

RESEARCH ARTICLE

Differences in mobility at the range edge of an expanding invasive population of *Xenopus laevis* in the west of France

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ABSTRACT

Theoretical models predict that spatial sorting at the range edge of expanding populations should favor individuals with increased mobility relative to individuals at the center of the range. Despite the fact that empirical evidence for the evolution of locomotor performance at the range edge is rare, data on cane toads support this model. However, whether this can be generalized to other species remains largely unknown. Here, we provide data on locomotor stamina and limb morphology in individuals from two sites: one from the center and one from the periphery of an expanding population of the clawed frog *Xenopus laevis* in France where it was introduced about 30 years ago. Additionally, we provide data on the morphology of frogs from two additional sites to test whether the observed differences can be generalized across the range of this species in France. Given the known sexual size dimorphism in this species, we also test for differences between the sexes in locomotor performance and morphology. Our results show significant sexual dimorphism in stamina and morphology, with males having longer legs and greater stamina than females. Moreover, in accordance with the predictions from theoretical models, individuals from the range edge had a greater stamina. This difference in locomotor performance is likely to be driven by the significantly longer limb segments observed in animals in both sites sampled in different areas along the range edge. Our data have implications for conservation because spatial sorting on the range edge may lead to an accelerated increase in the spread of this invasive species in France.

KEY WORDS: Frog, Locomotion, Invasion, Stamina

INTRODUCTION

Dispersal, typically defined as a permanent movement away from a site of birth and/or reproduction (Clobert et al., 2009), may be due to discrete and repeated introduction of propagules beyond ecological barriers. Alternatively, evolutionary mechanisms that make new ecological niches accessible may also spur dispersal (Wilson et al., 2009). Dispersal is dependent on many factors including an organism's phenotype, sex, age, reproductive output, the intensity of competition and environmental conditions (Stevens et al., 2010). The synergistic influence of these parameters may result in the spatial differentiation of expanding populations (Shine et al., 2011). Spatial sorting and lower population density have been documented at the invasion front of expanding populations (e.g. Phillips et al., 2010). Theoretical models based on these observations have

subsequently predicted increased dispersal and reproductive rates along the edge of the expansion range (Hallatschek and Nelson, 2007; Excoffier and Ray, 2008; Excoffier, 2009; Burton et al., 2010; Travis et al., 2010). Lower predation pressure by specialist predators and reduced competition (Burton et al., 2010; Phillips et al., 2010; Brown et al., 2013), in addition to an increased risk of kin competition resulting from low population density (Kubisch et al., 2013), may also encourage an increased dispersal rate at the colonization front. However, processes such as mutation surfing (Travis et al., 2010), Allee effects (Travis and Dytham, 2002) or allocation trade-offs (Bishop and Peterson, 2006; Fronhofer and Altermatt, 2015) may prevent this from happening. Thus, predictions from theoretical models may not always hold and these predictions remain to be tested. The increase of reproductive output at the range edge, for example, remains controversial (Hughes et al., 2003; Karlsson and Johansson, 2008; Bonte et al., 2012; Hudson et al., 2015). However, the allocation of resources to dispersal has been relatively well documented. For example, the fast dispersal rate and associated phenotypic traits that are observed in vanguard populations of the invasive cane toad *Rhinella marina* in Australia (Brown et al., 2007; Alford et al., 2009; Phillips et al., 2008) provide a nice illustration of a dispersal phenotype in a rapidly expanding population.

The present study focuses on another highly and globally invasive amphibian, the African clawed frog *Xenopus laevis* Daudin 1802. The use of *X. laevis* as a model system in developmental and cellular biology (Gurdon and Hopwood, 2000) has resulted in the presence of this species in laboratories world-wide. Invasive populations of *X. laevis* have since become established globally as a result of accidental as well as voluntary releases from research facilities and through the release of animals from the pet trade (Measey et al., 2012). Despite a growing body of literature on the invasion range and the impacts of this species on autochthonous ecosystems (Lafferty and Page, 1997; Lillo et al., 2005, 2011; Lobos and Jaksic, 2005; Eggert and Fouquet, 2006; Fouquet and Measey, 2006; Robert et al., 2007; Faraone et al., 2008; Rebelo et al., 2010; Measey et al., 2012; De Busschere et al., 2016), this species has never been used to test the predictions of dispersal models. Our study focuses on an invasive population of *X. laevis* in the west of France. Its introduction has been suggested to be associated with the presence of a research laboratory where *Xenopus* were bred and maintained until the facility closed in the early 1980s (Fouquet and Measey, 2006). Animals were officially first reported in 1998 when they were observed in few ponds around the likely site of introduction. However, residents of the area subsequently suggested that animals had been in these ponds since the early 1980s. Since then, animals have been expanding at a steady rate and they now occupy an area of over 2000 square kilometers. The aim of the present study was to test whether *X. laevis* at the range edge show evidence of dispersal phenotypes. Specifically, we test whether animals at the range edge have longer limbs and greater

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locomotor performance than animals near the likely site of release. To investigate this, we analyzed terrestrial endurance capacity and limb morphology for individuals from the center and the periphery of the range.

