

Differences in standard metabolic rate at the range edge versus the center of an expanding invasive population of *Xenopus laevis* in the West of France

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Abstract

Empirical and theoretical studies have investigated the trade-offs between reproduction, dispersal and/or survival that may arise between individuals at the range edge of an expanding population. The differential allocation of resources to these life-history traits may then be constrained by the metabolism of an individual. Previous studies of an invasive expanding population of the frog *Xenopus laevis* in the West of France showed an increase in allocation of resources to dispersal and a decrease in allocation to reproduction in individuals from the range front. The present study focuses on physiological variation through an analysis of the standard metabolic rate (SMR). SMR was analyzed through measurements of oxygen consumption and carbon dioxide production under resting conditions. Our results show a positive correlation between SMR and individual size and weight, but no difference in body condition is observed between individuals from the center and those from the periphery of the range. Moreover, a decrease in SMR at the periphery was observed in both sexes. Yet, a significant interaction effect between sex and site was observed. Males had a higher SMR than females at the center while females from the periphery showed a higher SMR than males. A lower SMR may allow animals from the periphery to allocate more resources to other functions, such as locomotion, and therefore dispersal. In contrast, the relatively higher SMR in females from the periphery (compared to males) is likely to be driven by the important energetic cost of reproduction in addition to the environmental and demographic constraints at the edge of an expanding population. From the perspective of conservation biology, these results attest to the importance of understanding the biological and evolutionary mechanisms underpinning the selection of traits to estimate the invasive potential of exotic species.

Introduction

Biological invasions are considered as an important threat to aquatic and terrestrial biodiversity on a global scale together with habitat destruction, pollution, and climate change (i.e. Alford & Richards, 1999; Collins & Storfer, 2003; Banci *et al.*, 2013). A growing body of studies has demonstrated the role of the introduction and spread of invasive exotic organisms in the disappearance, if not the extinction, of many species worldwide (e.g. Fritts & Rodda, 1998; McNeely, 2001; Clavero & Garcia-Berthou, 2005; Barun, Simberloff & Budinski, 2010; Ellis *et al.*, 2016). One of the main challenges in the conservation of native ecosystems is the understanding of the mechanisms underlying the expansion of an organism beyond its original range. Range expansions and range shifts are closely related to the capacity of an organism to reproduce,

disperse, and survive (Burton, Phillips & Travis, 2010). Theoretical and empirical studies have highlighted the differential allocation of resources to these life-history traits between individuals living at the edge, and those living at the core of the range of expanding populations (Burton *et al.*, 2010; Hughes, Hill & Dytham, 2003; Karlsson & Johansson, 2008; Llewelyn *et al.*, 2011; Bonte *et al.*, 2012; Brown *et al.*, 2015; Hudson *et al.*, 2015; Chuang & Peterson, 2016). For example, a preferential allocation of resources toward dispersal and associated phenotypic traits (e.g. limb dimensions) in vanguard populations of the invasive cane toad *Rhinella marina* in Australia has been documented (Brown *et al.*, 2007; Alford *et al.*, 2009; Phillips *et al.*, 2008). However, these trade-offs may be influenced and constrained by the metabolism of individuals.

An important marker of an organism's metabolic performance is the basal metabolic rate, or standard metabolic rate

(SMR) in ectotherms. These minimal metabolic rates represent a fixed cost that every organism faces. This corresponds to the energetic cost of organismal maintenance, including maintenance of the mitochondrial H^+ gradient, protein turnover, ion transport, hormone production, blood circulation, and ventilation (Bennett, 1988; Hulbert, 2000; Hulbert & Else, 1981; Rolfe & Brown, 1997). Nevertheless, SMRs appears highly variable in vertebrates, not only between populations (Wikelski *et al.*, 2003), but also among individuals within a population (O'Steen & Janzen, 1999; Steyermark & Spotila, 2000; Burton, Killen & Metcalfe, 2011). Variation in SMR may have consequences for the fitness of individuals (Boratyński *et al.*, 2013), thus raising questions about the mechanisms involved in the selection and maintenance of such variation. Two contrasting hypotheses have been proposed in the literature: the 'compensation hypothesis' and the 'increased intake hypothesis' (Nilsson, 2002).

