Do muscle contractile properties drive differences in locomotor performance in invasive populations of Xenopus laevis *in France?*

Pablo Padilla, Jason Tallis, Josh Hurst, Julien Courant, Rob S. James & Anthony Herrel

Journal of Comparative Physiology B
Biochemical, Systems, and
Environmental Physiology

ISSN 0174-1578

J Comp Physiol B
DOI 10.1007/s00360-020-01310-4

Springer

Journal of Comparative Physiology B
https://doi.org/10.1007/s00360-020-01310-4

ORIGINAL PAPER

Do muscle contractile properties drive differences in locomotor performance in invasive populations of *Xenopus laevis* in France?

Pablo Padilla[1,2] · Jason Tallis[3] · Josh Hurst[3] · Julien Courant[1] · Rob S. James[3] · Anthony Herrel[1,4]

Received: 28 June 2020 / Revised: 31 August 2020 / Accepted: 9 September 2020

Abstract

Jumping and swimming are key locomotor traits in frogs intimately linked to survival and dispersal. French populations of the frog *Xenopus laevis* from the invasion front are known to possess greater terrestrial locomotor endurance. Here, we tested whether individuals from the invasion front show differences in their muscle physiology that may underlie the observed whole-organism performance differences. We measured muscle contractile properties of the isolated gastrocnemius muscle in vitro, including isometric stress, activation and relaxation time, and work loop power output, both before and during a period of fatiguing contractions. We found that frogs from the centre of the range can produce tetanus force in their gastrocnemius muscle faster than animals from the periphery of the range, which could contribute to higher performance in one-off jumps. Yet, populations did not differ in muscle endurance. These results, coupled with previous work on this invasive population of *Xenopus laevis*, suggest that the greater stamina observed in individuals from the periphery may be more due to anatomical differences such as longer hind limbs and larger hearts along with potentially other as of yet untested physiological differences rather than differences in the mechanical properties of skeletal muscle.

Keywords *Xenopus laevis* · Muscle · Frog · Adaptation · Locomotion · Performance

Introduction

Whole-organism performance traits are commonly measured as they are fitness-relevant (Arnold 1983; Garland and Losos 1994; Irschick and Garland 2001; Le Galliard et al. 2004; Miles 2004). Among these, locomotor performance has been extensively studied due to its direct implications in predator escape (Husak 2006), territory defence (Husak et al. 2006), prey capture (Irschick and Losos 1998) and dispersal (Courant et al. 2019a). Muscle architecture (Inbar et al. 1981; Vanhooydonck et al. 2006; Lowie et al. 2019), limb dimensions (Losos 1990; Herrel et al. 2008), metabolism (Garland and Else 1987; Coyle 1999; Seebacher and Walter 2012), and muscle contractile properties (James et al. 2007; Vanhooydonck et al. 2014) are all likely drivers of variation in locomotor performance. Studying these properties and their interactions is crucial if one is to understand the evolution of locomotion. Moreover, an understanding of the underlying drivers of whole-organism performance is important in pinpointing how selection drives variation in performance.

The study of locomotor performance is particularly relevant in the case of invasive species as locomotion is linked to dispersal capacity which is a driver of range expansion (Phillips et al. 2006; Stevens et al. 2010; Louppe et al. 2017; Courant et al. 2019a). As intraspecific variation in dispersal capacity is often great (Stevens et al. 2010), this may lead to spatial segregation of individuals, with individuals showing high levels of locomotor performance typically being present at the range edge (Shine et al. 2011; Louppe et al. 2017). It has been demonstrated previously that this spatial sorting results in differences in limb length, endurance capacity, and

---

Communicated by G. Heldmaier.

✉ Pablo Padilla
pablo.padilla@doct.uliege.be

[1] Département Adaptations du Vivant, UMR 7179 C.N.R.S/M.N.H.N., 55 rue Buffon, 75005 Paris, France

[2] Laboratory of Ecology and Conservation of Amphibians (LECA), Behavioural Biology Group, U. R. Freshwater and OCeanic Science Unit of reSearch (FOCUS), University of Liège, 22 Quai van Beneden, 4020 Liège, Belgique

[3] Centre for Sport, Exercise and Life Sciences, Coventry University, Coventry CV1 5FB, UK

[4] Evolutionary Morphology of Vertebrates, Ghent University, 9000 Ghent, Belgium

muscle architecture between individuals at the centre and the periphery of the invasive range (Phillips et al. 2006; Louppe et al. 2017; Padilla et al. 2019). However, whether spatial sorting also impacts other traits such as muscle physiology has not been investigated. In vitro measures of muscle contractile properties are of particular interest as they allow to investigate whether differences in whole-organism performance are due to variation in the contractile properties of the muscle.

In the present study we examine the contractile properties of an important ankle extensor muscle, i.e. the gastrocnemius (Tracy et al. 2012), in an invasive population of the African clawed frog (*Xenopus laevis*) in France. Previous work has demonstrated differences in terms of morphology with animals from the periphery showing longer hind limbs, a greater muscle physiological cross-sectional area, and a greater terrestrial endurance capacity (Louppe et al. 2017; Padilla et al. 2019). Moreover, animals at the periphery also show greater dispersal as measured experimentally or in the field (Courant et al. 2019a, b).

