The Company of Biologists

RESEARCH ARTICLE

Does aquatic performance predict terrestrial performance: a case study with an aquatic frog, *Xenopus laevis*

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ABSTRACT

The physical properties of the environment impose strong selection on organisms and their form–function relationships. In water and on land, selective pressures differ, with water being more viscous and denser than air, and gravity being the most important external force on land for relatively large animals such as vertebrates. These different properties of the environment could drive variation in the design and mechanics of the locomotor system of organisms. Animals that use multiple environments can consequently exhibit locomotion conflicts between the demands imposed by the media, leading to potential trade-offs. Here, we tested for the presence of such locomotor trade-offs depending on the environment (water or land) in a largely aquatic frog, *Xenopus laevis*. We focused on terrestrial and aquatic exertion capacity (time and distance swum or jumped until exhaustion) and aquatic and terrestrial burst capacity (maximal instantaneous swimming velocity and maximal force jump) given the ecological relevance of these traits. We tested these performance traits for trade-offs, depending on environments (water versus air) and locomotor modes (i.e. exertion and burst performance). Finally, we assessed the contribution of morphological traits to each performance trait. Our data show no trade-offs between the performance traits and between the environments, suggesting that *X. laevis* is equally good at swimming and jumping thanks to the same underlying morphological specialisations. We did observe, however, that morphological predictors differed depending on the environment, with variation in head shape and forelimb length being good predictors for aquatic locomotion and variation in hindlimb and forelimb segments predicting variation in jumping performance on land.

KEY WORDS: Locomotion, Morphology, *Xenopus laevis*, Exertion, Burst performance, Physical environment

INTRODUCTION

The environment induces strong selection on organisms and their form–function relationships (Kardong, 1997). Indeed, depending on the nature of the environment, the physical properties may differ and may lead to variation in the design of organisms and their locomotor strategies. When moving in a fluid – air or water – resisting forces are applied on the body in the opposite direction to the movement (Vogel, 1994). This friction drag depends on the viscosity of the fluid, its density, the size and shape of the body and its velocity (Vogel, 1994). For relatively large animals such as vertebrates moving in a terrestrial environment, gravity is the most important external force acting on an animal's body and probably drives the design and mechanics of the locomotor system. Water, in contrast, is viscous and dense and imposes different forces on an organism and its movement (Gillis and Blob, 2001; Nauwelaert et al., 2007; Biewener et al., 2018). Given the differences in physical properties between water and land, differences in muscle function and kinematics can be expected (Clarac et al., 1987; Johnston and Bekoff, 1996; Gillis and Blob, 2001). For example, in ducks, the ankle extensor shows a similar pattern of activation and shortening in water and on land, yet the absolute levels of muscle stress and strain are greater during terrestrial locomotion (Biewener and Gillis, 1999). In eels, the transition from water to land elicited changes in the kinematics of body undulation coupled to changes in the duration of muscle activity and the relative timing of muscle activation (Gillis, 1998a,b).

However, some animals move and use multiple environments and their locomotor system thus probably reflects a compromise between the demands imposed by both media. Amphibians, and more specifically frogs, are an interesting model to explore the potential trade-offs and compromises in animals using multiple locomotor environments, as most are able to jump or hop on land and swim in the aquatic environment. Frogs exhibit a highly derived morphology with elongated ilia and hindlimbs, and a shortened trunk, adapted for jumping (Emerson, 1979). Frog jumping and swimming has been studied in detail, with studies focusing on the kinematics and mechanics of locomotion in different environments (Astley and Roberts, 2012, 2014; Robovska-Havelkova et al., 2014; Richards, 2008; Aerts and Nauwelaerts, 2009; Gillis and Blob, 2001). Previous studies have highlighted that hindlimb extension produces thrust during both jumping and swimming (Gillis and Biewener, 2000; Aerts and Nauwelaerts, 2009), suggesting similar demands on locomotion in the two media. Moreover, Nauwelaerts and Aerts (2003) found that anurans adjust limb kinematics, allowing them to move in both environments. Indeed, during jumping, first the hip, then the knee and finally the ankle are activated; during swimming, the knee extension initiates the movement, followed by the hip and then the ankle (Gillis and Biewener, 2000). Interestingly, Nauwelaerts and colleagues (2007) found no correlation between burst locomotor performance in a semi-aquatic frog moving in water and on land, suggesting a decoupling between performance in these two media.

