



HAL
open science

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, Anthony Herrel

► To cite this version:

Laurie Araspin, Anna Serra Martinez, Carla Wagener, Julien Courant, Vivien Louppe, et al.. Rapid shifts in the temperature dependence of locomotor performance in an invasive frog, *Xenopus laevis*, implications for conservation. *Integrative and Comparative Biology*, 2020, 10.1093/icb/icaa010 . hal-02514099

HAL Id: hal-02514099

<https://hal.science/hal-02514099>

Submitted on 7 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Laurie Araspin^{1,2}, Anna Serra Martinez¹, Carla Wagener², Julien Courant¹, Vivien Louppe³, Pablo
4 Padilla^{1,4}, John Measey^{2*} and Anthony Herrel^{1*}

5 1. UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie
6 Comparée, 55 rue Buffon, 75005, Paris, France.

7 2. Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University,
8 Stellenbosch, 7602, South Africa.

9 3. Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle,
10 CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP 51, 75231, Paris, Cedex 5,
11 France.

12 4. Laboratory of Fish and Amphibian Ethology, Behavioural Biology Group, Freshwater and Oceanic
13 science Unit of reSearch (FOCUS), University of Liège, Liège, Belgium.

14

15 * Contributed equally

16

17 # pages: 18

18 # tables: 8

19 # figures: 2

20

21

22

23

24

25

26

27 **Address for correspondence:**

28 Anthony Herrel

29 UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée,
30 55 rue Buffon, 75005, Paris, France

31 e-mail: anthony.herrel@mnhn.fr - phone: ++33-140798120 - fax: ++33-140793773

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
35 may limit population expansion unless organisms can physiologically respond to changes in
36 temperature either through plasticity or by adapting to their novel environment. Here, we studied
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
46 environment. These data may allow the refinement of physiologically informed species distribution
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
65 by enabling them to outcompete indigenous species (Catford et al. 2008; Cortes et al. 2016), others
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

82 traits), and dispersal (endurance capacity). In ectotherms, locomotor performance is directly
83 dependent on temperature and as such variation in the temperature range in a novel area may
84 determine the success of establishment and spread of an invasive species. However, the thermal
85 environment often varies seasonally and daily, resulting in an intrinsic plasticity in the response of
86 most animals to temperature (Osborn and Briffa 2006). Consequently, a greater plasticity in the
87 dependence of locomotor performance on temperature may predispose certain organisms to
88 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
96 al. 2018, Padilla et al. 2019a,b), locomotor performance, (Louppe et al. 2017), reproduction (Courant
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
113 performance in addition to critical thermal limits differ between populations. To do so we analysed

114 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
126 population were housed in 65L aquaria with five to ten individuals per tank. Animals were fed thrice
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*

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

135 *Critical minimal and maximal temperatures*

136 Individuals were placed in individual containers with some water (to prevent dehydration) and put in
137 an incubator (Aqualytic-LIEBHERR, TC 256 G/256 L/2-40°C) where temperature was decreased or
138 increased slowly (an average of 2°C each 45 minutes and 1°C each 45 minutes from 6°C downwards
139 for minimal temperature and from 28°C upwards for maximal temperature). Animals were warmed
140 up slowly as their thermal inertia was substantial and faster rates resulted in animals being cooler or
141 warmer than the temperature set on the incubator. Animals were inspected regularly and checked
142 for the lack of a righting response. As soon as animals were no longer able to turn over after having

143 been placed on their back, we considered that temperature (measured with a thermocouple inserted
144 into 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*

170 In order to fulfil assumptions of normality and homoscedasticity, all data were \log_{10} transformed
171 before analyses. Analyses were performed using R (version i386 3.4.2; R core team). To test for
172 differences in locomotor performance (burst and stamina) between populations, univariate analyses

173 (ANOVAs) were run. Within populations (i.e. South Africa and France) we further tested for effects of
174 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
181 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 ($F_{3,54} =$
189 $58.87, P < 0.001$;) and invasive *X. laevis* ($F_{1,32} = 42,68; P < 0.001$; Fig. 1, Table 3). Snout-vent length had
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
193 spent jumping was dependent on the mass of the individuals ($F_{3,54} = 2.98, P = 0.04$). In the invasive
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.