We here test for differences in muscle contractile properties and muscle endurance capacity between frogs from the centre and periphery of the range. Breeding migrations and dispersal events involve the overland dispersal of these frogs to new water-bodies (Courant et al. 2019a). This depends strongly on terrestrial endurance, even for aquatic species such as *Xenopus sp.* (Measey 2016). During these events animals will move quickly overland to new ponds while minimising the risk of predation. To test whether the observed in vivo differences in stamina can be explained by differences in muscle contractile physiology, muscle endurance capacity can be simulated in vitro through repeated muscle work loops at a frequency similar to what is observed in situ. The gastrocnemius muscle was used in these experiments as it is a major ankle extensor muscle important during both jumping and swimming (Richards 2008).

We also tested for differences between the sexes in muscle physiology as sexes are known to differ in limb length and endurance capacity (Louppe et al. 2017) which may be driven by differences in contractile physiology. As trade-offs between skeletal muscle burst performance and endurance capacity have been previously demonstrated between individuals in different ectotherms including *Xenopus* (e.g., Wilson et al. 2002; Vanhooydonck et al. 2014), we predicted that the higher endurance capacity in frogs from the periphery of the range may come at a cost to burst performance. Consequently, we predicted that frogs from the centre of the range will show higher muscle isometric stress, faster contractile kinetics, and a higher power output as selection likely favours burst performance. Conversely, we predicted that frogs from the periphery should be able to maintain muscle power output over a significantly greater number of work loop cycles compared to frogs from the centre of the range as spatial sorting will select for animals with greater endurance capacity at the periphery of the range.

Materials and methods

Animals

Ten *Xenopus laevis* from the centre and ten animals from the periphery of the range in Western France ("Deux-Sèvres") were brought to the Faculty of Health and Life Sciences at Coventry University, England, for analysis of muscle contractile performance. Frogs were housed at their optimal temperature for locomotion (23 °C; Araspin et al. 2020) before being used in muscle mechanics experiments. Ethics approval for the muscle mechanics experiments was provided by Coventry University (# P66560).

Muscle mechanics

The biggest female of the sample was used to set up the system. This animal was consequently not used in the analyses ($N = 19$; 9 females and 10 males). Frogs were killed by transection of the spinal cord, followed by pithing in accordance with the British Home Office regulations for the use of Animals (Scientific Procedures) Act 1986, Schedule 1. Dissections were performed in a refrigerated oxygenated Ringer's solution (composition: mmol L^{-1}: 115 NaCl, 2.5 KCl, 2.15 Na_2HPO_4, 0.85 NaH_2PO_4, 10.0 glucose and 1.8 $CaCl_2$, pH 7.4 at 20 °C prior to oxygenation). The medial section of the muscle was isolated with its tendons attached to the distal part of the femur on one side and the calcaneus-astragalus complex at the other side. Individuals were selected randomly to minimize the influence of the experimenter or test order.

Isometric assessments were used to determine the twitch and tetanus force of the medial gastrocnemius. The whole preparation was maintained in circulating oxygenated Ringer's solution at 23 °C, similar to animals' aquaria temperature and the preferred temperature of the species as well as their optimal temperature for locomotor performance (Casterlin and Reynolds 1980; Araspin et al. 2020). The femur was clipped into a crocodile clip attached to a strain gauge (UF1, Pioden, Controls Ltd, Canterbury Kent, UK) and the calcaneus/astragal complex was clipped into a crocodile clip attached to a motor arm (V201, Ling Dynamics Systems, Royston, Hertfordshire, UK) connected to a LVDT (Linear Variable Displacement Transformer, DFG 5.0, Solartron, Metrology, Bognor Regis, Sussex, UK). Twitch responses were generated by 1 ms stimulus pulses delivered by two parallel platinum wire electrodes. Muscle length and stimulation voltage was adjusted to maximise isometric twitch force. Isometric tetanic force was elicited via a stimulation of 200 ms burst duration using the muscle length and stimulation parameters found to elicit maximal twitch force. Stimulation frequency was altered between 90 to 120 Hz in subsequent tetani to optimise the stimulation frequency for maximal tetanic force (Seebacher et al. 2014). The maximal tetanus force, the time from stimulus to half peak tetanus force (THPT), and time from the last stimulus to half tetanus force relaxation (LSHR) were measured similar to other studies (Seebacher et al. 2014; James et al. 2015). The muscle was given a five-minute period of rest between each tetanic stimulation.

To determine the power output of the gastrocnemius muscle during cyclical length changes we used the work loop technique (Josephson 1993) at cycle frequencies of 2, 3, 4, 5 and 6 Hz. This allowed us to determine the cycle frequency that produced maximal power output, with three work loops generated per run. The strain during each work loop was set at 0.11, representing a total strain of 11% of resting muscle length (James et al. 2012). Stimulus phase and burst duration values were optimized for the muscle to produce maximal work at each cycle frequency. Control runs were performed every three to five runs to correct work loop power for possible deterioration in muscle performance over time. The gastrocnemius was given a five-minute rest between each run of three work loops.

