

Rapid shifts in the temperature dependence of locomotor performance in an invasive frog, Xenopus laevis, implications for conservation

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1 2	Rapid shifts in the temperature dependence of locomotor performance in an invasive frog, <i>Xenopus laevis</i> , implications for conservation.
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32 Abstract

33 Temperature is a critical abiotic factor impacting all aspects of the biology of organisms, especially in 34 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 35 temperature either through plasticity or by adapting to their novel environment. Here, we studied 36 37 the African clawed frog, Xenopus laevis, which has become invasive on a global scale. We compared 38 adults from an invasive population of western France to individuals from two populations in the 39 native range in South Africa. We measured the thermal dependence of locomotor performance in 40 adults given its relevance to dispersal, predator escape, and prey capture. Our results show 41 significant differences in the limits of the 80% performance breadth interval for endurance with the 42 French population showing a left shift in its limits congruent with the colder climate experienced in 43 France. The French invasive population was introduced only about 40 years ago suggesting a rapid 44 shift in the thermal physiology. Given that all individuals were acclimated under laboratory 45 conditions at 23 °C for two months this suggests that the invasive frogs have adapted to their new environment. These data may allow the refinement of physiologically informed species distribution 46 47 models permitting better estimates of future ranges at risk of invasion.

48 Key words: Invasion biology, *Xenopus laevis*, thermal performance curves, dispersal, adaptation

49 Introduction

50 Biological invasions have increased dramatically over the past two centuries (Seebens et al. 2017). 51 These invasions are due to anthropogenic causes (Liendo et al. 2015) and have changed patterns of 52 biodiversity at a global scale (Simberloff et al. 2013). However, most introductions do not lead to 53 invasions and a species can be invasive in one locality but not another (Mack et al. 2000). Indeed, in 54 many cases intraspecific variation in invasion success has been demonstrated, raising the question of 55 its drivers (Zenni and Nunez 2013). Species are often introduced in regions that differ dramatically in 56 climate or habitat from their native ranges (Facon et al. 2006; Lodge 1993). Consequently, introduced 57 species will face novel environments, stressors and a host of additional selective pressures that are 58 different from those encountered in their native range (Novak 2007). Subsequently, these introduced 59 populations tend to evolve different traits in their introduced compared to their native ranges 60 (Maron et al. 2004). Many organisms that have established in novel environments have shown the 61 potential for rapid adaptation (Richardson and Pysek 2006; Lavergne and Molofski 2007; Urban et al. 62 2007), which can occur within 20 generations or less (Prentis et al. 2008). For example, invasive cane 63 toads have been shown to rapidly evolve dispersal phenotypes due to spatial sorting (Shine et al. 64 2011). Whereas certain life history and phenotypic traits of invading species may facilitate expansion by enabling them to outcompete indigenous species (Catford et al. 2008; Cortes et al. 2016), others 65 66 may prove to be disadvantageous to the invader when environmental conditions change (Simberloff 67 and Gibbons 2004). This suggests that a high degree of plasticity or adaptability would be beneficial 68 for invasive species.

69 Selection on dispersal capacity, particularly locomotor traits (Stevens et al. 2010), can be expected to 70 occur in expanding invasive populations once established. However, the dispersal ability of an 71 individual depends on many features, including temperature (Bestion et al. 2015). Understanding 72 how temperature impacts locomotion and dispersal is thus critical to predict future range 73 expansions. Temperature is a characteristic of an animal's habitat and one of the dimensions of the 74 ecologic niche (Magnuson et al. 1979). Cellular responses to temperature are linked to the 75 metabolism supplying ATP for cellular maintenance, membrane and protein synthesis (Hulbert and 76 Else 2000) and play a role in growth, reproduction, locomotor performance. Thus, these processes 77 have direct fitness consequences (Johnston and Temple 2002; Guderley 2004). Temperature 78 performance curves describe the physiological capacity of an organism to respond to variation in 79 temperature (Sinclair et al. 2016; Angilletta 2006) and are a useful tool to quantify the potential for a 80 species to thrive under varying thermal conditions. Locomotor performance is particularly relevant as 81 it is fitness-relevant (Arnold 1983), impacting survival and prey capture (i.e. burst performance

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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.