MATERIALS AND METHODS

All individuals ($N=164$; 84 from the periphery and 80 from the center of the range) were caught in ponds and bodies of standing water within their current range using fykes. The range of *X. laevis* in western France is identified through regular monthly trapping campaigns by local fish and wildlife officers and currently covers three departments (Vienne, Deux-Sèvres and Maine-et-Loire) and an area of ~ 2000 km² (Fig. 1). Two pairs of sites were used in this study: one site at the center of the range, near the introduction point, and one site at the periphery. For each site, all individuals were caught in a single pond. Individuals from the first pair ($N=87$; 53 from the periphery and 34 from the center; sites 1 and 2, respectively, in Fig. 1) were caught, brought back and housed at the Function and Evolution (FUNEVOL) laboratory at the Muséum National d'Histoire Naturelle in Paris, France. Specimens were housed in groups of 6–10 individuals in 50 liter aquaria at a temperature of 23°C and fed with beef heart and mosquito larvae. All individuals were pit-tagged (Nonatec, Lutonic International, Rodange, Luxembourg), allowing unambiguous identification of each individual during study. Individuals from the second pair of sites ($N=77$; 31 from the

periphery and 46 from the center; sites 3 and 4, respectively, in Fig. 1) were killed in the field using an overdose of anesthetic (MS222) according to institutional guidelines, preserved in formaldehyde and used for morphometric analyses.

Morphometrics

All individuals were weighed (Ohaus, Brooklyn, NY, USA; precision ± 0.1 g) and measured using a digital caliper (Mitutoyo; precision ± 0.01 mm). Body dimensions were measured following Herrel et al. (2012). A summary of the morphometric data is provided in Table 1.

Performance

Stamina tests were performed at 22°C, which is considered the optimal temperature for the species (Casterlin and Reynolds, 1980; Miller, 1982). Animals (sites 1 and 2) were placed in individual containers with some water for 1 h in an incubator set at 22°C prior to each test. The body temperature (T_b) of each individual was recorded using a K-type thermocouple before and after stamina trial as the room temperature was slightly lower than the temperature of the incubator (19°C) causing the animals' body temperature to drop slightly during the trials. Between trials, animals were returned to their aquaria, fed, and allowed to rest for at least 24 h. Three trials per individual were performed and only the single best trial was retained for further analysis. Stamina was measured by chasing each