During swimming, the size and the speed of extension of the hindlimbs are important in generating propulsion (Richards and Clemente, 2010; Gillis, 2007; Aerts and Nauwelaerts, 2009). Moreover, in some species such as the pipid *Xenopus laevis*, the ilio-sacral joint allows the sliding of the pelvis along the vertebral

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column and has been suggested to contribute to locomotion by increasing the hindlimb stroke (Videler and Jorna, 1985). Jumping is dependent on the contraction of the hindlimb muscles causing rapid hip, knee and ankle extension (Emerson and De Jongh, 1980). The forelimbs, in contrast, are thought to play an important role in positioning the body during take-off (Toro et al., 2004; Biewener et al., 2018), and in damping the kinetic energy from the jump during landing (Nauwelaerts and Aerts, 2006; Sigurdsen et al., 2012; Herrel et al., 2016). Thus, the traits that are important for locomotion in different media may not be the same, yet this remains poorly understood (but see Nauwelaerts et al., 2007).

Locomotion is diverse and different locomotor modes are used in different contexts. For example, whereas exertion or endurance capacity is likely to be under selection during dispersal, burst performance is probably relevant in the context of prey capture or predator escape. Previous studies on anuran locomotion have compared swimming and jumping performance (Lutz and Rome, 1994; Astley and Roberts, 2012; Herrel et al., 2014; James et al., 2007; Richards, 2008; Richards and Clemente, 2013; Gillis, 2007), but only rarely across locomotor media for the same individuals (but see Nauwelaerts et al., 2007). Additionally, other studies have compared locomotor modes (Herrel and Bonneaud, 2012b; Wilson et al., 2002) but have rarely explored the possible interaction with locomotor environment (but see Gillis and Blob, 2001). Whereas most of these studies have suggested that trade-offs may exist between different types of locomotion (endurance versus burst performance; Herrel and Bonneaud, 2012b), these trade-offs are not always observed.

In the present study, we asked whether an animal that is a good performer in the aquatic environment is also a good performer in the terrestrial environment. Given that the physical properties differ between the two media, trade-offs in locomotion could occur. Alternatively, individual quality may dominate and cause animals to be good performers irrespective of the medium they move in (Van Damme et al., 2002). Finally, locomotion in different media may be decoupled and locomotor performance in one medium may not be a good predictor of locomotor performance in the other medium (Nauwelaerts et al., 2007). We studied *Xenopus laevis*, a principally aquatic frog from sub-Saharan Africa (Measey et al., 2004; Furman et al., 2015; Premachandra et al., 2023), that uses both aquatic and terrestrial locomotion to disperse (Measey and Tinsley, 1998; Lobos and Jaksic, 2005; Measey, 2016; De Villiers and Measey, 2017; Courant et al., 2019; Elepfandt et al., 2022). We measured exertion capacity and burst performance in both the aquatic and the terrestrial environment for 63 individuals of both sexes. Specifically, we predicted that burst performance traits would be correlated irrespective of the locomotor medium as both are dependent on rapid limb extension and thus are likely to require similar morphological adaptations (Nauwelaerts et al., 2007). In contrast, we expected exertion capacity in the two media to be less strongly correlated than burst performance as different morphological traits are likely to be important for locomotion in the two media. Moreover, the functional demands on the energetics of locomotion in these two media may trade-off with one another. As *X. laevis* is principally aquatic, selection may have favoured the energetics of locomotion in an aquatic environment to the detriment of terrestrial endurance capacity. Finally, we predicted that whereas terrestrial locomotor performance should be most strongly determined by hindlimb (generating propulsion) and forelimb (buffering impact) dimensions, head dimensions may be important drivers of aquatic locomotor performance in addition to limb dimensions, given the importance of streamlining in reducing drag and the energetic cost of locomotion.

MATERIALS AND METHODS

Adults of *Xenopus laevis* (Daudin 1802) used in this study were caught in autumn 2018 and 2019 in two different areas in South Africa (*N*=25, 14 females and 11 males; KwaZulu-Natal *N*=13, 8 females and 5 males; and Western Cape *N*=12, 6 females and 6 males) and in France (Deux-Sèvres, *N*=38; 19 females and 19 males). Upon arrival in the laboratory in Paris, each individual was pit-tagged, allowing unique identification. Animals were housed at the Function and Evolution Laboratory of the National Museum of Natural History (MNHN) in Paris, France. Specimens from South Africa were maintained in 30 l tanks, two per aquarium, and those from France were maintained in 65 l tanks with 5–10 individuals per aquarium. Animals were fed twice weekly with frozen beef heart or mosquito larvae. The temperature of the water was maintained at 23°C.

