

## Swimming and jumping in a semi-aquatic frog

SANDRA NAUWELAERTS<sup>1,\*</sup>, EIZE STAMHUIS<sup>2</sup>, PETER AERTS<sup>1</sup>

<sup>1</sup> *Department of Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Wilrijk (Antwerpen), Belgium*

<sup>2</sup> *Department of Marine Biology, University of Groningen, Biologisch centrum, Haren, The Netherlands*

**Abstract**—Locomotion has a clear ecological relevance for many animals. As animals need to move in order to escape from predators, find food, defend territories, etc., it is expected that locomotor performance might affect an individual's survival and reproduction. Clear links have also been found between an animal's performance and its morphology. A function analysis can unravel the underlying mechanistic facets of this link.

Frogs are interesting model species because they add an extra element to this topic; they have to perform in two entirely different physical environments, particularly semi-aquatic species. However, no trade-off was found between jumping and swimming performance. Morphological correlates were found but, to understand causations, a thorough understanding of the mechanics of locomotion is required.

When comparing the mechanics of jumping and swimming, the question arises of how to ensure a sound comparison. Ideally, some measure of 'effort' has to be added to the analysis. We suggest the use of the propulsive impulse. Unexpectedly, the impulse of swimming proved to be significantly smaller than the jumping impulses during locomotion in a semi-aquatic frog, *Rana esculenta*, even when maximal performance had been induced in both media.

To verify our impulse calculations, we analysed the external forces during both locomotor modes. The forces during terrestrial locomotion can be measured directly using a force plate; determining the forces in water requires a more complex set-up. For that reason, we performed a DPIV (Digital Particle Image Velocimetry) analysis on the flow generated by swimming frogs. These experiments confirmed the results of our impulse calculations.

**Keywords:** Anura; forces; kinematics; morphology; optimal design; *Rana esculenta*.

### INTRODUCTION

Locomotion is considered to be one of the major functions within the ecology of an animal because of its importance during activities such as feeding, social in-

---

\*Corresponding author; e-mail: [sandra.nauwelaerts@ua.ac.be](mailto:sandra.nauwelaerts@ua.ac.be)

teractions and predator avoidance (Brana, 2003). Many animals move through complex and heterogeneous physical environments at varying speeds and using different modes of locomotion (Nauwelaerts, 2002). Obviously, animals must modulate their locomotor behaviour to adjust for changes in the external environment, resulting in changes of direction, speed or posture (Irschick and Jayne, 1998; Biewener and Corning, 2001). The changes in locomotor behaviour are expected to be most extreme for species that move through different physical environments, such as water vs. land (Biewener and Gillis, 1999).

Water and air represent the fluid media in which organisms must survive and reproduce, and the many physical disparities (density, viscosity, gravitational load) between these environments can have important consequences for organismal design and function (Gillis and Blob, 2001). The medium defines the structural biomechanical requirements necessary for ecologically effective movement (Seebacher et al., 2003). Water is 800 times denser and 60 times more viscous than air, causing similar movements of the limbs to be more strenuous when they are performed in water. Primary forces that govern aquatic locomotion are drag and buoyancy. In contrast, during locomotion on land, the animal has to deal primarily with gravitational forces acting on the body (Williams et al., 2002; Nauwelaerts and Aerts, 2003), as air resistance is considered negligible for a jumping animal larger than a flea (Bennet-Clark, 1977).

Semi-aquatic animals represent a transition between terrestrial and aquatic lifestyles. This transition state requires biomechanical adaptations in order to make locomotion both on land and in water possible (Seebacher et al., 2003). Simultaneous optimisation of two tasks that require mutually incompatible morphologies or physiologies is impossible, because a trade-off will cause specialisation in one aspect to come at the expense of performance in other(s). In such cases, natural selection will result in some compromise, i.e., an intermediate phenotype that can perform both tasks reasonably, but never as optimally as a specialised phenotype. Because such trade-offs may be widespread, information on phenotypic traits under such conflicting selective forces may provide general insights into the nature of adaptive compromises (Shine et al., 2003).