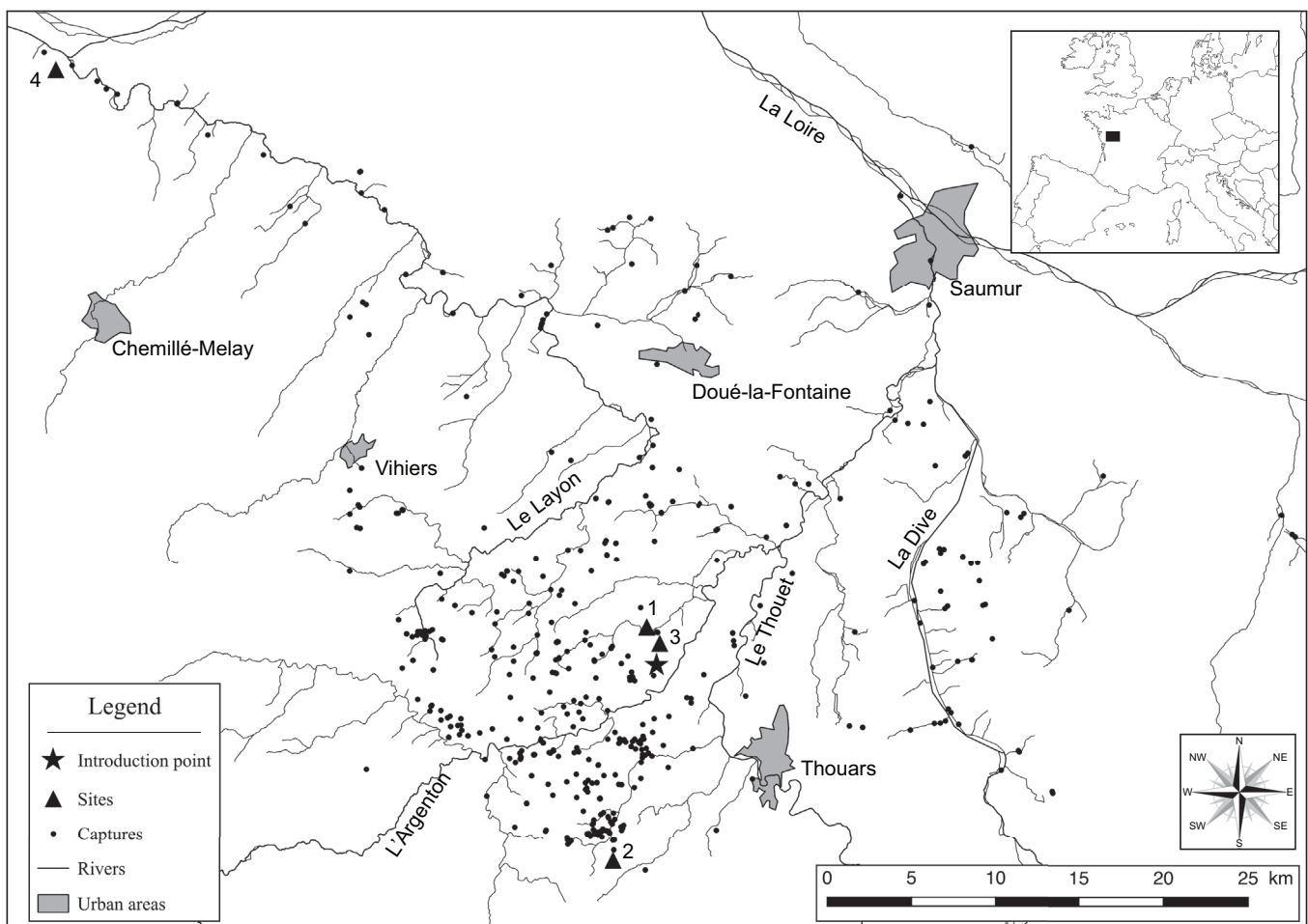


Fig. 1. Current distribution of the invasive population of *Xenopus laevis* in the west of France. Indicated are the point of introduction and the four sites used in this study. Small dots indicate ponds where *X. laevis* are present.

Table 1. Morphometric traits (means±s.e.) measured for each site and sex

	Sex	Site 1 (center)	Site 2 (periphery)	Site 3 (center)	Site 4 (periphery)
SVL (mm)	Female	83.37±1.03	65.01±1.03	86.70±1.04	80.54±1.04
	Male	70.15±1.04	59.84±1.02	69.50±1.03	63.53±1.04
Femur length (mm)	Female	27.93±1.02	28.84±1.01	27.73±1.02	27.80±1.01
	Male	29.65±1.02	30.34±1.01	30.41±1.02	31.48±1.02
Tibia length (mm)	Female	24.32±1.03	26.24±1.02	24.38±1.08	25.23±1.05
	Male	27.35±1.03	26.61±1.02	25.59±1.07	23.71±1.07
Astragalus length (mm)	Female	15.67±1.03	17.82±1.02	14.55±1.03	15.45±1.02
	Male	18.54±1.03	18.28±1.02	15.14±1.03	15.31±1.03
Longest toe length (mm)	Female	26.73±1.02	26.67±1.02	30.06±1.26	31.55±1.01
	Male	29.11±1.02	28.12±1.02	31.05±1.02	32.66±1.02
Humerus length (mm)	Female	10.59±1.04	11.86±1.03	11.22±1.32	12.02±1.19
	Male	13.49±1.04	13.21±1.03	20.51±1.29	13.15±1.29
Radius length (mm)	Female	9.89±1.04	9.68±1.03	12.05±1.03	13.58±1.02
	Male	12.13±1.04	11.80±1.03	11.80±1.03	14.39±1.03
Hand length (mm)	Female	4.00±1.04	4.31±1.03	4.52±1.05	5.16±1.03
	Male	4.41±1.03	4.38±1.03	4.41±1.05	5.19±1.05
Longest finger length (mm)	Female	10.02±1.03	9.35±1.02	11.25±1.03	12.42±1.02
	Male	11.04±1.03	10.35±1.02	10.84±1.03	12.94±1.03
Ilium width (mm)	Female	15.78±1.02	16.63±1.02	15.07±1.03	15.10±1.02
	Male	15.17±1.02	16.07±1.02	15.31±1.02	15.59±1.03
Mass (g)	Female	29.51±1.03	36.14±1.03	28.84±1.06	26.915±1.04
	Male	30.13±1.03	36.64±1.02	27.54±1.06	25.76±1.06

Site 1, $N=14$ males and $N=20$ females; site 2, $N=33$ males and $N=20$ females; site 3, $N=31$ males and $N=15$ females; site 4, $N=20$ males and $N=20$ females.

individual down a 3 m long circular track covered with cork. Animals were chased until exhaustion, which was identified by the lack of a righting response. Note that individuals recovered quickly from these trials and were immediately ready to eat when placed back in their home aquaria. For each individual, we recorded both the total distance covered and time spent moving until exhaustion. Statistical analyses were performed using the maximum distance covered and the maximum time spent moving for each individual out of the three trials (Table 2).