Each muscle was then subjected to a fatigue run at a 3 Hz cycle frequency for 50 continuous work loop cycles using a stimulation frequency of half that found to deliver a maximal tetanus, similar to the approach taken by Seebacher and co-authors (2014). Only one fatigue run was performed for each individual. All individuals showed near zero values of work at the end of the fatigue run. The muscle was then given a ten-minute rest after which an assessment of recovery was performed using three work loop cycles at the same parameters as used during the fatigue runs. On average muscle performance had recovered to 59.1% (± 11.6% S.D.) of the power output delivered at the start of the fatigue run. No differences between populations (centre vs. periphery) were detected in the recovery ($P > 0.05$).

At the end of the experiments the gastrocnemius muscle was cleaned by removal of any dead fibres, tendons and bone. The muscle was then dried with absorbent paper and the muscle mass was determined using an electronic balance (Mettler-Toledo B204-S, Greifensee, Switzerland). Mean muscle cross-sectional area was calculated for each muscle from mass, length and an assumed density of 1060 kg m^{-3} (Mendez and Keys 1960). Maximal twitch and tetanus stress (kN m^{-2}) values were calculated by dividing the maximal twitch and tetanus force values by the mean cross-sectional area for that muscle. Maximum normalised muscle power output (W kg^{-1}) was calculated as average net power output per length change cycle divided by muscle mass. The power output of each work loop in a fatigue run was converted to a percentage of the maximal power output generated by that muscle during the fatigue run.

Statistical analysis

Assumptions of normality of the residuals of each model were verified using quantile–quantile plots (Q–Q plots) and Shapiro tests. As THPT and LSHR did not follow normality we logarithmically transformed them. A correlation test was performed between each variable and snout-vent length (SVL) to examine allometric effects. Since the time to half peak tetanus and the time from last stimulation to half relaxation were correlated with SVL we performed analysis of covariance (ANCOVA) for THPT and LSHR using SVL as co-variable with sex, locality, and their interaction as factors. We then performed multivariate analysis of variance (MANOVA) for twitch and tetanus stress and twitch and tetanus force with sex, locality, and their interaction as factors. We used a maximal Linear Mixed Effect Model (LMEM) using normalized power output as variable, with sex, locality, and frequency as fixed factors and ID number as a random factor as the same muscle was tested at different frequencies. The model residuals were normally distributed. We then used Tukey's pairwise analyses on the fitted means of normalized power output to test for significant differences. Differences in fatigue were tested using analysis of variance (ANOVA) with the 24th work loop power output as our variable, since it was from that cycle onwards that we graphically observed the beginning of a differentiation in the interaction between sex and locality with the muscle still generating net power in all individuals (Fig. 1). Tests at other cycle numbers also showed no differences between populations (all $P > 0.05$). We used the model that best fitted our data by estimating their AIC. All analyses were performed in R (R Core Team 2017).

Results

Twitch and tetanus

The best model for twitch and tetanus stress retained only locality ($F_{1,\,15} = 6.89$, $P < 0.01$). However, only the effect of twitch stress was significant ($P = 0.016$; tetanus stress $P = 0.73$). Individuals from the centre (mean ± S.D. 99.40 ± 19.62) had higher twitch stresses than those from the periphery (79.02 ± 12.43; Fig. 2; Table 1). Regarding absolute muscle force, the only significant explanatory variable in the multivariate analysis was locality ($F_{1,15} = 7.91$, $P < 0.01$; Sex: $F_{1,15} = 1.38$, $P = 0.28$; Interaction: $F_{1,15} = 1.08$, $P = 0.36$). However, when testing twitch and tetanus force separately, no significant differences were detected (all $P > 0.05$; Table 1).

