observed here.

Individuals from periphery represent the migration front and are first to colonize new environments. Therefore, they may be encountering variations in the environment which may induce phenotypic plasticity in their response to temperature as well as other traits. On the other hand, population from the center remains at the same place and experiences more stable conditions and may effectively adapt and specialize, losing some of its plasticity and narrowing its temperature performance breadth. Why, however only females show this pattern remains unclear. One of the possible explanations is that as the cost of reproductive investment in females is high and they may not be able to shift their physiological parameters. Despite the interesting initial results from our study, additional experiments at different temperatures are needed to establish a full temperature~performance curve for individuals from the two environmentally different populations. Moreover, testing the ability of the individuals from the two populations to acclimation would be worth investigating.

6. Conclusion

This study showed significant differences in locomotor performance in sexes, as well as between central and peripheral populations of *Xenopus laevis*. These results indicate that, like in other invasive species, individuals with improved locomotion are situated on the periphery of the habitat. Although the individuals are sensitive to temperature change, this study suggests that further invasion of species will not be disrupted due to their capability to adapt to new temperature regimes.

Whereas our results are restricted to only one physiological trait in adult individuals, they demonstrate the complexity of how temperature affects the physiological processes of this species.

Our data note differences in locomotor performance only for higher temperature amongst females, indicating that lower tested temperature might be thermal optima for locomotion of this species.

Whether these differences imply the possibility of trade-offs with other traits such as reproductive investment, needs to be tested, however.

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8. Curriculum Vitae

I was born on 31st of July 1993 in Zagreb where I had attended classical elementary school 'Izidor Kršnjavi'. I had continued my education in 2008 in Classical Gymnasium in Zagreb and during that period I acted as a delegate in European Youth Parliament in Croatia. In 2012 I had enrolled at the Faculty of Science, Division of Biology as Environmental Science student. In 2015 I completed undergraduate studies with thesis ‘Isotope stratigraphy of the Upper Cretaceous rudist bivalves' and enrolled in graduate studies at Faculty of Science. Same year I took part in organizing international conference on environmental sciences ISCES '15 at the Faculty of Science in Zagreb and also did an internship at the Department of Zoology. In 2016 I had visited Moscow Lomonosov State University in Russia for winter biology school and field work. Later I had studied a semester at AgroParisTech, Paris Institute of Technology for Life, Food and Environmental sciences in France. During my academic stay in Paris I had worked at Natural History Museum. That same year I had obtained Rector's Reward of University of Zagreb for work 'Patterns of migration of macrozoobenthic communities in interstitial zone of tufa barriers’. In 2017 I did laboratory practice and training at Ruđer Bošković Institute, at the Division of Molecular Biology. During several years of my studying I have actively taken part in numerous manifestations and projects such as Night of Biology event, acted in BIUS student organisation and been an exhibitor at 2nd Symposium on Freshwater Biology in Zagreb.

Rođena sam 31. srpnja 1993. u Zagrebu gdje sam pohađala klasičnu osnovnu školu ‘Izidor Kršnjavi’. 2008. godine nastavila sam obrazovanje u Klasičnoj gimnaziji u Zagrebu, te sam tada bila članica i delegat Europskog Parlamenta Mladih u Hrvatskoj. Maturirala sam 2012. i iste godine upisala preddiplomski studij Znanosti o okolišu na Biološkom odsjeku Prirodoslovno-matematičkog fakulteta u Zagrebu. 2015. godine završila sam preddiplomski studij završnim radom ‘Izotopna stratigrafija gornjokrednih rudista’, te upisala diplomski studij istog usmjerenja kao i preddiplomski. Iste godine sudjelovala sam u organiziranju međunarodne konferencije na temu znanosti o okolišu, ISCES ’15 na Prirodoslovno-matematičkom fakultetu u Zagrebu, te radila laboratorijsku stručnu praksu na Zavodu za zoologiju. 2016. godine posjetila sam Moskovsko državno sveučilište Lomonosov u Rusiji radi zimske škole biologije i terenskog usavršavanja. Kasnije sam provela 6 mjeseci u

Francuskoj na pariškoj visokoj školi AgroParisTech. Tijekom akademskog boravka u Parizu radila sam u Prirodoslovnom muzeju. Iste godine sam osvojila Rektorovu nagradu Sveučilišta u Zagrebu za rad 'Obrasci migracija makrozoobentosa u plitkom intersticiju sedrenih barijera'. Tijekom 2017. radila sam laboratorijsku praksu na institutu Ruđer Bošković na Zavodu za molekularnu biologiju. Tijekom godina studiranja sam izlagala na 2. Simpoziju o biologiji slatkih voda u Zagrebu, te aktivno sudjelovala u brojnim manifestacijama i organizacijama poput Noći biologije i BIUS studentske organizacije.