All protocols are in accordance with the guidelines of the institutional animal care and use committee at the MNHN. Research and capture permits were provided by the Préfet of the Deux-Sèvres department (France). Capture and export permits for *X. laevis* from KwaZulu-Natal (iSimangaliso National Park) were provided under permit number OP 3169/2018 from KwaZulu-Natal Wildlife; capture and export of *X. laevis* from the Western Cape was made possible under permit CN15-31-5189 from CapeNature. Animal ethics clearance application ACU-2021-19215 in Research Ethics, Animal Care and Use was provided by the Ethics Committee in Stellenbosch University.

Morphometrics
Body dimensions of animals were measured following Herrel et al. (2012). The mass was measured with a digital scale (Ohaus, Brooklyn, NY, USA; precision ±0.1 g). Snout–vent length (SVL), head dimensions (height, width and length), lower jaw length, ilium dimensions (length and width), femur, tibia, foot, toe, humerus, radius, hand and finger (Fig. 1) were measured using a pair of digital callipers (Mitutoyo; precision ±0.01 mm).

Performance
Terrestrial exertion capacity was measured at 23°C by chasing animals by hand until exhaustion across a 3 m long graduated circular track with a humidified cork substrate to prevent dehydration (Herrel and Bonneaud, 2012a; Louppe et al., 2017; Araspin et al., 2020). Animals were considered exhausted when they were no longer able to right themselves when put on their back. As soon as an animal appeared exhausted, it was put on its back and if able to turn over again, the measurements were continued. Typically, animals were put on their backs between two and three times during a trial. The maximal distance jumped was recorded as the number of complete laps plus the distance covered as indicated by the graduations on the track (precision: 5 cm). The time to exhaustion was recorded using a stopwatch to the nearest second. Trials were repeated twice per individual and the maximal time and distance were retained for further analyses.

Terrestrial burst performance was quantified by measuring maximal jump force at 23°C using a force plate (Kistler Instruments AG, Type 5691A) connected to a charge amplifier (Kistler Charge Amplifier type 9865), following previous protocols (Herrel et al., 2014). Animals were stimulated to jump on the force plate five or six times within a 1 min recording session. Forces were recorded at 500 Hz and Kistler Bioware software was used to extract peak *X*, *Y* and *Z* forces (in N). The vector sum of these three forces was calculated and the resultant force was used in all analyses. Trials were repeated three times and the single highest jump force was retained for further analyses (Araspin et al., 2020).
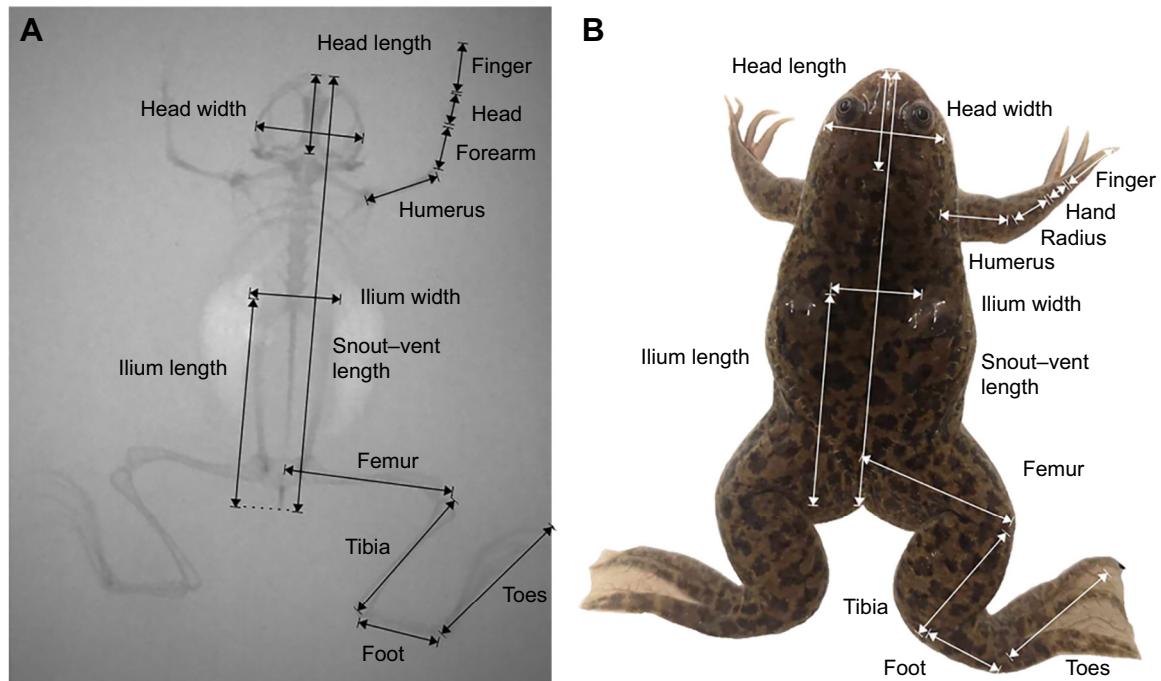
Fig. 1. Illustration of the morphometric data taken from _Xenopus laevis_. Illustrated are the measurements taken on a live animal (B) and the corresponding underlying bones in the radiograph (A). Not illustrated are head height and lower jaw length.