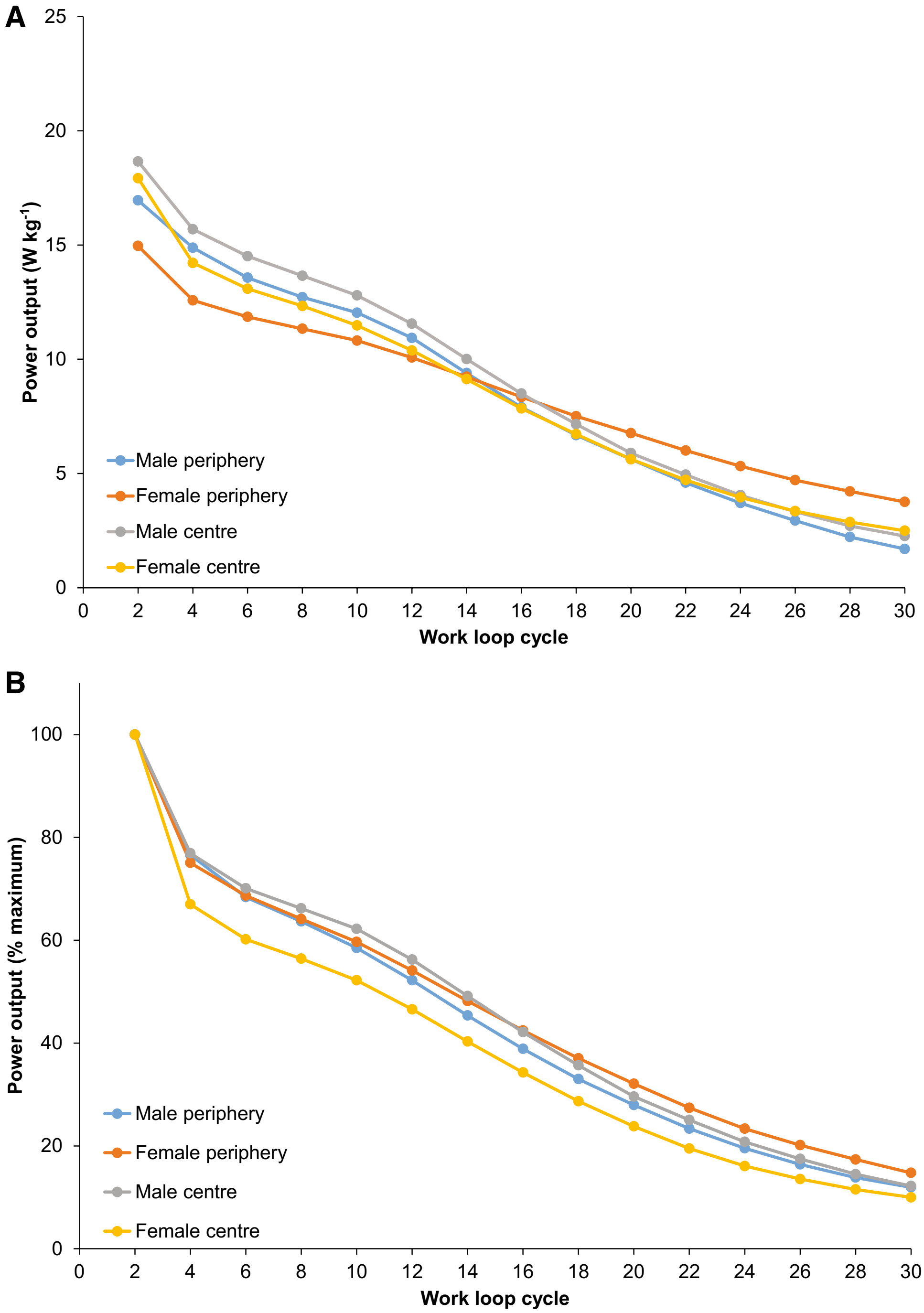

Fig. 1 Fatigue runs illustrating how muscle power output declines as a function of work loop number (**a**). Although females from the periphery appear to have lower power output, they appear to maintain power better during the fatigue runs. The lower graph shows the power output of each work loop as a percentage of the maximal power output generated by that muscle during the fatigue run (**b**). Each coloured point represented the mean of the group

Isometric activation times

ANCOVAs performed on the log transformed variables with SVL as covariable showed that only locality impacted THPT (SVL: $F_{1,15} = 0.01$, $P = 0.90$; Locality*Sex: $F_{1,15} = 0.73$, $P = 0.4$; Sex: $F_{1,15} = 0.98$, $P = 0.33$; Locality: $F_{1,15} = 7.84$, $P = 0.01$) and only sex for LSHR (SVL: $F_{1,15} = 1.45$, $P = 0.24$; Locality*Sex: $F_{1,15} = 0.11$, $P = 0.74$; Sex: $F_{1,15} = 9.39$, $P < 0.01$; Locality: $F_{1,15} = 0$, $P = 0.96$). Individuals from the centre of the range had a THPT that was on average 14.77% shorter than individuals from the periphery. In females, the time needed to relax the gastrocnemius muscle was ion average 19.93% shorter than males (Fig. 3; Table 1).

Cycle frequency—power output

The LMEM on normalized power output showed no differences between locality or sex (Locality: $P = 0.86$; Sex: $P = 0.84$; Locality*Sex: $P = 0.4$). However, cycle