Statistical analyses

All data were \log_{10} transformed to meet assumptions of normality and homoscedasticity. To test for differences in size [snout–vent length (SVL)] between sexes, and between center and edge sites, univariate analyses (ANOVAs) were performed. Differences in body mass, the morphology of the ilium and limb dimensions were tested between sexes and populations using multivariate ANOVAs with the SVL as a covariate (MANCOVA). These analyses were performed independently within each pair of sites (comparison of site 1 with site 2, and site 3 with site 4) to avoid potential biases due

to preservation of the animals (sites 3 and 4). An ANOVA was performed to test for differences in the body temperature of the animals from sites 1 and 2 after the trials. Given that both SVL (sites 1 and 2: $F_{1,83}=47.92$; $P<0.01$; sites 3 and 4: $F_{1,73}=6.35$; $P=0.01$) and body temperature ($F_{1,83}=20.65$; $P<0.001$) were different between animals from different sites they were incorporated as covariates in our multivariate analyses. Next, a multivariate analysis (MANCOVA), with SVL and body temperature as covariates, was performed to test whether stamina, identified here as the maximum time and the maximum distance moved until exhaustion, differed between sexes and sites. All analyses were performed using SPSS v.22 (IBMSPSS, Chicago, IL, USA).

RESULTS

Snout–vent length was significantly different between males and females from sites 1 and 2 ($F_{1,83}=18.80$; $P<0.01$), with females being on average 16% larger than males. Similarly, females were on average 20% larger when comparing preserved animals from sites 3 and 4 ($F_{1,73}=50.32$; $P<0.01$; Table 3). SVL was also significantly different between populations, with individuals from the center being larger than individual from the periphery (sites 1 and 2: $F_{1,83}=47.92$; $P<0.01$; sites 3 and 4: $F_{1,73}=6.35$; $P=0.01$). Individuals from site 1 (center of the range) are on average 20% larger than those from site 2 (periphery) (Table 1, Fig. 2). Individuals from site 3 (center of the range) are on average 8% larger than those from site 4 (periphery; Table 1, Fig. 2).

Table 2. Mean performance trait and body temperature at the end of the trial

	Population	Sex	Mean±s.e.
T_b (°C)	Center	Female	22.28±1.01
		Male	21.83±1.01
	Periphery	Female	20.89±1.01
		Male	21.63±1.01
Distance (cm)	Center	Female	1241.65±1.12
		Male	1137.63±1.12
	Periphery	Female	1300.17±1.11
		Male	1721.87±1.09
Time (s)	Center	Female	75.51±1.12
		Male	91.62±1.11
	Periphery	Female	110.15±1.10
		Male	148.59±1.08

Center, $N=14$ males and $N=20$ females; periphery, $N=33$ males and $N=20$ females.

Table 3. Results of univariate analyses testing for differences in SVL and body temperature at the end of the stamina trial between populations and sexes

Variable	Source	F	d.f.	Error	P -value
SVL	Population	47.92	1	83	<0.01
	Sex	18.80	1	83	<0.01
	Population×sex	2.18	1	83	0.14
T_b	Population	20.65	1	83	<0.01
	Sex	0.88	1	83	0.35
	Population×sex	12.51	1	83	<0.01