Aquatic exertion capacity was performed using the same 3 m long graduated circular track used to measure terrestrial exertion, but filled with 20 cm of water at 23°C. Animals were chased individually by hand until exhaustion (i.e. unable to recover their ventral position when placed on their back). The total distance swum was recorded using the graduated circular track and time to exhaustion was recorded using a stopwatch. Trials were repeated twice per individual and the maximal time and distance were retained for further analyses (Araspin et al., 2023).

Aquatic burst performance was estimated by quantifying the instantaneous swimming velocity. To do so, we recorded escape swimming responses using a Phantom Miro M310 high-speed camera set at 800 Hz (resolution of 1280×800 pixels). Frogs were placed in a rectangular tank 2 m long, 20 cm wide and 30 cm tall, filled with 20 cm of water at 23°C. Animals were put in the tank and startled by slightly touching their back. The camera recorded at least two complete swimming cycles for each individual from a dorsal view and swimming trials were repeated three times. Videos were analysed with ProAnalyst and X and Y coordinates were exported following the protocol described in Herrel and Bonneaud (2012a,b). Maximal instantaneous velocity was calculated after filtering (low-pass Butterworth filter, implemented in Excel by Sam Van Wassenbergh; https://www.uantwerpen.be/en/staff/sam-vanwassenbergh/my-website/excel-vba-tools/) and numerical differentiation of the cumulative displacement profiles. The single highest peak instantaneous velocity across all trials was retained for further analyses.

After each locomotor trial, animals were returned to their home tank, fed, and left to rest for at least 2 days.

Statistical analyses

In order to fulfil assumptions of normality and homoscedasticity, all data were $\log_{10}$ transformed before analyses. Residuals of a regression of each performance and each morphological trait on SVL were used in all subsequent statistical analyses. We first tested for correlations between the different residual performance traits within and across media using Pearson correlations. We used correlations rather than regressions as no directionality is expected in the relationships between traits. As each correlation tests a specific hypothesis, no corrections for multiple testing were performed. However, all results remained significant when adjusting the P-value for multiple testing (adjusted P=0.003). Next, stepwise multiple regression analyses using the Akaike information criterium to test model fit were run using the 'MASS' package in R (Venables and Ripley, 2002) to assess which residual morphological traits best predicted variation in residual performance traits. All analyses were performed using R (version i386 4.1.2; http://www.R-project.org/).

RESULTS

The mean performance and morphological measurements are listed in Table 1; raw individual measurements are available from https://doi.org/10.48579/PRO/NIV1ET (Table S1).

Performance relationships

All residual performance traits were positively and significantly correlated to one another. The most strongly correlated traits were the time swum until exhaustion versus the aquatic exertion (r=0.99; P<0.001). The least correlated performance traits were terrestrial burst performance versus aquatic exertion (r=0.73; P<0.001) and terrestrial burst versus the time swum until exhaustion (r=0.75; P<0.001; Table 2). No trade-offs were observed between performance in different media (i.e. aquatic versus terrestrial; Fig. 2) or between the different types of performance (i.e. exertion versus burst performance; Fig. 3).

Morphology and performance

Overall residual morphological traits were excellent predictors of residual performance in _X. laevis_. Stepwise regression analyses with the residual performance traits as dependent variables and the

Table 1. Performance and morphological traits for all individuals

Trait	Value
Performance traits	
Aquatic burst performance (velocity in cm s^{-1})	213±6.64
Terrestrial burst performance (jump force in N)	1.05±0.07
Aquatic exertion (distance in cm)	8525±540
Aquatic exertion (time in s)	250±18.9
Terrestrial exertion (distance in cm)	2477±102
Terrestrial exertion (time in s)	210±14.5
Morphological traits (mm)	
Ilium width	15.8±0.25
Ilium length	31.8±0.52
Femur length	26.7±0.48
Tibia length	30.2±0.45
Foot length	16.8±0.46
Toe length	30.6±0.53
Head width	22.5±0.32
Head length	20.5±0.30
Head height	12.5±0.28
Jaw length	21.2±0.27
Humerus length	12.3±0.38
Radius length	7.79±0.25
Hand length	3.69±0.17
Finger length	11.6±0.30