89 The African clawed frog, Xenopus laevis, is a principally aquatic frog native to sub-Saharan Africa 90 (Furman et al. 2015) and is widely used in laboratories worldwide. This species shows important 91 phenotypic differentiation between populations in its native range (Du Preez et al. 2009) suggesting 92 that it is particularly plastic in its physiology. The escape or voluntary release of individuals has led to 93 the establishment of populations on four continents: Asia, Europe, South America, and North 94 America (Measey et al. 2012). The invasive population from France is of particular interest due to its 95 ongoing expansion and has been well studied in terms of its morphology and physiology (Louppe et al. 2018, Padilla et al. 2019a,b), locomotor performance, (Louppe et al. 2017), reproduction (Courant 96 97 et al. 2017), behaviour (Kruger et al. 2019) and genetic composition (De Busschere et al. 2016). 98 Moreover, negative impacts on native biota have been demonstrated (Courant et al. 2018a,b). 99 Interestingly, the invasive population in France faces a different climate (Oceanic temperate) 100 compared to the native climate in South Africa (Rödder et al. 2017; Table 1). Given that the 101 population has expanded rapidly over the past 40 years (Vimercati et al. 2019) this suggests that they 102 either show broad thermal tolerance and plasticity or that they have adapted to the local climate.

103 Previous studies have suggested that future distribution scenarios for global invasions will be 104 improved by the investigation of traits leading to invasiveness coupled to the dynamics of introduced 105 species (Courchamp et al. 2017). Moreover, a comparison of suites of morphological or physiological 106 traits from native and non-native populations may help to understand the relationship between 107 adaptive responses and successful invasions (Garcia et al. 2013). Studies of the thermal sensitivity of 108 locomotor performance can provide a useful means to understand how physiological traits can limit 109 species distributions and may help to identify and characterise future range expansions (Chown et al. 110 2010). The aim of the present study is to test whether the thermal sensitivity of locomotor 111 performance differs in invasive and native populations (France and South Africa) of Xenopus laevis. 112 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 analysed 113

- terrestrial endurance and jumping capacities for individuals from the invasive (France) and native
- 115 (South Africa) ranges.

116 Materials and methods

117 Individuals used in this study were caught in two different areas in South Africa (N = 30, 12 males and 118 18 females; KwaZulu-Natal N = 15, 8 females and 7 males; Western Cape N = 15, 10 females and 5 119 males). Animals from the two regions in South Africa showed no differences in their thermal 120 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 121 pooled for all subsequent analyses. Individuals from the invasive population originated from western 122 France (Deux-Sèvres; N = 43, 23 males and 20 females). Upon arrival in the laboratory in Paris each 123 individual was pit-tagged allowing a unique identification. Animals were housed at the Function and 124 Evolution laboratory of the National Museum of Natural History in Paris, France. Specimens from the 125 native population were maintained in 30L aquaria, two per tank and those from the invasive population were housed in 65L aquaria with five to ten individuals per tank. Animals were fed thrice 126 127 weekly with frozen heart beef or mosquito larvae. The temperature of water was maintained at 23°C 128 and animals were acclimated at this temperature for two months before starting the experiments. All 129 protocols were in accordance with the guidelines of institutional animal care and use committee at 130 the MNHN.

131 Morphometrics

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

135 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 minutes and 1°C each 45 minutes from 6°C downwards for minimal temperature and from 28°C upwards 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 insertedinto the cloaca) to be that animal's critical temperature.

145 *Performance*

146 Stamina tests were performed at 19, 23, 27 and 31°C. We were unable to measure stamina at 16°C as 147 animals warmed up during the stamina tests often up to 2°C above their initial temperature of 16°C. 148 The muscle contractions occurring during repeated jumping likely produce enough heat to warm up 149 the animals over the course of a stamina trial which lasted often five to six minutes at these low 150 temperatures. Individuals were placed in individual containers with some water (to prevent 151 dehydration) for 3h hours in an incubator set at the desired test temperature. For each trial, body 152 temperature was recorded using a K-type thermocouple before and after performance. The room 153 temperature was set as close as possible to the test temperature. Measures of stamina were 154 performed by chasing animals individually until exhaustion (animals unable to right themselves when 155 put on their back) across a 3m long circular track with a humified cork substrate (Herrel and 156 Bonneaud 2012; Louppe et al. 2017). The total distance and time to exhaustion at the end of the trial 157 were recorded. After each trial animals were returned to their tank, fed and left to rest for at least 2 158 days. Trials were repeated twice per individual and the maximal time and distance were retained for 159 further analyses.

160 Burst performance was measured at 16, 19, 23, 27 and 31°C. Individuals were placed in small 161 containers with some water for 3 hours in an incubator set at the desired test temperature. Jump 162 force data were obtained via a force plate (Kistler Instruments AG, Type 5691A; see Herrel et al. 163 2014). Animals were placed on the force plate and were stimulated to jump five or six times within a 164 one-minute recording session. Forces were recorded at 500Hz and we used the Kistler Bioware 165 software to extract peak X, Y and Z forces (in Newtons). We then calculated the vector sum of the 166 three forces and used the resultant force in all further analyses. Three trials per individual were 167 recorded and the maximum jump force across all jumps and all trials was retained for further 168 analyses.