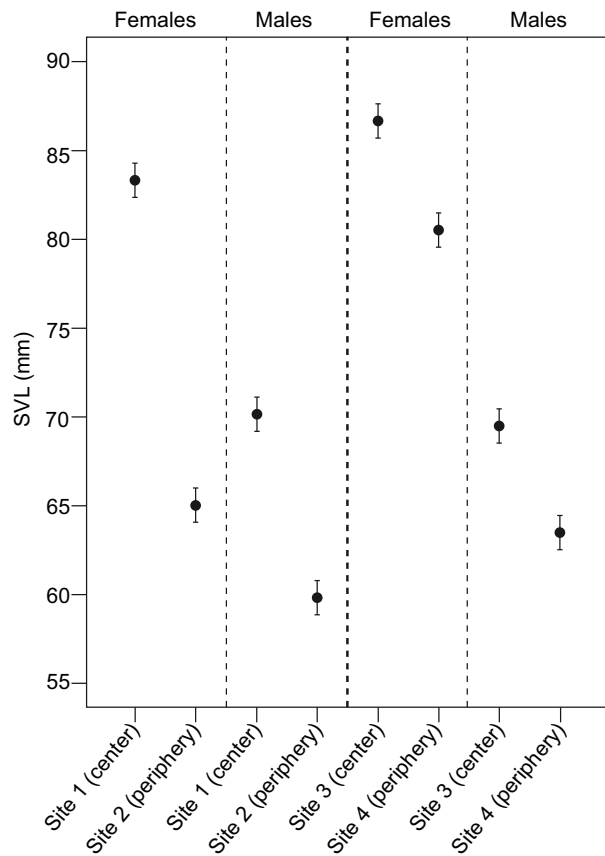


Fig. 2. Snout-vent length for males and females from sites at the center and the periphery of the range. Values are means±s.d. Site 1, N=14 males and N=20 females; site 2, N=33 males and N=20 females; site 3, N=31 males and N=15 females; site 4, N=20 males and N=20 females.

Size-corrected limb dimensions were also significantly different between males and females from sites 1 and 2 (Wilks' lambda=0.53; $F_{11,72}=5.84$; $P<0.01$; Table 4), and sites 3 and 4 (Wilks' lambda=0.59; $F_{14,59}=2.88$; $P<0.01$; Table 5). Within sites 1 and 2, all morphological traits except for hand length were significantly greater for males (Table 4). Male forelimbs are on average 15% longer and hind limbs 7% longer than those of females of a given body size (Table 1). For sites 3 and 4, the toe, radius, hand and finger

Table 4. MANCOVA performed on the morphometric data from sites 1 and 2 with SVL as covariate

Effect	Variable	Wilks' lambda	F	d.f.	Error	P-value
Population		0.61	4.25	11	72	<0.01
	Mass		40.48	1	82	<0.01
	Astragalus		4.56	1	82	0.04
	Ilium width		6.00	1	82	0.02
	Finger		6.55	1	82	0.01
Sex		0.53	5.84	11	72	<0.01
	Femur		11.37	1	82	<0.01
	Tibia		7.71	1	82	0.01
	Astragalus		16.75	1	82	>0.01
	Longest toe hind		11.49	1	82	>0.01
	Humerus		26.00	1	82	>0.01
	Radius		33.09	1	82	>0.01
	Longest toe front		18.56	1	82	>0.01
	Hand		2.43	1	82	0.12
	Population×sex			0.79	1.73	11

Table 5. MANCOVA performed on the morphometric data from sites 3 and 4 with SVL as covariate

Effect	Variable	Wilks' lambda	F	d.f.	Error	P-value
Population		0.59	2.88	14	59	<0.01
	Femur		38.68	1	72	<0.01
Sex		0.48	4.66	14	59	<0.01
	Toe		4.34	1	72	0.04
	Radius		23.61	1	72	<0.01
	Hand		7.53	1	72	<0.01
	Finger		16.03	1	72	<0.01
Population×sex		0.78	1.19	14	59	0.31

length are significantly longer in males compared with females (Table 1). Limb dimensions were significantly different between populations as well (sites 1 and 2: Wilks' lambda=0.61; $F_{11,72}=4.25$; $P<0.01$; Table 4; sites 3 and 4: Wilks' lambda=0.48; $F_{14,59}=4.62$; $P<0.01$; Table 5). Individuals from site 2 (the range edge) have significantly longer astragali (on average 5% longer), a wider ilium (on average 5% wider) and a higher body mass (on average 18% heavier) than individuals from site 1 (center). Individuals from site 4 (periphery) have significantly longer femurs (on average 10% longer; Tables 1, 5) than individuals from site 3 (center).

Stamina, with body length and temperature as covariates, is significantly different between males and females (Wilks' lambda=0.91; $F_{2,80}=4.11$; $P<0.02$), with males being capable of moving an average of 23% longer for a given body size and temperature (Table 6). Stamina is also significantly different between individuals from the center and the periphery (Wilks' lambda=0.83; $F_{2,80}=8.09$; $P<0.01$), with individuals from the range edge moving 35% longer before exhaustion (Fig. 3, Table 6). Moreover, the distance moved also showed a trend for animals from the periphery to move a greater distance for a given body size compared with animals from the center of the range ($P=0.06$; Table 6).

DISCUSSION

Our results show significant differences in stamina and limb morphology for two sites in the range of *X. laevis* in France, one from the center and one on the edge of the range. Individuals at the range edge showed greater stamina and had longer legs. Our analyses of the limb morphology in a second set of populations also show longer limbs for animals from the range edge, suggesting that this is a more general phenomenon. However, measurements of locomotor performance in frogs from additional sites are needed to better understand whether the longer limbs observed in animals from these additional sites also result in differences in endurance capacity.