The 'compensation hypothesis' suggests that selection may favor the maintenance of a low SMR, because this may provide a benefit in terms of energy allocation and risk moderation. Having a low SMR may allow an individual to dedicate more energy to other processes, such as growth (Blackmer *et al.*, 2005), or reproduction (Jackson, Trayhurnt & Speakman, 2001; Ketola & Kotiaho, 2009). Likewise, should the energetic intake change, a low SMR would imply a lower daily energetic expenditure, resulting in less foraging time and thus less risk of predation (Steyermark *et al.*, 2005). On the other hand, the 'increased intake hypothesis' proposes that SMR reveals the general efficiency of energy acquisition (Blackmer *et al.*, 2005; Boratyński & Koteja, 2010). Selection may then favor high SMR because this may be functionally linked to an increased daily energetic expenditure capacity (Hammond & Diamond, 1997; Meerlo *et al.*, 1997; Speakman *et al.*, 2003; Tinbergen & Verhulst, 2000) which may be related to an increased lactation, thermoregulation capacity, or aerobic scope, for example. A high SMR is typically associated with proportionally bigger organs, such as intestines, liver, kidneys, and heart (Garland, 1984; Garland & Else, 1987; Daan, Masman & Groenewold, 1990; Konarzewski & Diamond, 1995; Speakman & McQueenie, 1996; Chappell, Bech & Buttemer, 1999; Hammond *et al.*, 2000). Thus, an individual with a higher SMR may be able to allocate more energy to different processes than an individual with a lower SMR. This hypothesis is supported by various studies reporting positive correlation between SMR and body mass (anurans: Steyermark *et al.*, 2005; birds: Piersma, Cadée & Daan, 1995), body-mass adjusted organ size (anurans: Steyermark *et al.*, 2005; birds: Daan *et al.*, 1989, 1990; Chappell *et al.*, 1999), and cell size (anurans: Hermaniuk, Rybacki & Taylor, 2016). Although a significant number of studies have explored the correlations between SMR and anatomical characteristics, few studies investigated the variations of SMR among individuals in expanding populations (Seebacher & Franklin, 2011).

This work focuses on an invasive population of *X. laevis*, a large aquatic frog introduced in several localities on 4 continents (Measey *et al.*, 2012). Since its introduction in the West of France in the early 1980s (Fouquet & Measey, 2006) this population has expanded and now covers an area of up to

2000 km². Previous studies have highlighted the preferential allocation of resources to dispersal (Louppe, Courant & Herrel, 2017), and a lower allocation to reproduction (Courant *et al.*, 2017) in individuals from the periphery of the range of this population. The aim of the present study was to test whether *X. laevis* at the range edge show evidence of physiological differences. To do so, we investigated the SMR of individuals from the center and the periphery of the range. SMR was analyzed through measurements of oxygen consumption and carbon dioxide production under resting conditions. Data obtained in a previous study on the mobility of the same individuals (Louppe *et al.*, 2017) allowed for the analysis of correlations between locomotor capacity and SMR.

Materials and methods

All individuals ($N = 53$; 26 from the center and 27 from the periphery of the range) were caught in ponds 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 3 departments (Vienne, Deux-Sèvres, and Maine-et-Loire) and an area of approximately 2000 km² (Fig. 1). Two sites are used in this study: 1 site from the center of the range, near the introduction point, and 1 site at the periphery, both sites being about 20 km apart (Fig. 1). For each site, all individuals were caught in a single pond. Individuals 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 L 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. All experiments were performed in accordance to the institutional animal use and care regulations.

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 dimension were measured following Herrel *et al.*, (2012). A summary of the morphometric data is provided in Fig. 2.

Metabolism

Standard metabolic rate was measured at 22°C which is considered the optimal temperature for the species (Casterlin & Reynolds, 1980; Miller, 1982). After trials, animals were returned to their aquaria, fed, and allowed to rest. SMR is here quantified by measuring carbon dioxide production and oxygen consumption under constant low light conditions, using an open-flow, push-through respirometry system (Sable Systems, Las Vegas, NV, USA). Prior to each test, carbon dioxide and oxygen within the air flow were calibrated with a Flow Measurement System (FB8; Sable Systems). During tests, individuals were placed in 1192 mL cylindrical