203 *Burst performance*

204 Temperature significantly affected burst performance in the native population ($F_{4,70} = 20.854$; $P <$
205 0.001 ; Fig. 2, Table 5). Snout-vent length and mass also significantly impacted jump force in these
206 animals (SVL: $F_{1,17} = 10.77$, $P = 0.004$; mass: $F_{1,17} = 7.17$, $P = 0.015$). In the invasive population,
207 temperature also significantly affected jump force ($F_{4,118} = 17.73$, $P < 0.001$; Fig. 2, Table 5). Jump
208 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 ($T_{opt_{France}}: 19.36^{\circ}\text{C}$;
215 $T_{opt_{South\ Africa}}: 21.56^{\circ}\text{C}$; $F_{1,56} = 28.3$, $P < 0.001$; Table 7). For burst performance no differences in
216 optimal temperature were detected, however ($T_{opt_{France}}: 23.94^{\circ}\text{C}$; $T_{opt_{South\ Africa}}: 24.48^{\circ}\text{C}$; $P > 0.05$).
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
221 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

233 al. 2011). In our study thermal limits did not differ significantly between the native and invasive
234 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
236 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
238 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 (Rödger 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

265 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*

273 In addition to the shift in the thermal optimum for endurance capacity, a shift in the 80% thermal
274 performance limits for endurance capacity was observed between the native and invasive
275 populations. Indeed, the thermal performance curve shows a left-shift towards cooler temperatures
276 of about two degrees in the invasive population. Consequently, the invasive French population
277 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.
298 endurance) in the invasive population of *X. laevis* that are not taken into account in these SDMs.
299 Although the future distribution of *X. laevis* is likely to increase with climate change (Ilhow et al.
300 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.

304 **Acknowledgements**

305 The authors would like to thank Lance McBrayer, Eric McElroy and Diego Sustaita for organising the
306 symposium entitled 'Applied Functional Biology: linking ecological morphology to conservation and
307 management' supported by DAB, DCB, DEE, DNNSB, DVM as well as the Company of Biologists. We
308 would like to thank them for inviting us to present our work on invasive amphibians. We would also
309 like to thank two anonymous reviewers for helpful and constructive comments on an earlier version
310 of the paper. JM and CW would like to thank the DSI-NRF Centre of Excellence for Invasion Biology
311 and Stellenbosch University. Research and capture permits were provided by the Préfet of the Deux-
312 Sèvres department (France); capture and export permits for *Xenopus laevis* from KZN (iSimangaliso
313 National Park) were provided under permit number OP 3169/2018 from KZN Wildlife; capture and
314 export of *Xenopus laevis* from the Western Cape was made possible under permit CN15-31-5189
315 from CapeNature. We would like to thank Xander Combrink and Scotty Kyle for sharing information
316 about iSimangaliso NP.

317 **Funding**

318 This work was supported by an ERA-Net BiodivERsA grant INVAXEN, with the national funders ANR,
319 DFG, BELSPO and FCT, as part of the 2013 BiodivERsA call for research proposals. INVAXEN 'Invasive
320 biology of *Xenopus laevis* in Europe: ecology, impact and predictive models' [ANR-13-EBID-0008-01]
321 to A.H. and J.M.; the National Research Foundation of South Africa [NRF Grant No. 87759 and
322 incentive funding] to J.M.

323 **Author contributions**

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
325 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.

327 **References**

328 Angilletta MJ. 2006. Estimating and comparing thermal performance curves. *J Therm Biol* 31:541–45.

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

331 Arnold SJ. 1983. Morphology, Performance and Fitness. *Am Zool* 23:347–61.

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

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

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

338 Catford JA, Jansson R, Nilsson C. 2009. Reducing redundancy in invasion ecology by integrating
339 hypotheses into a single theoretical framework. *Div Distr* 15:22–40.

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

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

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

346 Courant J, Secondi J, Vollette J, Herrel A, Thirion J-M. 2018. Assessing impacts of the invasive *Xenopus*
347 *laevis* on amphibians in western France. *Amph Rept* 39:219-227.