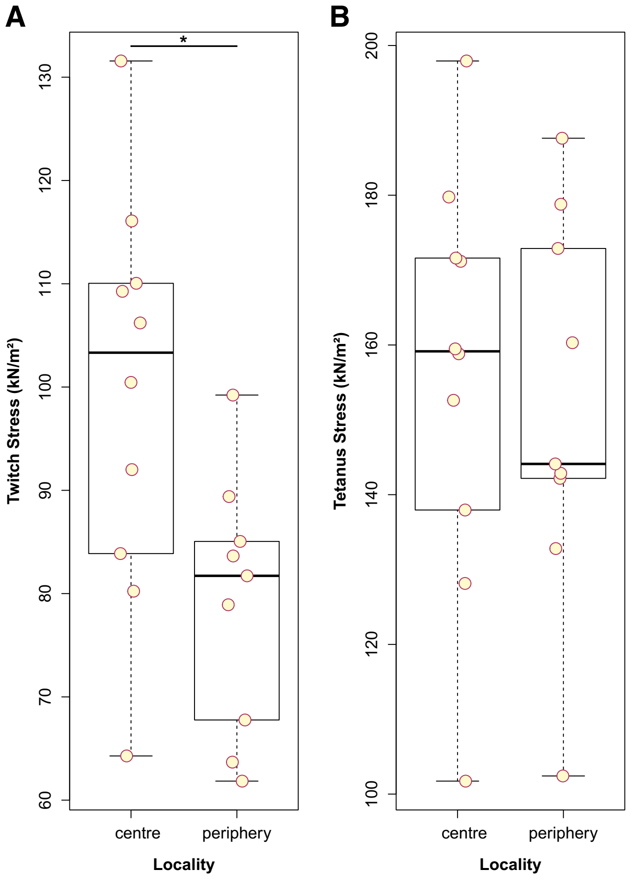

Fig. 2 Effect of locality (centre vs. periphery of the range) on twitch (**a**) and tetanic (**b**) stress. Whereas animals from the centre of the range produced significantly higher twitch stresses, no difference in tetanic stress was observed. Significant differences are indicated with asterisks ($* < 0.05$)

frequency had a significant effect ($P < 0.01$), with animals showing lower power output at a frequency of 2 Hz (mean ± SE = 25.5 ± 1.33 W kg^{-1}) compared to either 4 Hz (32.8 ± 1.24 W kg^{-1}), 5 Hz (32 ± 1.24 W kg^{-1}), or 6 Hz (29.7 ± 1.27 W kg^{-1}; Fig. 4; Table 1).

Fatigue runs

None of the factors tested had a significant effect on power output at the 24th work loop of the fatigue run (Locality: $F_{1, 15} = 0.24$, $P = 0.63$, Sex: $F_{1, 15} = 0.68$, $P = 0.42$, Locality*Sex: $F_{1, 15} = 0.98$, $P = 0.33$). However, females from the periphery showed a greater variability in power output at the 24th work loop compared to other groups.

Discussion

Overall, the lack of significant differences in maximal tetanus force, maximal power output, and endurance between *X. laevis* from the centre or the periphery of the range in France suggest that the physiological properties of the gastrocnemius, an important ankle extensor muscle, cannot explain the variation in in vivo terrestrial locomotor endurance. Indeed, differences between localities were only observed for twitch stress (Fig. 2a) and the time needed to reach half peak tetanus (Fig. 3a). Animals from the centre of the range showed greater twitch stress and shorter time to half peak tetanus compared to animals at the periphery. If a trade-off exists between skeletal muscle burst and endurance performances, then animals at the centre of the range (which hypothetically should have a lower skeletal muscle endurance) should excel in burst performance. However, only differences in twitch stress and tetanus activation time, but not in tetanus force or power output

Table 1 Summary of the physiological traits measured

	Center ($N = 9$)	Periphery ($N = 10$)	Female ($N = 9$)	Male ($N = 10$)
Twitch force (N)	1.87 ± 0.52	1.69 ± 0.43	1.94 ± 0.58	1.64 ± 0.33
Tetanus force (N)	2.98 ± 0.91	3.19 ± 0.67	3.38 ± 0.84	2.81 ± 0.67
Twitch stress (kN/m^2)	99.4 ± 19.62	79.02 ± 12.43	85.64 ± 20.47	93.45 ± 18.35
Tetanus stress (kN/m^2)	155.92 ± 27.64	151.55 ± 26.36	150.07 ± 28.52	157.25 ± 25.32
THPT (ms)	24.16 ± 3.58	28.36 ± 2.55	25.24 ± 2.94	26.96 ± 4.32
LSHR (ms)	110.16 ± 19.78	109.84 ± 22.05	97.27 ± 17.34	121.48 ± 15.74
Power output at 2 Hz (W kg^{-1})	25.92 ± 3.44	24.70 ± 4.40	25.95 ± 3.70	24.94 ± 4.14
Power output at 3 Hz (W kg^{-1})	30.49 ± 2.97	28.62 ± 4.35	29.94 ± 3.45	29.20 ± 4.15
Power output at 4 Hz (W kg^{-1})	33.98 ± 5.19	31.42 ± 6.00	34.09 ± 6.23	31.60 ± 5.11
Power output at 5 Hz (W kg^{-1})	33.62 ± 6.28	30.45 ± 7.17	33.95 ± 7.05	30.52 ± 6.44
Power output at 6 Hz (W kg^{-1})	30.62 ± 5.57	28.53 ± 8.07	31.73 ± 7.10	28.19 ± 6.41
Power output after 24th work-loop (W kg^{-1})	4.00 ± 1.37	4.42 ± 2.26	4.56 ± 2.06	4.28 ± 2.02