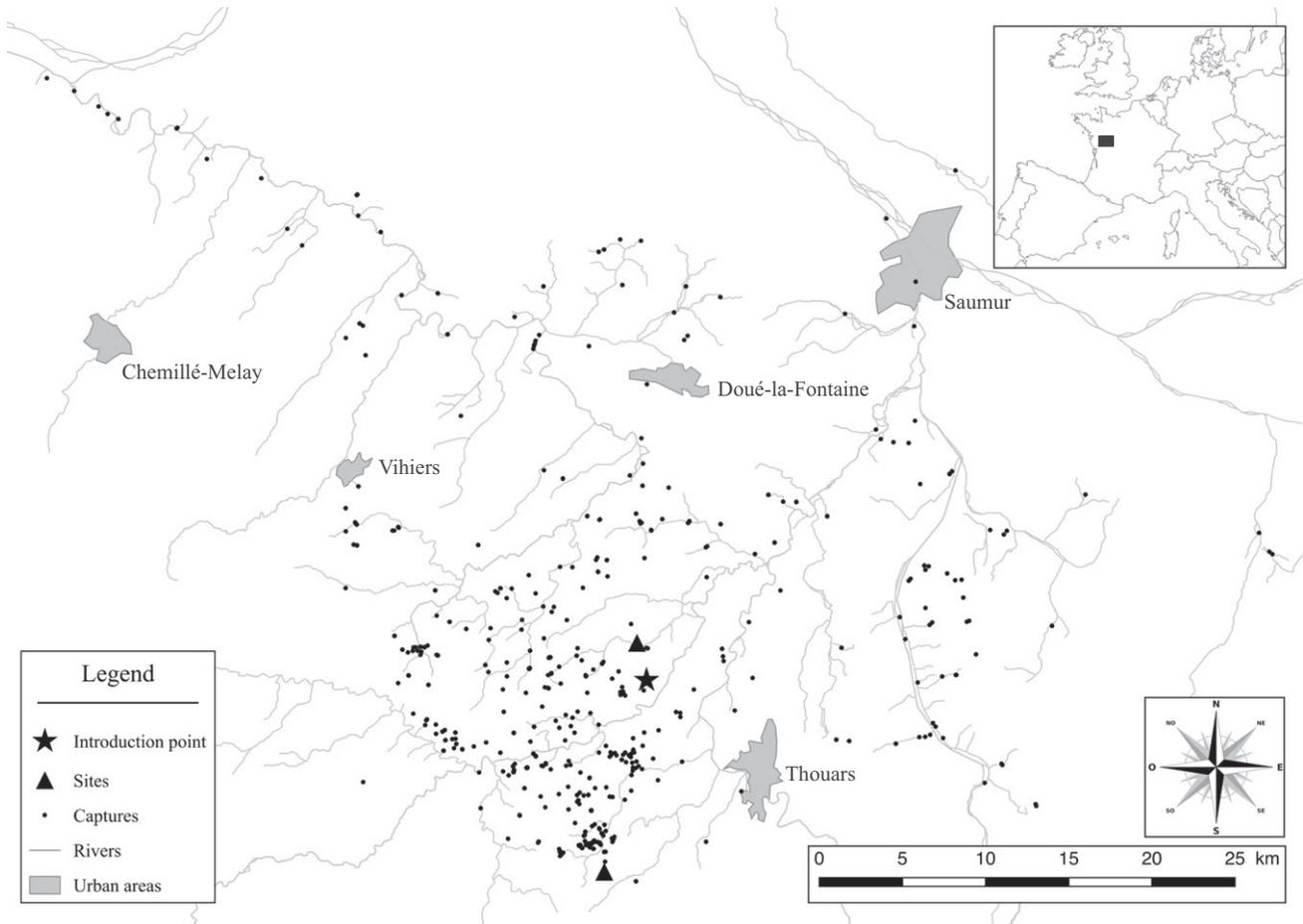


Figure 1 Current distribution of the invasive population of *Xenopus laevis* in the West of France. Indicated are the point of introduction and the 2 sites used in this study. Small dots indicate ponds where *X. laevis* is present.