Table 6. MANCOVA performed on the performance traits with SVL and temperature as covariates

Effect	Variable	Wilks' lambda	F	d.f.	Error	P-value
Population		0.83	8.09	2	80	<0.01
	Distance		3.74	1	81	0.06
Sex		0.91	15.08	1	81	<0.01
	Time		4.11	2	80	0.02
Population×sex		0.95	0.90	1	81	0.35
	Distance		6.75	1	81	0.01
Population×sex	Time		2.27	2	80	0.11

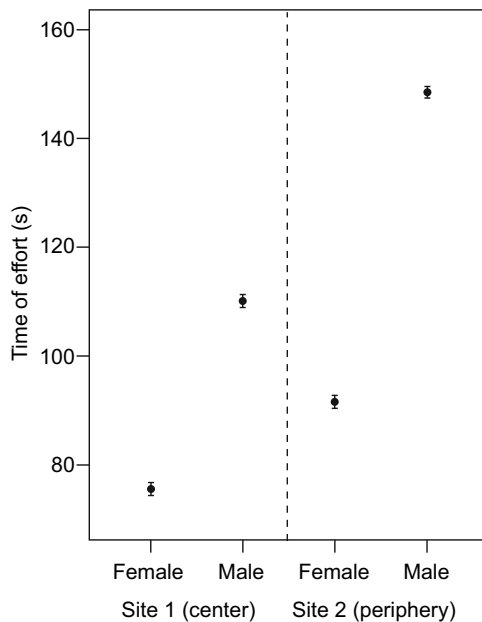


Fig. 3. Mean time until exhaustion for males and females from populations at the center versus the periphery of the range. Values are means \pm s.d. Site 1, $N=14$ males and $N=20$ females; site 2, $N=33$ males and $N=20$ females.

In addition, our results highlight morphological and locomotor differences between males and females in *X. laevis*. Females are significantly larger than males (Fig. 2, Table 2) as is common in frogs and in *Xenopus* species more specifically (Zug, 1978; Measey and Tinsley, 1998; Herrel et al., 2012). Males also possess relatively longer forelimbs and hind limbs than females (Table 2). Furthermore, males show a better endurance capacity (specifically the time until exhaustion) than females (Fig. 3, Table 6) similar to observations for *Xenopus tropicalis* (Herrel et al., 2012). The greater endurance capacity in males relative to females may be explained by their relatively larger limbs and lower body mass allowing them to keep moving longer than females for their body size. This could be beneficial for males during courting and reproduction. The longer forelimbs observed in males may additionally provide males an advantage during mating, allowing them to maintain their grasp on females during amplexus (Measey and Tinsley, 1997).

In addition to the differences between sexes, our data also show significant differences in body size and endurance capacity between the center and the periphery of the range (Fig. 3, Table 6). Individuals from the edge of the expansion range are smaller and have a higher endurance than those from the center of the range. Our results also highlight differences in body dimensions, particularly in limb segments involved in locomotion, such as the astragalus and ilium for individuals from site 2, and the femur for individuals from site 4. The difference in the specific skeleton elements impacted is intriguing and may be due to specific differences between populations. Whereas individuals from site 2 got to this locality by overland migration, animals from site 4 may have been taking advantage of waterways to reach their current site. Although the limb segments involved are different, these results suggest a common response: hind limbs are longer in individuals from the periphery, which is likely to enhance their locomotor capacity. Indeed, previous studies have demonstrated a relationship between limb dimensions and locomotor performance. Higher endurance abilities are attributed to relatively longer hind limbs in *X. tropicalis*

(Herrel et al., 2012) and *R. marina* (Phillips et al., 2006). The length of the foot could also play a key role in aquatic locomotion, because foot size and rotation are crucial for the generation of thrust in aquatic frogs (Richards, 2010). The ilium may also play an important role in aquatic locomotion, as it has been suggested that the sliding of sacral vertebrae along the ilia during swimming improves swimming speed in *Xenopus* frogs (Videler and Jorna, 1985). Therefore, in addition to having a better terrestrial locomotor endurance, frogs from the range edge may also have an improved swimming performance compared with individuals from the center of the range. However, this remains to be tested for individuals from the four sites included in this study.

From the perspective of conservation biology, it is of particular importance to pay attention to the rapid evolution of morphological and physiological traits observed in *X. laevis*. As highlighted in the case of the invasion of *R. marina* in Australia (Brown et al., 2007; Alford et al., 2009; Phillips et al., 2006, 2008), the fast optimization of dispersal abilities can lead to situations that can be unmanageable for conservation biologists. Our study demonstrates an improved terrestrial locomotor performance at the range edge but also suggests better locomotor abilities in an aquatic environment. In order to optimize the conservation efforts and the preservation of autochthonous ecosystems, a better understanding of the physiological, evolutionary and behavioral responses of invasive species that can impact dispersal and colonization is key.