Data are means±s.e.m. (N=63).

residual morphological traits as independent variables resulted in highly significant models. For aquatic exertion, the model retained head width and radius length as explanatory variables (R^2=0.88; $F_{5,57}$=93.1; P<0.001; Table 3). Terrestrial exertion was best predicted by tibia, foot, radius and hand length (R^2=0.93; $F_{7,55}$=113.8; P<0.001; Table 3). Aquatic burst performance was best predicted by the ilium dimensions (width and length) and foot radius length (R^2=0.94; $F_{7,55}$=129; P<0.001; Table 3). For terrestrial burst performance the model retained ilium width and radius length as the principal explicatory variables (R^2=0.66; $F_{3,59}$=129; P<0.001; Table 3). Aquatic time to exhaustion was best predicted by foot, humerus and radius length as well as head width (R^2=0.91; $F_{7,55}$=92.54; P<0.001; Table 3). Finally, terrestrial time

Table 2. Pearson correlations of residual performance traits across all individuals

Performance	r	P
Aquatic		
Aquatic time versus aquatic distance	0.99	<0.001
Aquatic burst versus aquatic distance	0.90	<0.001
Aquatic burst versus aquatic time	0.92	<0.001
Terrestrial		
Terrestrial time versus terrestrial distance	0.98	<0.001
Terrestrial burst versus terrestrial distance	0.78	<0.001
Terrestrial burst versus terrestrial time	0.78	<0.001
Burst performance		
Aquatic burst versus terrestrial burst	0.80	<0.001
Mixed		
Aquatic distance versus terrestrial distance	0.92	<0.001
Aquatic time versus terrestrial time	0.95	<0.001
Aquatic burst versus terrestrial distance	0.93	<0.001
Terrestrial burst versus aquatic distance	0.73	<0.001
Aquatic time versus terrestrial burst	0.75	<0.001
Aquatic time versus terrestrial distance	0.94	<0.001
Terrestrial time versus aquatic burst	0.95	<0.001
Terrestrial time versus aquatic distance	0.93	<0.001

All correlations remained significant after sequential Bonferroni correction. Indicated are the Pearson correlation coefficient and the significance of the relationship. N=63.
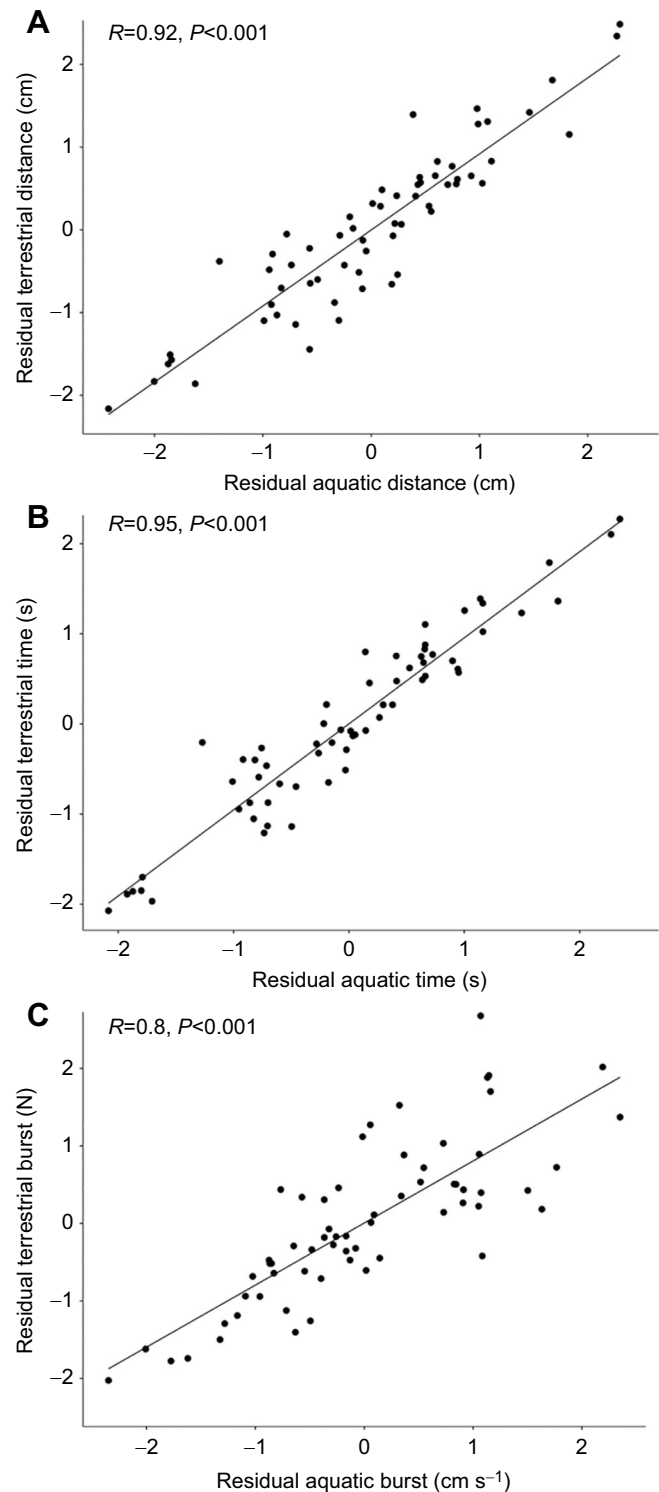