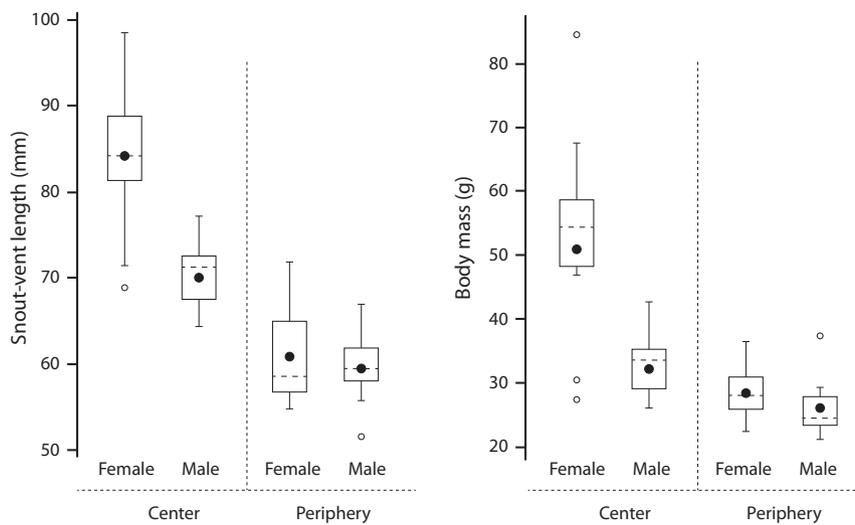


Figure 2 Snout-vent length and body mass of *Xenopus laevis* measured for each site and sex (center, $N = 14$ females and $N = 13$ males; periphery, $N = 13$ females and $N = 13$ males). Black dots indicate mean values.

containers, and the temperature of the air inside these containers was recorded by the respirometry system. Air was pumped with a Dual Pumped System (PP2; Sable Systems) from a Dewpoint Generator (DG-4; Sable System) allowing to humidify air before entering the animal chambers to prevent desiccation. The air flow passed through the Flow Measurement System (FB8; Sable Systems) at a rate of 200 mL min^{-1} and was split into 7 paths, 6 of which were directed into animal chambers, and 1 was used for baseline measurements. Then, the air entered a Flow Multiplexer (MUX; Sable Systems) allowing to sample one chamber air stream independently from the others. Water vapor and barometric pressure, flow rate, temperature, oxygen and carbon dioxide volumes were recorded with a Field Metabolic System (FMS; Sable Systems) at 1 sample per second for 300 s successively for the 7 chambers. This sampling was repeated 5 times, giving 6 series of 300 s samples for each chamber. The first 2 series of samples were not used in the following analyses to avoid biases relative to the animals stress and activity after being put in the chamber.

Mean values of temperature, oxygen volume consumed (VO_2), and carbon dioxide volume produced (VCO_2) were calculated for each series. Mean VCO_2 and VO_2 were repeatable across all series (Pearson correlation; all $P < 0.01$) except between series 4 and 6 for the VO_2 ($P = 0.15$). The minimal mean carbon dioxide and oxygen volume ($\text{VO}_2 \text{ min}$ and $\text{VCO}_2 \text{ min}$ in Fig. 3), as well as the average of all series means (VO_2 and VCO_2 in Fig. 3) were used in further statistical analyses. Temperature varied slightly along series, by a rate of change in 0.5°C on average.

Statistical analyses

All data were Log_{10} -transformed to meet assumptions of normality and homoscedasticity. A correlation test was performed to test whether stamina, identified as the maximum time and distance moved until exhaustion (Louppe *et al.*, 2017), weight, snout-vent length, carbon dioxide production and oxygen consumption were correlated. Next, to test for differences in SMR between sexes and between sites (center