CONCLUSION

This study showed significant differences in performance and morphology in *X. laevis* from sites in the center versus the periphery of the range. Moreover, these differences have evolved since their introduction less than 40 years ago. This suggests that, as in other invasive amphibians, spatial sorting has resulted in the evolution of locomotor capacity, improving the dispersal ability of individuals on the range edge. Although experiments are needed to test the genetic basis of these differences, the fact that there is more than 15 km between the sites from the center to the periphery suggests that gene flow may be limited and thus these subpopulations may have diverged significantly. Finally, our results are consistent with models predicting the allocation of resources to dispersal at the range edge of expanding populations. However, it remains to be tested whether this implies trade-offs with other traits such as reproductive investment, immunity or competitive ability.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

A.H. devised the study; J.C. captured animals in the field; V.L. performed the locomotor trials; V.L. and A.H. analyzed the data; all authors contributed to the writing of the manuscript.

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References

Alford, R. A., Brown, G. P., Schwarzkopf, L., Phillips, B. and Shine, R. (2009). Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildl. Res.* **36**, 23–28.

- Bishop, M. J. and Peterson, C. H.** (2006). When r-selection may not predict introduced-species proliferation: predation of a non-native oyster. *Ecol. Appl.* **16**, 718–730.
- Bonte, D., Dyck, H. V., Bullock, J. M., Coulon, A., Delgado, M., Gribbs, M., Lehouch, V., Matthysen, E., Mustin, K., Saastamoinen, M. et al.** (2012). Costs of dispersal. *Biol. Rev.* **87**, 290–312.
- Brown, G. P., Shilton, C., Phillips, B. L. and Shine, R.** (2007). Invasion, stress, and spinal arthritis in cane toads. *Proc. Natl. Acad. Sci. USA* **104**, 17698–17700.
- Brown, G. P., Kelehear, C. and Shine, R.** (2013). The early toad gets the worm: cane toads at an invasion front benefit from higher prey availability. *J. Anim. Ecol.* **82**, 854–862.
- Burton, O. J., Phillips, B. L. and Travis, J. M. J.** (2010). Trade-offs and the evolution of life-histories during range expansion. *Ecol. Lett.* **13**, 1210–1220.
- Casterlin, M. E. and Reynolds, W. W.** (1980). Diel activity and thermoregulatory behavior of a fully aquatic frog: *Xenopus laevis*. *Hydrobiologia* **75**, 189–191.
- Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. and Massot, M.** (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209.
- De Busschere, C., Courant, J., Herrel, A., Rebelo, R., Rödder, D., Measey, G. J. and Backeljau, T.** (2016). Unequal contribution of native South African phylogeographic lineages to the invasion of the African clawed frog, *Xenopus laevis*, in Europe. *PeerJ* **4**, e1659.
- Eggert, C. and Fouquet, A.** (2006). A preliminary biotelemetric study of a feral invasive *Xenopus laevis* population in France. *Alytes* **23**, 144–149.
- Excoffier, L.** (2009). Patterns of DNA sequence diversity and genetic structure after a range expansion: lessons from the infinite-island model. *Mol. Ecol.* **13**, 853–864.
- Excoffier, L. and Ray, N.** (2008). Surfing during population expansion promotes genetic revolutions and structuration. *Trends Ecol. Evol.* **23**, 347–351.
- Faraone, F. P., Lillo, F., Giaccone, G. and Valvo, M. L.** (2008). The large invasive population of *Xenopus laevis* in Sicily, Italy. *Amphib-Reptilia* **29**, 405–412.
- Fouquet, A. and Measey, G. J.** (2006). Plotting the course of an African clawed frog invasion in Western France. *Anim. Biol.* **56**, 95–102.
- Fronhofer, E. A. and Altermatt, F.** (2015). Eco-evolutionary feedbacks during experimental range expansions. *Nat. Commun.* **6**, 6844.
- Gurdon, J. B. and Hopwood, N.** (2000). The introduction of *Xenopus laevis* into developmental biology: of empire, pregnancy testing and ribosomal genes. *Int. J. Dev. Biol.* **44**, 43–50.
- Hallatschek, O. and Nelson, D. R.** (2007). Gene surfing in expanding populations. *Theor. Pop. Biol.* **73**, 158–170.
- Herrel, A., Gonwouo, L. N., Fokam, E. B., Ngundu, W. I. and Bonneaud, C.** (2012). Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *J. Zool.* **287**, 311–316.