Table entries are means ± standard deviations

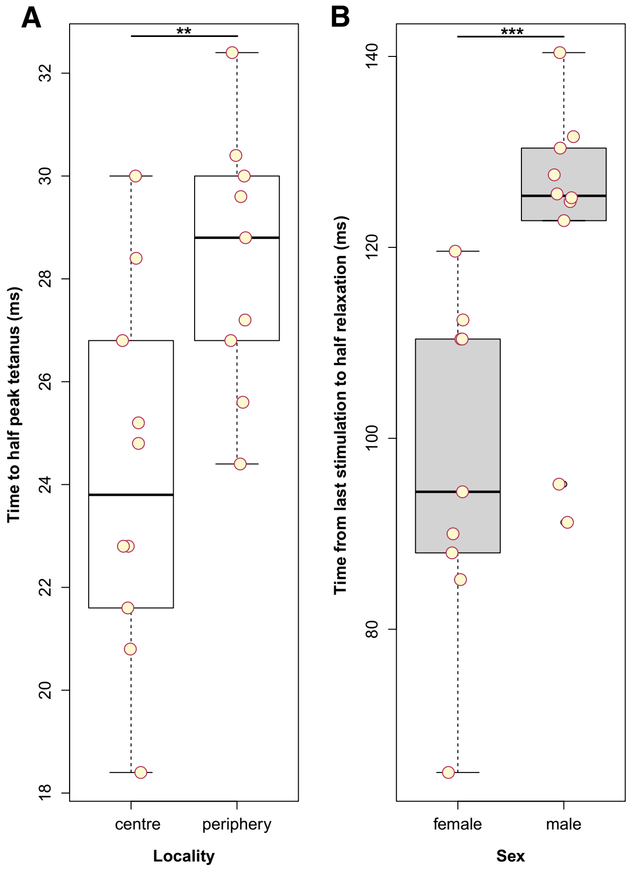

Fig. 3 Impact of locality (**a**) and sex (**b**) on the time to half peak tetanus and the time from peak tetanus to half relaxation, respectively. Although animals from the centre of the range produced tetanus force faster in their gastrocnemius muscle, no differences between sexes were observed (**a**). Conversely, whereas females showed faster muscle relaxation than males, no differences between the centre and the periphery were observed (**b**). Significant differences are indicated with asterisks (** <0.01, *** <0.001)

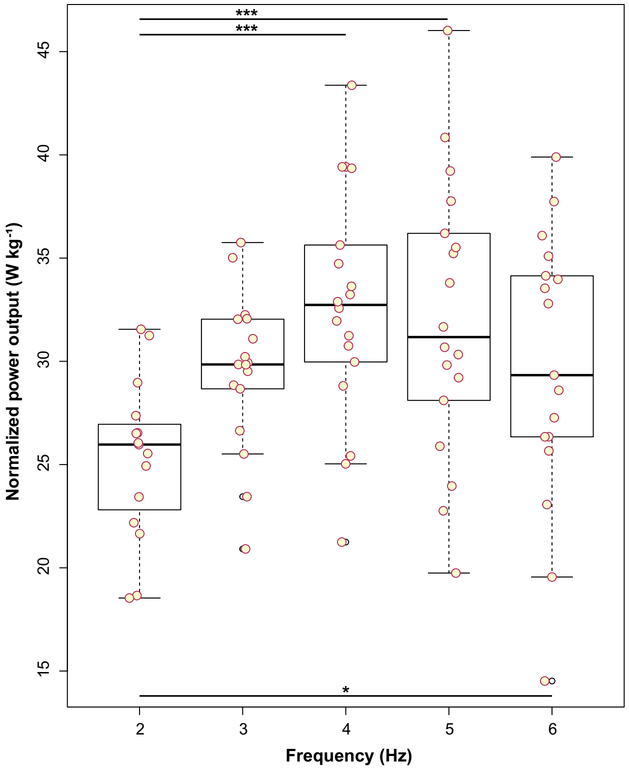

Fig. 4 Power output—cycle frequency plot illustrating that power output gradually increases with cycle frequency to reach an optimum around 4–5 Hz. Significant differences are indicated by asterisks (* <0.05, *** <0.001). No differences between localities or sexes were observed

were observed demonstrating that at the level of contractile function this trade-off was not apparent. The lack of differences between each locality in tetanus stress compare to what was found in peak twitch stress could be explained by our experimental methods. During tetanus stimulation we chose to use the muscle length that optimised twitch force. Muscles do operate across a force–length curve which may differ according to their activation level (i.e. the number of active motor units) (Holt and Azizi 2016), with lower activation level typically being at a longer optimal length. If so, the optimal length for tetanic stimuli might be shorter and as such this may have impacted our results. In contrast to the in vivo differences in stamina observed between populations (Louppe et al. 2017), no differences were observed in fatigue resistance at the muscular level. Other factors including cardiovascular performance, muscle architecture (Padilla et al. 2019), or the activation and coordination of the hind limb muscles may be important drivers of the observed variation in whole-organism performance.