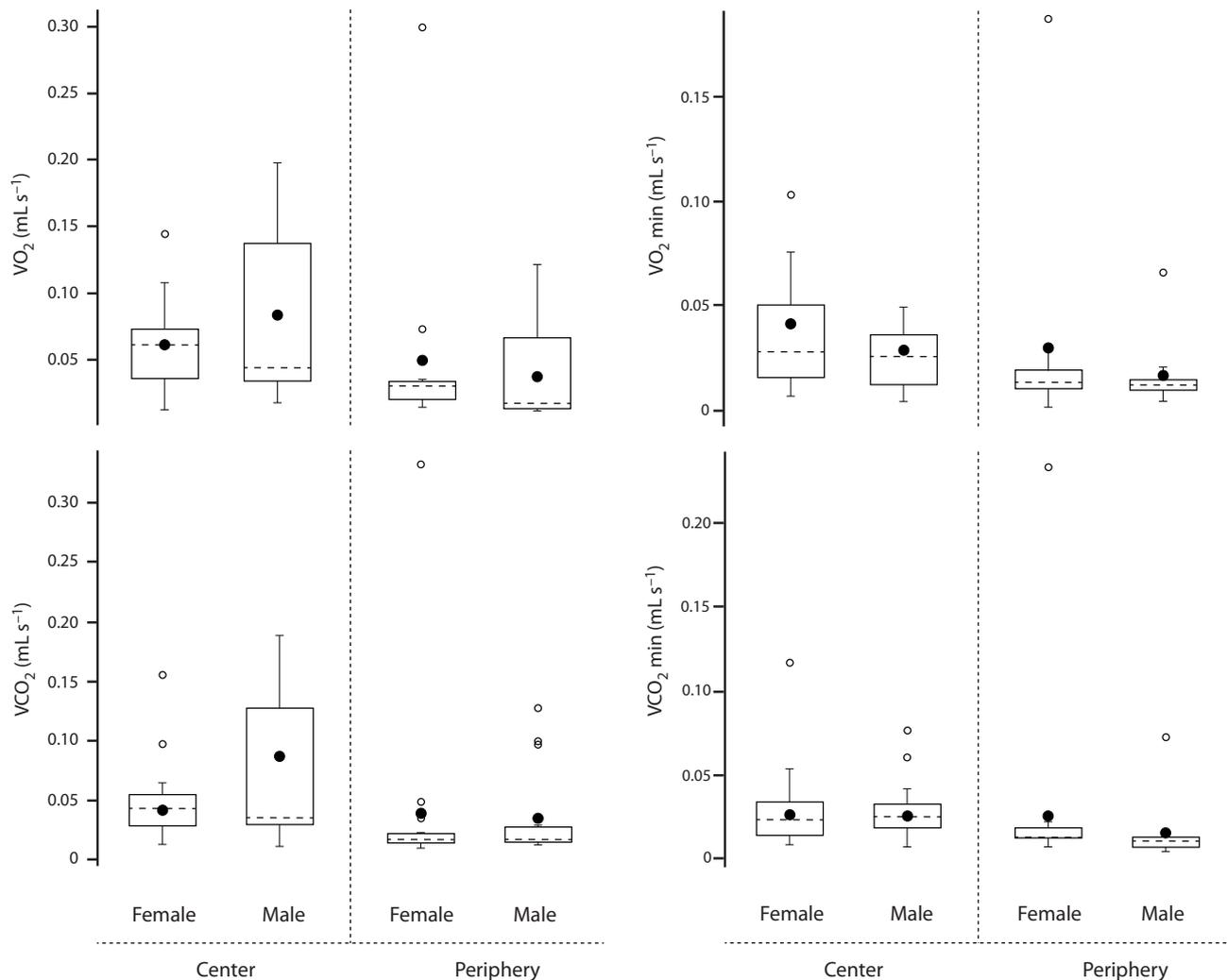


Figure 3 Mean oxygen volume consumed and carbon dioxide volume produced for individuals of *Xenopus laevis* from each site and sex.

and periphery), multivariate analyses of co-variance (MANCOVA) were performed with snout-vent length and temperature as covariates. Next, both effects were analyzed independently through analyses of co-variance (ANCOVA). Snout-vent length was incorporated as a covariate in the model testing the effect of site for males, yet its effect was not significant (Wilk's Lambda = 0.63; $F_{6,17} = 1.7$; $P = 0.18$), so only the temperature was maintained as a covariate in analysis for males (Wilk's Lambda = 0.31; $F_{6,18} = 6.68$; $P < 0.01$). All analyses were performed using SPSS V.22 (IBMSPSS Inc., Chicago, IL, USA).

Results

Correlations and multiple regressions between locomotor performances, morphology and metabolism

Correlation tests showed significant negative correlations between snout-vent length and time moved until exhaustion (Pearson Correlation = -0.33 ; $P < 0.02$) and distance covered (Pearson Correlation = -0.27 ; $P < 0.05$) for the animals included in our analysis. Furthermore, snout-vent length was positively correlated with all metabolic variables (VO_2 : Pearson Correlation = 0.29 ; $P < 0.04$; VO_2 min: Pearson Correlation = 0.42 ; $P < 0.01$; VCO_2 : Pearson Correlation = 0.34 ; $P < 0.02$; VCO_2 min: Pearson Correlation = 0.43 ; $P < 0.01$) and to weight (Pearson Correlation = 0.95 ; $P < 0.01$). Weight was also positively correlated with minimal metabolic variables (VO_2 min: Pearson Correlation = 0.41 ; $P < 0.01$; VCO_2 min: Pearson Correlation = 0.38 ; $P < 0.01$) and VCO_2 (Pearson Correlation = 0.28 ; $P < 0.05$) (Table 1). However, the time moved until exhaustion (hereafter endurance) was not significantly correlated with metabolic variables (VO_2 : Pearson Correlation = -0.13 ; $P = 0.36$; VO_2 min: Pearson Correlation = -0.06 ; $P = 0.55$; VCO_2 : Pearson Correlation = -0.14 ; $P = 0.33$; VCO_2 min: Pearson