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

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

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

355 Angilletta MJ. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University
356 Press.

357 Du Preez LH, Kunene N, Hanner R, Giesy JP, Solomon KR, Hosmer A, Van Der Kraak GJ. 2009.
358 Population-specific incidence of testicular ovarian follicles in *Xenopus laevis* from South Africa: A
359 potential issue in endocrine testing. *Aquatic Toxicol* 95:10–16.

360 Facon B, Genton B, Shykoff J, Jarne P, Estoup A, David P. 2006. A general eco-evolutionary framework
361 for understanding bioinvasions. *Trends Ecol Evol* 21:130–35.

362 Fick SE, Hijmans RJ. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land
363 areas. *Int J Climatol* 37:4302–4315.

364 Furman BLS, Bewick AJ, Harrison TL, Greenbaum E, Gvoždík V, Kusamba C, Evans BJ. 2015. Pan-
365 African phylogeography of a model organism, the African clawed frog '*Xenopus laevis*.' *Mol Ecol*
366 24:909–25.

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

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

371 Guderly H. 2004. Metabolic responses to low temperature in fish muscle. *Biol Rev* 79:409–427.

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

374 Herrel A, James RS, Van Damme R. 2007. Fight versus flight: physiological basis for temperature
375 dependent behavioral shifts in lizards. *J Exp Biol* 210:1762-1767.

376 Herrel A, Gonwouo LN, Fokam EB, Ngundu WI, Bonneaud C. 2012. Intersexual differences in body
377 shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *J Zool* 287:311–16.

378 Herrel A, Vasilopoulou-Kampitsi M, Bonneaud C. 2014. Jumping performance in the highly aquatic
379 frog, *Xenopus tropicalis*: sex-specific relationships between morphology and performance. *PeerJ*
380 2:e661

381 Hirano M, Rome LC. 1984. Jumping performance of frogs (*rana pipiens*) as a function of muscle
382 temperature. *J Exp Biol* 108:429-439.

383 Huey RB, Kingsolver JG. 1993. Evolution of resistance to high temperature in ectotherms. *Am Nat*
384 142:S21–46.

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

387 Hulbert AJ, Else PL. 2000. Mechanisms underlying the cost of living in animals. *Annu Rev Physiol*
388 62:207–35.

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

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

394 James RS, Tallis J, Herrel A, Bonneaud C. 2012. Warmer is better: thermal sensitivity of both maximal
395 and sustained power output in the iliotibialis muscle isolated from adult *Xenopus tropicalis*. *J Exp Biol*
396 215:552–58.

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

399 Johnston IA, Temple GK. 2002. Thermal plasticity of skeletal muscle phenotype in ectothermic
400 vertebrates and its significance for locomotory behaviour. *J Exp Biol* 205:2305–2322.

401 Kruger N, Measey J, Herrel A, Secondi J. 2019. Anti-predator strategies of the invasive African clawed
402 frog, *Xenopus laevis*, to native and invasive predators in western France. *Aqua Invas* 14: 433–443.

403 Lavergne S, Molofsky J. 2007. Increased genetic variation and evolutionary potential drive the
404 success of an invasive grass. *Proc Natl Acad Sci* 104:3883–88.

405 Liendo D, Biurrun I, Campos JA, Herrera M, Loidi J, García-Mijangos I. 2015. Invasion patterns in
406 riparian habitats: The role of anthropogenic pressure in temperate streams. *Plant Biosyst* 149:289–
407 97.

408 Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends Ecol Evol* 8:133-137.

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

411 Louppe V, Courant J, Videlier M, Herrel A. 2018. Differences in standard metabolic rate at the range
412 edge versus the center of an expanding invasive population of *Xenopus laevis* in the West of France. *J*
413 *Zool* 305:163-172.

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

416 Magnuson JJ, Crowder LB, Medvick PA. 1979. Temperature as an ecological resource. *Am Zool*
417 19:331–43.

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

420 Martin TL, Huey RB. 2008. Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal
421 preferences. *Am Nat* 171:E102–18.

422 Measey GJ, Rodder D, Green SL, Kobayashi R, Lillo F, Lobos G, Rebelo R. 2012. Ongoing invasions of
423 the African clawed frog, *Xenopus laevis*: a global review. *Biol Inv* 14 :2255–2270.