Fig. 2. Correlations between performance traits across media (aquatic versus terrestrial). Illustrated are residual performance measures corrected for variation in overall size (snout–vent length). (A) Terrestrial exertion (distance) against aquatic exertion (distance). (B) Terrestrial exertion (time) against aquatic exertion (time). (C) Terrestrial burst performance (jump force) against aquatic burst performance (peak instantaneous velocity). Indicated are the Pearson correlation coefficient and the P-value.

to exhaustion was best explained by ilium, femur, tibia, foot, toe, humerus and radius length (R^2=0.93; $F_{7,55}$=115.3; P<0.001; Table 3).
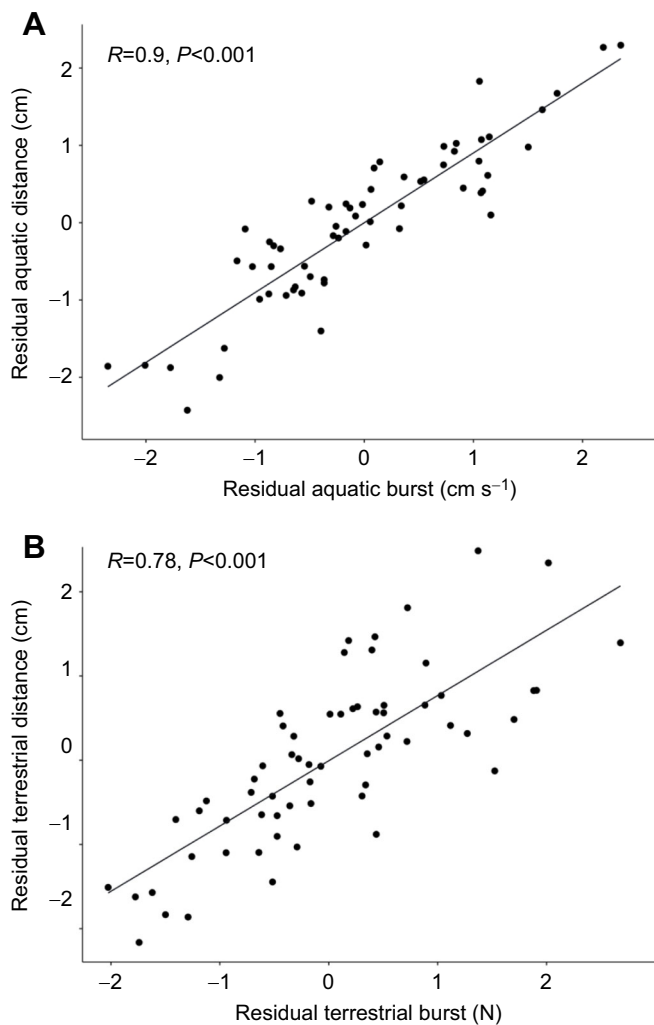
Fig. 3. Correlations between performance traits across types of performance (burst versus exertion capacity). Illustrated are residual performance measures corrected for variation in overall size (snout–vent length). The relationship between aquatic burst performance and aquatic exertion (measured as the distance swum before exhaustion) is strong (A), whereas it is less so for terrestrial performance (B). Indicated are the Pearson correlation coefficient and the P-value.