Table 1 Significant Pearson correlations between morphometric, metabolic and performance data of *Xenopus laevis*

Variables	Pearson correlation	<i>P</i>
Endurance		
Distance	0.73	<0.01
Snout-vent length	-0.33	<0.02
Snout-vent length		
Distance	-0.27	<0.05
Mass	0.95	<0.01
VO_2	0.29	<0.04
VO_2 min	0.42	<0.01
VCO_2	0.34	<0.02
VCO_2 min	0.43	<0.01
Body mass		
VO_2 min	0.41	<0.01
VCO_2	0.28	<0.05
VCO_2 min	0.38	<0.01

Correlation = -0.1 ; $P = 0.49$), and multiple regression showed no significant effect of metabolic variables on endurance (VO_2 : $F_{1,51} = 0.87$; $P = 0.36$; VO_2 min: $F_{1,51} = 0.21$; $P = 0.65$; VCO_2 : $F_{1,51} = 0.97$; $P = 0.33$; VCO_2 min: $F_{1,51} = 0.48$; $P = 0.49$).

Differences in SMR between sexes and between sites

MANCOVAs performed showed significant interaction effects of sex and sites on SMR (Wilk's Lambda = 0.72; $F_{7,43} = 2.37$; $P < 0.04$; Fig. 4). Consequently, both effects were analyzed independently.

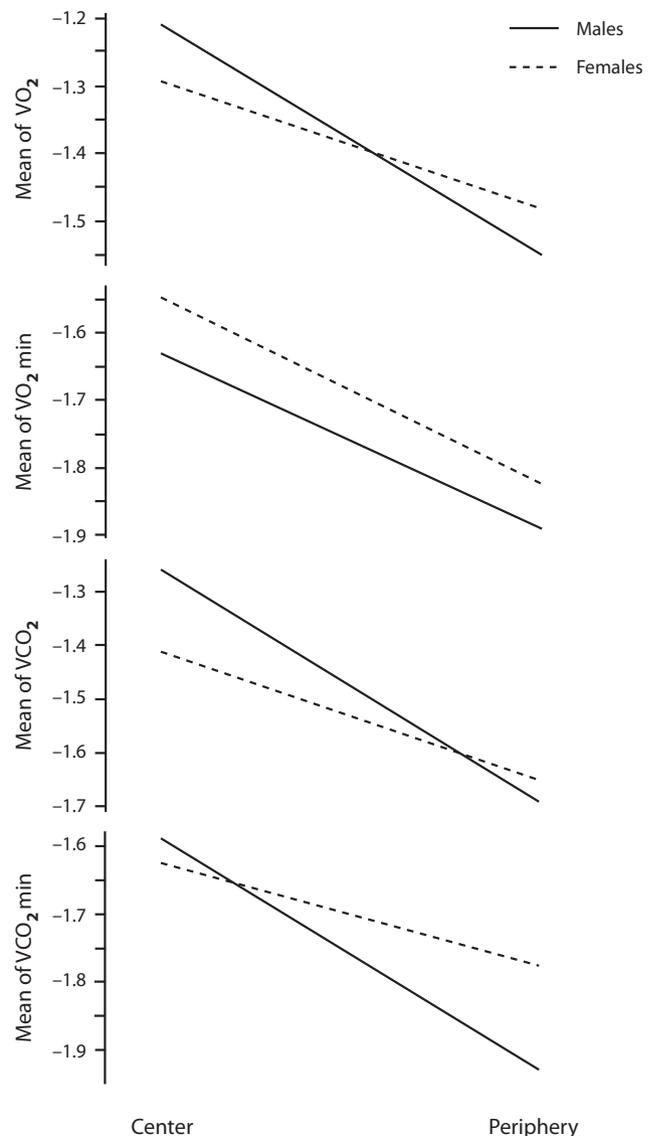


Figure 4 Graphic representation of the interaction between sex and site on metabolic variables (after \log_{10} transformation; in $mL s^{-1}$) of *Xenopus laevis*.