169 *Statistical analyses*

In order to fulfil assumptions of normality and homoscedasticity, all data were log₁₀ transformed
before analyses. Analyses were performed using R (version i386 3.4.2; R core team). To test for
differences in locomotor performance (burst and stamina) between populations, univariate analyses

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- 173 (ANOVAs) were run. Within populations (i.e. South Africa and France) we further tested for effects of
- temperature, mass, sex, snout-vent-length (SVL) and their interactions on locomotor performance
- 175 using repeated measures multivariate analyses of variance (MANOVAs). Next, pairwise multiple
- 176 comparisons tests (pairwise.t.test, "Stats" package version 3.4.2) with Bonferroni-Holm adjusted p-
- 177 values to test which temperatures differed from one another (temperature range: Stamina
- 178 [19,23,27,31°C]; Burst [16,19,23,27,31°C]). For each individual thermal performance curves
- 179 (Angilletta, 2009) were created using the minimum convex polygon method (van Berkum, 1986).
- 180 Optimal temperatures as well as temperature breadths T_{pb80} and T_{pb95} were analysed using univariate
- analyses of variance (ANOVAs) to test for differences between populations and performance traits.

182 Results

183 Within the native population (South Africa) a significant difference in snout-vent-length (SVL) ($F_{1,24}$ = 184 36.56; P < 0.001;) and mass ($F_{1,24}$ = 40.22; P < 0.001) was observed with females being larger than

- 185 males (Table 2). No differences in mass and SVL were observed between sexes in our sample of the
- 186 invasive population (France).

187 Stamina

188 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; Fig. 1, Table 3). Snout-vent length had 189 190 a significant effect on the maximum distance jumped in native X. laevis ($F_{3,96}$ = 159.04, P < 0.001). 191 Temperature also had a significant impact on the time spent jumping until exhaustion for the native 192 (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 193 194 population, a significant interaction between sex and temperature was observed ($F_{3,96}$ = 3.76, P = 195 0.013). Post-hoc tests showed that, in terms of distance, French frogs performed significantly 196 differently between each temperature (P < 0.001) in contrast to frogs from South Africa which 197 differed for some but not all temperatures (Table 4). Post-hoc tests on the time to exhaustion 198 showed significant differences between all temperatures for both populations (Invasive: P < 0.001; 199 native: P < 0.05). Native frogs performed significantly better than invasive frogs at 23 °C ($F_{1,64}$ = 47.91, 200 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 ($F_{1,64}$ = 201 0.448, P = 0.51). The time to exertion further differed significantly between populations at all tested 202 temperature (P < 0.001, for all temperatures) with invasive frogs becoming exhausted sooner.

- Temperature significantly affected burst performance in the native population ($F_{4,70}$ = 20.854; P < 0.854
- 205 0.001; Fig. 2, Table 5). Snout-vent length 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; Fig. 2, Table 5). Jump
- force was further also dependent on snout-vent length and sex in the invasive population (SVL: $F_{4,118}$
- 209 = 2.94, P = 0.023; sex: $F_{4,118}$ =5.25, P < 0.001). Post-hoc tests demonstrated significant differences
- 210 between some, but not all, temperatures irrespective of the population of origin (Table 6). No
- 211 significant differences in burst performance were detected between populations at the different test
- 212 temperatures (*P* > 0.05; Table 5).

213 Optimal temperature, critical temperatures, and performance breadths

- 214 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; P > 0.05).
- 217 There were no significant differences between populations in their 80 and 95% thermal performance
- 218 breadths (all *P* > 0.05). However, there are significant differences in the upper and lower limits of the
- 219 performance breadth interval (80%: $F_{1,56}$ =6.87, P < 0.01; 95%: $F_{1,56}$ =35.07, P < 0.005; Table 7, Figs. 1,2)
- 220 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
- 222 8).

223 Discussion

224 Critical temperatures

225 When organisms are confronted with temperatures approaching their thermal tolerance limits, they 226 can often avoid these using behavioural strategies (Sinclair et al. 2016). Outside its physiological 227 range an organism cannot maintain locomotor function and ultimately cannot survive (Angilletta 228 2009). This is a direct consequence of the thermal sensitivity of metabolic processes (Gillooly et al. 229 2001). Behavioural modulation may be less easy for principally aquatic animals like X. laevis and 230 consequently the thermal tolerance limits can be expected to be broad. The thermal tolerance limits 231 measured here were relatively broad. However, ectotherms from high latitudes often have even 232 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 to 31.7 °C; South Africa: 4.3 to 31.4 °C) (Table 8). Thus, the invasive
- 235 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).
- 237 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.