Table 3. Stepwise AIC models retained for each performance trait highlighting the full model (R^2- and P-value) as well as the standardised partial regression coefficients (β) for the variables retained in the model

	β	P
Aquatic exertion (distance): R^2=0.88; $F_{5,57}$=97.13; P<0.001		
Head width	0.18	0.016
Radius length	0.42	<0.001
Aquatic exertion (time): R^2=0.91; $F_{7,55}$=92.54; P<0.001		
Foot length	0.19	0.05
Head width	0.20	0.005
Humerus length	0.23	0.008
Radius length	0.33	<0.001
Terrestrial exertion (distance): R^2=0.93; $F_{7,55}$=113.8; P<0.001		
Tibia length	−0.17	0.02
Foot length	0.18	0.02
Radius length	0.54	<0.001
Hand length	0.18	0.04
Terrestrial exertion (time): R^2=0.93; $F_{7,55}$=115.3; P<0.001		
Ilium length	0.11	0.02
Femur length	0.16	0.02
Tibia length	−0.23	0.004
Foot length	0.22	0.01
Toe length	0.17	0.02
Humerus length	0.16	0.03
Radius length	0.48	<0.001
Aquatic burst: R^2=0.94; $F_{7,55}$=129; P<0.001		
Ilium width	0.16	0.01
Ilium length	0.16	0.002
Foot length	0.25	0.004
Radius length	0.35	<0.001
Terrestrial burst: R^2=0.66; $F_{3,59}$=40.87; P<0.001		
Ilium width	0.46	<0.001
Radius length	0.28	0.01

DISCUSSION
Performance relationships
No significant trade-offs were detected between performance in different media (water versus land) or between different types of performance traits (burst versus exertion). A strong positive correlation was observed between our two measures of exertion capacity irrespective of the medium and variation in body size despite the differences in the mechanics of locomotion in the media. This correlation is not surprising as individuals that keep moving longer will probably swim or jump a greater overall distance until exhaustion (Table 2). Thus, the two measures (time and distance) appear to be complementary measures of exertion performance. Unexpectedly, and in contrast to previous studies (Herrel and Bonnead, 2012a,b), no conflict was observed between the two locomotor modes studied here (i.e. burst and exertion capacity) in either of the media (Table 2). Other studies on whole-animal performance also failed to detect trade-offs between speed and endurance (Wilson et al., 2002; Sorci et al., 1995; Vanhooydonck et al., 2014; de Albuquerque et al., 2015; Moen, 2019; Rebelo and Measey,

2019). Despite its physiological basis, no consensus on the presence of burst–endurance trade-offs in locomotion appears to emerge.

In our study, the different locomotion modes (i.e. burst performance and exertion) in the two media were significantly and positively correlated, meaning that individuals that perform well in the terrestrial environment also perform well in the aquatic environment. Although *X. laevis* are primarily aquatic, recent ecological studies have shown that they also disperse overland (Measey and Tinsley, 1998; Lobos and Jaksic, 2005; Measey, 2016; De Villiers and Measey, 2017; Courant et al., 2019; Elepfandt et al., 2022). Additionally, *X. laevis* is known to consume terrestrial prey at the water's edge (Measey, 1998), putting a premium on its ability to perform well in both media. Jumping is phylogenetically conserved in anurans (Shubin and Jenkins, 1995) and is probably related to selective pressures linked to prey capture and escape from predators (Emerson, 1978; Gomes et al., 2002; Citadini et al., 2018). This function has shaped the frog 'Bauplan', which has been retained in most living frogs (Shubin and Jenkins, 1995). Thus, in contrast to the idea that species using multiple locomotor modes will show intermediate phenotypes that provide reasonable performance at both tasks but optimal performance in neither (Shine and Olsson, 2003), *X. laevis* appears to be equally good at swimming and jumping. Although the reason for the lack of a compromise phenotype remains to be investigated further, we here propose that both aquatic and terrestrial performance traits benefit from the same underlying morphological specialisations as suggested previously for semi-aquatic frogs (Nauwelaerts et al. 2007). Moreover, variation in individual quality may drive the observed patterns observed, with some individuals just being excellent performers compared with others, irrespective of the task or the medium (Van Damme et al., 2002).

Morphology and performance

Unexpectedly, head dimensions such as width, as well as the morphology of the forelimb were important predictors of aquatic exertion. Although at first sight counter-intuitive, leg dimensions were not retained in our model. However, when running a linear regression, foot length was a significant and strong predictor of variation in performance (R^2=0.76; P<0.001) but not retained in our stepwise model. Variation in head dimensions (i.e. width) and radius length are likely to be important predictors as they are probably linked to hydrodynamic constraints: more optimal shape may generate less resistance and decrease drag (Biewener et al., 2018), yet this remains to be tested. In the terrestrial environment, limb dimensions such as foot and tibia length were good predictors of variation in performance. During jumping, an elongation of the distal elements such as the tibia and foot may contribute to jumping performance by increasing the time an animal can continue to push on the substrate during take-off (Aerts and Nauwelaerts, 2009; Gillis and Biewener, 2000). Variation in radius length was a good predictor of terrestrial exertion, probably because of the role of the forelimb in dampening landing forces (Nauwelaerts and Aerts, 2006).