Table 2 MANCOVAs and ANCOVAs performed on metabolic data (females: snout-vent length and temperature as covariates; males: temperature as covariate) of *Xenopus laevis*

Data	Effect	Variable	Wilk's Lambda	F	d.f.	Error	P
Females	Site		0.47	3.45	6	18	0.02
		VO ₂		0.35	1	23	0.56
		VO ₂ min		4.97	1	23	0.04
		VCO ₂		0.88	1	23	0.36
		VCO ₂ min		4.88	1	23	0.04
Males	Site		0.49	3.14	6	18	0.03
		VO ₂		5.97	1	23	0.02
		VO ₂ min		5.48	1	23	0.03
		VCO ₂		7.28	1	23	0.01
		VCO ₂ min		11.81	1	23	<0.01
Center	Sex		0.63	1.86	6	19	0.14
Periphery	Sex		0.59	2.20	6	19	0.09

Bold values indicate significant differences.

Differences between sexes

The analysis of the differences in metabolic variables values between sexes of individuals from the center, with temperature as covariate, showed no significant differences (Wilk's Lambda = 0.63; $F_{6,19} = 1.86$; $P = 0.14$). Also, metabolic variables in individuals from the periphery, were not significantly different between sexes (Wilk's Lambda = 0.59; $F_{6,19} = 2.2$; $P = 0.0$) (Table 2). Body condition (differences in body mass, with snout-vent length as covariate), was not different between males and females and this irrespective of site ($F_{1,48} = 2.84$; $P = 0.1$).

Differences between sites

Body condition was not different between sites irrespective of sex ($F_{1,48} = 1.8$; $P = 0.20$). However, metabolic variables were significantly different between females from the center and the periphery of the range when taking into account variation in snout-vent length and temperature (Wilk's Lambda = 0.47; $F_{6,18} = 3.45$; $P < 0.02$). VO₂ min and VCO₂ min are respectively 32% ($F_{1,23} = 4.97$; $P < 0.04$) and 29% ($F_{1,23} = 4.87$; $P < 0.04$) lower in females from the periphery (Table 2). Metabolic variables were also significantly different between males from the center and the periphery when taking into account variation in snout-vent length and temperature (Wilk's Lambda = 0.49; $F_{6,18} = 3.14$; $P < 0.03$). All metabolic variables were significantly higher for males from the center. VO₂ and VO₂ min were respectively 24% ($F_{1,23} = 5.97$; $P < 0.02$) and 14% ($F_{1,23} = 5.48$; $P < 0.03$) higher for males from the center. VCO₂ and VCO₂ min were respectively 28% ($F_{1,23} = 7.28$; $P < 0.01$) and 19% ($F_{1,23} = 11.81$; $P < 0.01$) higher for males from the center (Table 2).

Discussion

Our results showed a positive correlation between weight and size in all individuals, as well as a positive correlation between these traits and SMR. These results are consistent with other

studies reporting similar correlations in several vertebrate species, as well as positive correlations between SMR and body mass (anurans: Steyermark *et al.*, 2005; birds: Piersma *et al.*, 1995), body-mass adjusted organ size (anurans: Steyermark *et al.*, 2005; birds: Daan *et al.*, 1989, 1990; Chappell *et al.*, 1999), and cell size (anuran: Hermaniuk *et al.*, 2016). Furthermore, a negative correlation between size and endurance (referred to here as the time moved until exhaustion) was observed (Louppe *et al.*, 2017). Thus, smaller and lighter animals are characterized by a lower SMR, and a higher endurance. These results are in line with the 'compensation hypothesis' (Nilsson, 2002), where it is considered that individuals with low SMR may have more energy to allocate to other functions and processes, such as growth (Blackmer *et al.*, 2005), reproduction (Jackson *et al.*, 2001; Ketola & Kotiaho, 2009), or, as suggested by our results, locomotion and dispersal.

However, our data do not show significant differences in terms of body condition (estimated as size-adjusted weight) neither between males and females nor between sites. Nevertheless, SMR is significantly different between individuals living at the center and those living at the periphery of the range with animals at the periphery showing a lower SMR when correcting for differences in body size between sites (Fig. 4). Although body-mass adjusted organ size remains to be measured, anatomical characteristics do not seem to be the main factors leading to differences in SMR between populations. SMR is higher in females from the center in comparison to females from the periphery, yet SMR is relatively higher in males compared to females in the center, but relatively lower than that of females at periphery of the range. According to the 'compensation hypothesis', the lower SMR observed in males compared to females at the periphery may allow them to allocate more resources to other functions such as locomotion or dispersal. Our results do not show direct effects nor correlations between metabolic variables and endurance. Nevertheless, previous studies of these populations highlighted a better endurance (Louppe *et al.*, 2017), a lower investment in reproduction (Courant *et al.*, 2017), and an increased dispersal

(Courant pers. obs.) in individuals from the periphery. Therefore, our results suggest the males from the periphery can invest more of their energy towards locomotor performance not only by having a low SMR, but also investing less in reproduction (Courant *et al.*, 2017). This trade-off is then favorable to dispersal at the invasion front, but may also be an asset in mate searching, particularly in low population density conditions as is often the case at the margins of an expanding population (Burton *et al.*, 2010; Phillips, Brown & Shine, 2010; Brown, Kelehear & Shine, 2013; Kubisch *et al.*, 2013).