Gastrocnemius endurance cannot explain differences in locomotor performance

The differences in gastrocnemius muscle activation time and twitch stress between animals from the centre and the periphery of the range did not translate into differences in muscle endurance capacity. Moreover, other traits such as tetanus stress and work loop performance did not show any differences. Consequently, it is unlikely that differences in the physiology of the ankle extensor are responsible for the observed difference in stamina at the whole-organism level. Knee and hip extensors are also important during jumping and showed differences in muscle mass between populations (Padilla et al. 2019). Consequently, these muscles could be targets to test for differences in muscle endurance and may help explain the observed differences in whole-organism performance. Alternatively, the differences observed in vivo might not be due to differences in muscle physiology but other traits such as metabolism (James et al. 2012), muscle architecture (Lowie et al. 2019; Padilla et al. 2019), dispersal behaviour (Lindström et al. 2013; Gruber et al. 2017), cardiovascular performance (Dempsey et al. 2008), the availability and storage of nutrients, or lung volume. A previous study on muscle architecture demonstrated that animals at the periphery have heavier and longer muscles combined with a greater muscle cross-sectional area, with such differences apparent for the gastrocnemius muscle (Padilla et al. 2019). How this may contribute to greater endurance capacity at the whole organism level remains to be investigated. However, previous work has shown that females from the periphery of the range have larger hearts (Padilla et al. 2019) which may contribute to their increased endurance capacity.

Sex-specific effects on muscle relaxation

Our results also showed some evidence of sexual dimorphism in muscle relaxation with females relaxing their muscles faster than males (LSHR; see Fig. 3b). This suggests that females may have a greater proportion of fast fibres. Sexual dimorphism in muscle fibre type has been demonstrated previously for the forearm flexor muscles in frogs (Rubinstein et al. 1983; Navas and James 2007) with males having slower muscle relaxation. As males have a higher endurance than females (Louppe et al. 2017) this may explain why their gastrocnemius muscle could have slower muscle fibre types and longer relaxation times. Interestingly, females from the periphery showed a great variability in their gastrocnemius endurance capacity. The reason behind this increased variability compared to males is yet to be investigated.

In summary, we compared muscle contractile properties between invasive frogs from the centre and the periphery of the range in France. Despite minor differences in the contractile function of the gastrocnemius muscle, these results cannot explain previously observed differences in whole-organism performance (i.e. stamina, see Louppe et al. 2017) as we did not find any differences in muscle endurance or power output between frogs from the centre and the periphery of the range. However, previous studies showed differences in muscle architecture and organ size (e.g., female heart size) that may in part explain the in vivo differences in endurance capacity between the centre and periphery. These results in combination with results from previous studies (Louppe et al. 2017; Courant et al. 2017, 2019a, b; Padilla et al. 2019) show that integrative studies on the drivers of variation in dispersal capacity and locomotor performance in invasive species and the traits that impact the ability to move are key in understanding invasion dynamics.

Acknowledgements Research and capture permits were provided by the Préfet of the Deux-Sèvres department.

Author contributions Conceptualization: Anthony Herrel; Methodology: Rob S. James; Formal analysis and investigation: Pablo Padilla, Jason Tallis, Josh Hurst,Rob S. James, Anthony Herrel; Writing—original draft preparation: Pablo Padilla, Rob S. James, Anthony Herrel; Writing—review and editing: all authors; Funding acquisition: Anthony Herrel; Resources: Julien Courant; Supervision: Anthony Herrel, Rob S. James.

Funding This research was funded by the ERA-Net BiodivERsA, with the national funders ANR, DFG, BELSPO and FCT, as part of the 2013 BiodivERsA call for research proposals. INVAXEN "Invasive biology of *Xenopus laevis* in Europe: ecology, impact and predictive models" project ANR-13-EBID-0008-01.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Ethics approval for the muscle mechanics experiments was provided by Coventry University (# P66560).

References

Araspin L, Martinez AS, Wagener C, Courant J, Louppe V, Padilla P, Measey J, Herrel A (2020) Rapid shifts in the temperature dependence of locomotor performance in an invasive frog, *Xenopus laevis*, implications for conservation. Integr Comp Biol 60:456–466

Arnold SJ (1983) Morphology, performance and fitness. Am Zool 23:347–361

Casterlin ME, Reynolds WW (1980) Diel activity and thermoregulatory behavior of a fully aquatic frog: *Xenopus laevis*. Hydrobiologia 75:189–191

Courant J, Secondi J, Bezeiriat V, Herrel A (2017) Resources allocated to reproduction decrease at the range edge of an expanding population of an invasive amphibian. Biol J Linn Soc 122:157–165

Courant J, Secondi J, Guillemet L, Vollette E, Herrel A (2019a) Rapid changes in dispersal on a small spatial scale at the range edge of an expanding population. Evol Ecol 33:599–612

Courant J, Adil L, De Kegel B, Adriaens D, Herrel A (2019b) Conserved growth rate and age structure of *Xenopus laevis* in the edge and core of an expanding population. Biol J Linn Soc 128:122–129

Coyle EF (1999) Physiological determinants of endurance exercise performance. J Sci Med Sport 2:181–189

Dempsey JA, Amann M, Romer LM, Miller JD (2008) Respiratory system determinants of peripheral fatigue and endurance performance. Med Sci Sports Exerc 40:457–461

Garland TJr, Else PL (1987) Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. Am J Physiol 252:R439–R449

Garland TJr, Losos JB (1994) Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago, pp 240–302