Interestingly, the same morphological traits were good predictors of variation in both measures of exertion. For the time to exhaustion in the aquatic environment, foot length, head width and radius length explained most of the variation. The midfoot contributes to propulsion (Richards and Clemente, 2010) and provides most of the thrust during swimming through foot rotation (Richards and Clemente, 2010; Robovska-Havelkova et al., 2014). A more forceful propulsion may allow for more time to rest during the glide phase between each stroke. As exertion capacity relies strongly on the cardiovascular system, longer resting times may reduce the oxygen demand, which generally increases with increased swimming activity (Dewar et al., 1994). This may then allow animals to swim longer and further. For terrestrial exertion, both forelimb and hindlimb segments were good predictors of performance. Whereas longer hindlimb elements may provide a greater insertion area for the limb muscles and allow the animals to keep pushing on the substrate longer during take-off (Emerson and De Jongh, 1980), longer forelimb segments may be important in the absorption of landing forces and the positioning of the body during take-off (Nauwelaerts and Aerts, 2006). The ilium may play an important role by providing attachment for the ilio-sacral musculature. These muscles allow the pre-loading of tendons, increasing elastic energy storage, modulating jump direction (Richards et al., 2018) and aligning the centre of mass with the direction of the propulsive force (Emerson and De Jongh, 1980).

For burst performances, morphological predictors differed depending on the media (aquatic or terrestrial; Table 3). In aquatic burst performance (i.e. swimming velocity), the radius length, the foot length and the ilium dimensions (width and length) were the best predictors in explaining the variation in performance among individuals. The midfoot is probably important as it provides propulsion and thrust during foot rotation (Richards and Clemente, 2010; Robovska-Havelkova et al., 2014). Foot movement is the sum of the extension produced at the hip, the knee, the ankle and the tarsometatarsal joints, and foot translational and rotational velocity can vary from stroke to stroke (Richards, 2008). Body length increases during swimming as a result of the sliding pelvis, which moves antero-posteriorly, thus increasing the distance over which the hindlimbs can extend (Videler and Jorna, 1985). This may explain why ilium dimensions are retained as good predictors of aquatic burst performance. During swimming, the forelimbs are either held along the body or extended anteriorly (Gillis and Biewener, 2000), which could impact the hydrodynamic resistance of the animal and may explain why the radius length was also an important predictor. For terrestrial burst performance, the ilium width and the radius length are good predictors (Fig. 1). The forelimb has been suggested to play a role in adjusting the body position and lifting the upper body in order to optimize jumping take-off angle (Toro et al., 2004). Longer forelimbs may provide a greater range of body postures prior to take-off, but should not affect the resultant jump forces unless frogs tend to slide at lower jump angles. It is known that the ilio-sacral musculature is active during the take-off phase of a jump (Emerson and De Jongh, 1980) and may help transmit forces between hindlimbs and the axial skeleton (Shubin and Jenkins, 1995). This may allow alignment of the centre of mass of the frog in the direction of the jump propulsion (Emerson and De Jongh, 1980).

Conclusion

In summary, our results show no conflict between locomotion in different media (i.e. aquatic versus terrestrial) or between the different locomotion modes (i.e. exertion versus burst performance). Overall, our results suggest that individuals that perform well in the terrestrial environment also perform well in an aquatic environment. However, depending on the environment (aquatic or terrestrial), the morphological traits driving variation in locomotor performance differed. Whether these results can be generalized to other frogs or even other vertebrates remains to be tested. However, given the differences between our results and data for other semi-aquatic frogs (Nauwelaerts et al., 2007), this may not be the case.

Author contributions

Conceptualization: L.A., J.M., A.H.; Methodology: L.A.; Validation: L.A., J.M., A.H.; Formal analysis: L.A.; Investigation: L.A.; Resources: J.M., A.H., L.A.; Data curation: L.A.; Writing - original draft: L.A.; Writing - review & editing: L.A., J.M., A.H.; Visualization: L.A., A.H.; Supervision: J.M., A.H.; Project administration: J.M., A.H.; Funding acquisition: J.M., A.H.

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