Comparable results would be expected for females. Yet, females at the periphery showed a relatively higher SMR compared to males despite an absolutely lower SMR compared to animals from the center. These counter-intuitive results may, however, be explained by the differences in the energetic costs of reproduction between sexes. All animals must bear the cost of reproduction if they want to breed. This cost appears through various traits and processes, such as thermoregulation constraints, increased risk of predation, decreased prey consumption and mobility, and notably an increased energetic expenditure (Shine, 1980, 2003; Seigel *et al.*, 1987; Stearns, 1989; Gregory, Crampton & Skebo, 1999; Angilletta & Sears, 2000; Bonnet *et al.*, 2002; O'Donnell & Arnold, 2005; Harshman & Zera, 2007). In males of many species, this energetic expenditure meet the needs of spermatogenesis, but also mate searching, territorial defense, courtship, calling, and intra-sexual combat (Marler, Walsberg & Moore, 1995; Michener, 1998; Kunz & Orrell, 2004; Ophir, Schrader & Gillooly, 2010). In females, energy is allocated to oogenesis, and to the development and maintenance of the embryos during all or part of their development (Guillette, 1982; Beuchat & Vleck, 1990). In oviparous species, the production of eggs and their lipid rich content requires an important quantity of energy (Kunz & Orrell, 2004). Hence, in lizards, the amount of energy allocated to egg production represent 13 to 48% of the energy expended during the mating season; and 7 to 13% of the annual energy expenditure (Orrell & Carpenter, 2004; Kunz & Orrell, 2004). In the turtle *Chrysemys picta*, it represents 14% of the annual energy expenditure (Kunz & Orrell, 2004). Moreover, in the lizard *Zootoca vivipara*, oxygen consumption in females increases during pregnancy up to 46% in oviparous and up to 82% in viviparous populations (Foucart *et al.*, 2014). Thus, although the energetic cost of reproduction in males and females of *X. laevis* remains to be tested, our results suggest that the relatively higher SMR in females from the periphery (compared to males) may correspond to the cost of reproduction in addition to any investment into locomotion. At the center of the range, a lower investment in dispersal (and so in locomotion), may favor the maintenance of a relatively lower SMR in females compared to males, allowing more energy to be allocated to reproduction.

Optimization of dispersal capacity at the invasion front of an expanding exotic species is influenced by the allocation of energy to a wide range of life-history traits. Our results highlight this by showing differences in the metabolic characteristics of animals facing different environmental constraints and requirements at the center and the periphery of the range of an expanding population of a largely aquatic anuran,

X. laevis. As these constraints are different for each sex, metabolic characteristics may be different in males and females as well. Understanding the biological and evolutionary mechanisms underpinning this selection and optimization appears determinant in estimating the invasive potential of an exotic species.

Conclusion

This study shows a correlation between SMR and individual size and weight in an invasive population of *X. laevis*: bigger and heavier individuals present a higher SMR. Nevertheless, no difference in body condition is observed between individuals from the center and those from the periphery of the range. SMR is, however, different between sites. Males and females have lower SMR at the periphery. Moreover, males from the periphery show a relatively lower SMR than females, the inverse of what is observed at the center of the range. In concert with a lower investment in reproduction, this allows allocation of more energy to locomotion, and therefore dispersal. On the other hand, females from the periphery show a relatively higher SMR compared to males. The important energetic cost of reproduction for females, in addition to specific environmental and demographic constraints at the edge of an expanding population may explain the high SMR of females living at the periphery. Although more work appears necessary, including additional samples, the examination of maximum metabolic capacity, aerobic scope, and metabolic cost of reproduction, this study attests to the rapidity with which significant physiological differences may appear in expanding invasive populations. From the perspective of conservation biology, understanding of the mechanisms involved in selection of physiological traits underpinning dispersal in invasive species thus appears crucial.

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