239 Locomotor performance

240 Metabolism imposes strong constraints on resource allocation to fitness-relevant traits (Brown et al. 241 2004). Previous studies have suggested that thermal performance curves tend to have the same 242 shape, with performance increasing with increasing temperature until a maximum is reached at the 243 optimal temperature (T_{opt}) and then rapidly decreasing (Angilletta et al. 2002). Invasive and native 244 populations in our study showed similar shapes of the thermal performance curve (Figs. 1, 2). 245 Interestingly, the temperature optima differed between the different performance traits with burst 246 performance showing a higher optimal temperature than endurance capacity. This is in accordance 247 with previous studies showing that thermal optima and preferences can differ for different 248 performance tasks (Huey and Stevenson 1979; Van Damme et al. 1991, Martin and Huey 2008, Herrel 249 and Bonneaud 2012). Burst performance appears to be physiologically optimised at higher 250 temperatures than endurance capacity. In many animals jump performance increases with increasing 251 temperature (James et al. 2007, 2012) until a physiological limit threshold (Hirano and Rome 1984). 252 Moreover, it has been shown that the power produced by the iliotibialis muscle in *Xenopus tropicalis* 253 increases with temperature, suggesting that warmer is better for burst performance (Herrel and 254 Bonneaud 2012, James et al. 2012), in accordance with our results.

255 Optimal temperatures for endurance capacity differed between native and invasive populations 256 (South Africa: 21.56°C, France: 19.36°C). Moreover, the absolute endurance was significantly greater 257 in frogs from the native population, except at 19°C. Thus, invasive frogs performed relatively better 258 at cooler temperatures compared to the native South African frogs. In France, the climate is colder 259 than in South Africa (Table 1), a significantly different climatic niche compared to that in the native 260 range (Rödder et al. 2017). The observed differences in thermal optima appear correlated with 261 differences in environmental temperatures (Table 1), in accordance with the prediction that the 262 thermal optimum will be set at the temperature most encountered in the environment (Huey and 263 Kingsolver 1993; Navas et al. 2008). Variation in muscle contraction kinetics can explain variation in

264 locomotor speed (John-Alder 1989) and oxygen transport relevant for endurance capacity. In

amphibians, the maximal rate of oxygen consumption is strongly dependent on temperature

266 (Seymour 1972). Indeed, even the resting or basal metabolism in amphibians increases with

267 temperature (Whitford 1973). In contrast to endurance capacity, native and invasive populations

268 performed equally well for burst performance. It has been demonstrated previously that force

269 production is less temperature dependent compared to muscle contractive velocity or metabolic rate

270 (Herrel et al. 2007) and as such the lack of differences in the thermal dependence of jump force is

271 not unexpected.

272 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 towards 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

278 performance curve did not differ between populations showing that the overall shape of the

279 performance curve did not evolve. This may suggest a level of intrinsic constraint to the ability in *X*.

280 *laevis* to broaden its temperature performance curve beyond certain physiological limits.

281 Plasticity has a clear and ubiquitous role in promoting phenotypic changes in response to climate 282 variation (Pigliucci 2005, Urban et al. 2014). As temperature affects both locomotion and skeletal 283 muscle performance, some ectotherms show acclimation under different thermal environments in 284 order to maintain skeletal muscle and locomotor performance (Johnston and Temple, 2002; Padilla 285 et al., 2018a). However, other studies have shown that thermal physiology may evolve. For example, 286 in Limnodynastes peronii differences appear among populations with populations from cooler 287 environments tending to perform better at lower temperatures (Wilson 2001). As the invasive 288 population expressed differences in the optimal temperature for endurance and shifts in the thermal 289 limits despite being kept in a common environment for several months at identical temperatures, our 290 results suggest that X. laevis has effectively adapted to the thermal environment of its invasive range 291 in France. As French individuals are derived from two distinct genetic lineages from southern Africa 292 (De Busschere et al. 2016), the genetic admixture could have facilitated the observed thermal 293 adaptation.

294 Species distribution models (SDM) are commonly used in ecological and evolutionary studies and use 295 geographic information on species presence and absence in different climatic zones (Brown 2014) to

- 296 make predictions on future ranges under different scenarios of climate change (Ilhow et al. 2016).
- 297 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 (Ilhow et al.
- 2016), these predictions do not include the ability of *X. laevis* to rapidly adapt to different climatic
- 301 conditions and likely underestimate the future invasion potential of the species. Future modelling
- 302 efforts should focus on incorporating physiological information on the thermal dependence of
- 303 dispersal as well as potential for adaptation.

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323 Author contributions

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- 324 AH and J.M. conceived the study; L.A., A.S.M., and P.P. collected data; J.C., C.W. and J.M. collected
- animals in the field; L.A., P.P. and A.H. analysed the data; L.A. and A.H. wrote the article and all
- 326 authors contributed to and approved the final version of the paper.

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489 Figure legends

- 490 **Figure 1**: temperature performance curves illustrating the impact of temperature on endurance
- 491 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
- 493 represent means ± standard errors of the mean.
- 494 **Figure 2**: temperature performance curves illustrating the impact of temperature on jump force for
- 495 *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
- 497 mean.