Gruber J, Brown G, Whiting MJ, Shine R (2017) Is the behavioural divergence between range-core and range-edge populations of cane toads (*Rhinella marina*) due to evolutionary change or developmental plasticity? R Soc Open Sci 4:170789

Herrel A, Vanhooydonck B, Porck J, Irschick DJ (2008) Anatomical basis of differences in locomotor behavior in *Anolis* lizards: a comparison between two ecomorphs. Bull Mus Comp Zool 159:213–238

Holt NC, Azizi E (2016) The effect of activation level on muscle function during locomotion: are optimal lengths and velocities always used? Proc R Soc B 283:20152832

Husak JF (2006) Does speed help you survive? A test with collared lizards of different ages. Funct Ecol 20:174–179

Husak JF, Fox SF, Lovern MB, Van Den Bussche RA (2006) Faster lizards sire more offspring: sexual selection on whole-animal performance. Evolution 60:2122–2130

Inbar O, Kaiser P, Tesch P (1981) Relationships between leg muscle fiber type distribution and leg exercise performance. Int J Sports Med 2:154–159

Irschick DJ, JrT G (2001) Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. Ann Rev Ecol Syst 32:367–396

Irschick DJ, Losos JB (1998) A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. Evolution 52:219–226

James RS, Navas CA, Herrel A (2007) How important are skeletal muscle mechanics in setting limits on jumping performance? J Exp Biol 210:923–933

James RS, Tallis J, Herrel A, Bonneaud C (2012) Warmer is better: thermal sensitivity of both maximal and sustained power output in the iliotibialis muscle isolated from adult *Xenopus tropicalis*. J Exp Biol 215:552–558

James RS, Vanhooydonck B, Tallis JA, Herrel A (2015) Larger lacertid lizard species produce higher than expected iliotibialis muscle power output: the evolution of muscle contractile mechanics with body size. J Exp Biol 218:3589–3595

Josephson RK (1993) Contraction dynamics and power output of skeletal muscle. Ann Rev Physiol 55:527–546

Le Galliard J-F, Clobert J, Ferrière R (2004) Physical performance and Darwinian fitness in lizards. Nature 432:502–505

Lindström T, Brown GP, Sisson SA, Phillips BL, Shine R (2013) Rapid shifts in dispersal behavior on an expanding range edge. Proc Natl Acad Sci USA 110:13452–13456

Losos JB (1990) The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. Evolution 44:1189–1203

Louppe V, Courant J, Herrel A (2017) Differences in mobility at the range edge of an expanding invasive population of *Xenopus laevis* in the west of France. J Exp Biol 220:278–283

Lowie A, Gillet E, Vanhooydonck B, Irschick DJ, Losos JB, Herrel A (2019) Do the relationships between hindlimb anatomy and sprint speed variation differ between sexes in *Anolis* lizards? J Exp Biol 222:188805

Measey J (2016) Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review. PeerJ 4:e2474

Mendez J, Keys A (1960) Density and composition of mammalian muscle. Metabolism 9:184–188

Miles DB (2004) The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. Evol Ecol Res 6:63–75

Navas CA, James RS (2007) Sexual dimorphism of extensor carpi radialis muscle size, isometric force, relaxation rate and stamina during the breeding season of the frog *Rana temporaria* Linnaeus 1758. J Exp Biol 210:715–721

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

Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. Nature 439:803

R Core Team (2017) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Richards CT (2008) The kinematic determinants of anuran swimming performance: an inverse and forward dynamics approach. J Exp Biol 211:3181–3194

Rubinstein NA, Erulkar SD, Schneider GT (1983) Sexual dimorphism in the fibers of a "clasp" muscle of *Xenopus laevis*. Exp Neurol 82:424–431

Seebacher F, Walter I (2012) Differences in locomotor performance between individuals: importance of parvalbumin, calcium handling and metabolism. J Exp Biol 215:663–670

Seebacher F, Tallis JA, James RS (2014) The cost of muscle power production: muscle oxygen consumption per unit work increases at low temperatures in *Xenopus laevis*. J Exp Biol 217:1940–1945

Shine R, Brown GP, Phillips BL (2011) An evolutionary process that assembles phenotypes through space rather than through time. Proc Natl Acad Sci USA 108:5708–5711

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

Tracy CR, Christian KA, Baldwin J, Phillips BL (2012) Cane toads lack physiological enhancements for dispersal at the invasive front in Northern Australia. Biology Open 1:37–42

Vanhooydonck B, Herrel A, Van Damme R, Irschick DJ (2006) The quick and the fast: the evolution of acceleration capacity in *Anolis* lizards. Evolution 60:2137–2147

Vanhooydonck B, James RS, Tallis J, Aerts P, Tadic Z, Tolley KA, Measey GJ, Herrel A (2014) Is the whole more than the sum of its parts? Evolutionary trade-offs between burst and sustained locomotion in lacertid lizards. Proc R Soc B 281:20132677

Wilson RS, James RS, Van Damme R (2002) Trade-offs between speed and endurance in the frog *Xenopus laevis*: a multi-level approach. J Exp Biol 205:1145–1152