- Hudson, C. M., Phillips, B. L., Brown, G. P. and Shine, R.** (2015). Virgins in the vanguard: low reproductive frequency in invasion-front cane toads. *Biol. J. Linn. Soc.* **116**, 743–747.
- Hughes, C. L., Hill, J. K. and Dytham, C.** (2003). Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proc. R. Soc. B* **270**, S147–S150.
- Karlsson, B. and Johansson, A.** (2008). Seasonal polyphenism and developmental trade-offs between flight ability and egg laying in a pierid butterfly. *Proc. R. Soc. B* **275**, 2131–2136.
- Kubisch, A., Fronhofer, E. A., Poethke, H. J. and Hovestadt, T.** (2013). Kin competition as a major driving force for invasions. *Am. Nat.* **181**, 700–706.
- Lafferty, K. D. and Page, C. J.** (1997). Predation on the endangered tidewater goby, *Eucyclogobius newberryi*, by the introduced African clawed frog, *Xenopus laevis*, with notes on the frog's parasites. *Copeia* **1997**, 589–592.
- Lillo, F., Marrone, F., Sicilia, A., Castelli, G. and Zava, B.** (2005). An invasive population of *Xenopus laevis* (Daudin, 1802) in Italy. *Herpetozoa* **18**, 63–64.
- Lillo, F., Faraone, F. P. and Valvo, M. L.** (2011). Can the introduction of *Xenopus laevis* affect native amphibian populations? Reduction of reproductive occurrence in presence of the invasive species. *Biol. Inv.* **13**, 1533–1541.
- Lobos, G. and Jaksic, F. M.** (2005). The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile: causes of concern. *Biodivers. Conserv.* **14**, 429–439.
- Measey, G. J. and Tinsley, R. C.** (1997). Mating behavior of *Xenopus wittei* (Anura: Pipidae). *Copeia* **1997**, 601–609.
- Measey, G. J. and Tinsley, R. C.** (1998). Feral *Xenopus laevis* in South Wales. *Herpetol. J.* **8**, 23–27.
- Measey, G. J., Rödder, D., Green, S. L., Kobayashi, R., Lillo, F., Lobos, G., Rebelo, R. and Thirion, J.-M.** (2012). Ongoing invasions of the African clawed frog, *Xenopus laevis*: a global review. *Biol. Inv.* **14**, 2255–2270.
- Miller, K.** (1982). Effect of temperature on sprint performance in the frog *Xenopus laevis* and the salamander *Necturus maculosus*. *Copeia* **1982**, 695–698.
- Phillips, B. L., Brown, G. P., Webb, J. K. and Shine, R.** (2006). Invasion and the evolution of speed in toads. *Nature* **439**, 803–803.
- Phillips, B. L., Brown, G. P., Travis, J. M. J. and Shine, R.** (2008). Reid's paradox revisited: the evolution of dispersal kernels during range expansion. *Am. Nat.* **172**, S34–S48.
- Phillips, B. L., Brown, G. P. and Shine, R.** (2010). Life-history evolution in range-shifting populations. *Ecology* **91**, 1617–1627.
- Rebelo, R., Amaral, P., Bernardes, M., Oliveira, J., Pinheiro, P. and Leitão, D.** (2010). *Xenopus laevis* (Daudin, 1802), a new exotic amphibian in Portugal. *Biol. Inv.* **12**, 3383–3387.
- Richards, C. T.** (2010). Kinematics and hydrodynamics analysis of swimming anurans reveals striking inter-specific differences in the mechanism for producing thrust. *J. Exp. Biol.* **213**, 621–634.
- Robert, J., Abramowitz, L., Gantries, J. and Morales, H. D.** (2007). *Xenopus laevis*: a possible vector of *Ranavirus* infection? *J. Wildl. Dis.* **43**, 654–652.
- Shine, R., Brown, G. P. and Phillips, B. L.** (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proc. Natl. Acad. Sci. USA* **108**, 5708–5711.
- Stevens, V. M., Pavione, S. and Baguette, M.** (2010). Variation within and between closely related species uncovers high intra-specific variability in dispersal. *PLoS ONE* **5**, e11123.
- Travis, J. M. J. and Dytham, C.** (2002). Dispersal evolution during invasions. *Evol. Ecol. Res.* **4**, 1119–1129.
- Travis, J. M. J., Münkemüller, T. and Burton, O. J.** (2010). Mutation and the evolution of dispersal during range expansions. *J. Evol. Biol.* **23**, 2656–2667.
- Videler, J. J. and Jorna, J. T.** (1985). Functions of the sliding pelvis in *Xenopus laevis*. *Copeia* **1985**, 251–254.
- Wilson, J. R. U., Dormont, E. E., Prenais, J. P., Lowe, J. A. and Richardson, M. D.** (2009). Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.* **24**, 136–144.
- Zug, G. R.** (1978). Anuran locomotion—structure and function, 2: jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smithson. Contrib. Zool.* **276**, 1–31.