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

426 Novak SJ. 2007. The role of evolution in the invasion process. *Proc Natl Acad Sci USA* 104:3671–72.

427 Osborn TJ, Briffa KR. 2006. The spatial extent of 20th-century warmth in the context of the past 1200
428 years. *Science* 311:841–44.

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

432 Padilla P, Courant J, Herrel A. 2019. Allocation trade-offs impact organ size and muscle architecture in
433 an invasive population of *Xenopus laevis* in Western France. *J Anat* 235:1057-1064.

434 Pigliucci M. 2005. Evolution of phenotypic plasticity: where are we going now? *Trends Ecol Evol*
435 20:481–86.

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

438 Rödder D, Ihlow F, Courant J, Secondi J, Herrel A, Rebelo R, Measey GJ, Lillo F, Villiers FAD, Busschere
439 CD, Backeljau T. 2017. Global realized niche divergence in the African clawed frog *Xenopus laevis*.
440 *Ecology and Evolution* 7:4044–58.

441 R core team. 2019. R: A language and environment for statistical computing. R Foundation for
442 Statistical Computing, Vienna, Austria.

443 Richardson DM, Pyšek P. 2006. Plant invasions: merging the concepts of species invasiveness and
444 community invasibility. *Progr Phys Geogr: Earth and Environm* 30:409–31.

445 Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M,
446 Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Gradow L, Dawson W, Dullinger S,
447 Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D,
448 Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE,
449 Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka
450 T, Essl F. 2017. No saturation in the accumulation of alien species worldwide. *Nat Commun* 8:14435.

451 Seymour RS. 1972. Behavioral thermoregulation by juvenile green toads, *Bufo debilis*. *Copeia*
452 1972:572–75.

453 Shine, R., G.P. Brown and B.L. Phillips (2011) An evolutionary process that assembles phenotypes
454 through space rather than through time. *Proc Natl Acad Sci USA* doi: 0.1073/pnas.1018989108.

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

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

460 Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS. 2016. Can we predict ectotherm
461 responses to climate change using thermal performance curves and body temperatures? *Ecol Lett* 19:
462 1372–1385.

463 Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagran-Santa Cruz M, Lara-
464 Resendiz R, Martinez-Mendez N, Calderon-Espinosa ML, Meza-Lazaro RN, Gadsden H, Avila LJ,
465 Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Iburguengoytia N, Puntriano CA, Massot M,
466 Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW. 2010. Erosion of lizard
467 diversity by climate change and altered thermal niches. *Science* 328:894–99.

468 Stevens VM, Pavoine S, Baguette M. 2010. Variation within and between closely related species
469 uncovers high intra-specific variability in dispersal. *PLoS ONE* 5:e11123.

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

472 Urban MC, Phillips BL, Skelly DK, Shine R. 2007. The cane toad's (*Chaunus [Bufo] marinus*) increasing
473 ability to invade Australia is revealed by a dynamically updated range model. *Proc R Soc B* 274:1413–
474 19.

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

- 477 Van Berkum FH. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis*
478 lizards. *Evolution* 40:594–604.
- 479 Van Damme R, Bauwens D, Verheyen RF. 1991. The thermal dependence of feeding behaviour, food
480 consumption and gut-Passage time in the lizard *Lacerta vivipara*, Jacquin. *Funct Ecol* 5:507.
- 481 Vimercati G, Labadesse M, Dejean T, Secondi J. 2019. Assessing the effect of landscape features on
482 pond colonisation by an elusive amphibian invader using environmental DNA. *Freshwater Biol* doi:
483 10.1111/fwb.13446
- 484 Whitford WG. 1973. The effects of temperature on respiration in the amphibia. *Am Zool* 13:505–12.
- 485 Wilson RS. 2001. Geographic variation in thermal sensitivity of jumping performance in the frog
486 *Limnodynastes peronii*. *J Exp Biol* 204:4227–4236.
- 487 Zenni RD, Nuñez MA. 2013. The elephant in the room: the role of failed invasions in understanding
488 invasion biology. *Oikos* 122:801–15.

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,
492 D). Indicated are the 80% thermal performance breadths for each trait and each population. Symbols
493 represent means \pm 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
496 breadths for each trait and each population. Symbols represent means \pm standard errors of the
497 mean.