Most anurans use their hind limbs to generate propulsive forces during both jumping and swimming. The same apparatus, the legs, is used to perform the same task, but in two different media. If the two media impose different requirements on the morphology of a frog, the morphology of a semi-aquatic frog, such as *Rana esculenta*, is expected to be intermediate between the ideal morphology of an aquatic frog and that of a terrestrial frog, on the condition that no other constraints, which may be unrelated to locomotion, are imposed on its morphology. The same argument can be made in relation to behavioural aspects of an animal's biology, such as kinematic patterns. A first clue to whether the different media impose differing requirements upon the evolution of frogs can be found in a consistent difference in morphology between species that live in different habitats. Emerson (1987) found that the locomotor mode of a frog could be predicted by plotting the

fore limb length against the hind limb length. On this plot, swimming species were significantly different from jumping species, but this was mainly due to a difference in fore limb length. At first glance, there is no functional reason why a greater fore limb length should be beneficial for the propulsive abilities of a jumping species, but it will certainly improve the landing capacity of an animal. However, a relevant functional difference was found in the structure of the pelvis of an animal. A sliding pelvis in an aquatic frog, *Xenopus laevis*, proved to be beneficial during swimming, because it increased the distance over which the legs could accelerate (Videler and Jorna, 1985), while a jumping animal experienced vertical rotation of the pelvis, thus aligning the pelvis with the vertebral column (O'Reilly et al., 2000). However, this is not a consistent difference between species that live in different environments, because the sliding pelvis is restricted to the family of Pipidae.

An additional reason to study frogs in the context of locomotion through different physical environments is their terrestrial origin. This origin causes the frogs' bauplan mainly to have adaptations for saltatorial locomotion (Wake, 1998). The interpretation of the evolution of anurans has been based for a long time on *Triadobatrachus* as the common ancestor, and these findings are confirmed by the discovery of an even older anuran, *Prosalirus bitis*. The absence of a tail in the adult stage of life is explained by the fact that a tail would cause frictional drag and interfere with the movement of the legs. The backbone is short and rigid due to a reduced number of vertebral elements. Together with the fused and elongated tibia and fibula, these are thought to be adaptations developed to withstand the stresses of leaping. The long segments, together with an extra segment in the foot, enable the frog to accelerate over a longer distance. All these morphological characteristics seem to indicate a strong influence of the historical background of these frogs on their current morphology. It is possible that this imposes a major constraint on the adaptation of the frog to a more aquatic lifestyle.

In this paper, the morphological characteristics that determine performance during locomotion in a semi-aquatic frog, *Rana esculenta*, are discussed. The study will: *i*) investigate whether optimisation of performance in one locomotor mode through morphological adaptations is automatically detrimental for the performance in the other locomotor mode; and *ii*) explore form-function relationships by using a correlative analysis of morphology and performance among individuals within the chosen species (see Morphology). Because correlations do not demonstrate causations, more information is needed about the biomechanics underlying both locomotor modes. A first step in obtaining such knowledge is *iii*) a thorough comparison of the kinematics of the hind limbs during swimming and jumping (see Kinematics), substantiated by *iv*) studying the external forces generated by the hind limbs during propulsion (see Forces).

### *Performance*

Maximal performance was measured for each individual during both swimming and jumping by invoking an escape response in water and on land. Jumping performance

was estimated by inducing maximal jumps on a force plate that measured the ground reaction forces during the push-off phase. The maximal ground reaction force was then taken as an unequivocal performance measure. On the other hand, maximal swimming performance was estimated as the fastest 25 cm interval, registered by photocells, realised by the individual animal swimming through a 2 m long tunnel. To ensure the maximal possible performance of each animal, the escape response was tested ten times and the maximal velocity and ground reaction force of these ten trials were used in the further analysis.

No correlation was found between individual performance measurements for both locomotor modes, with or without the effect of size. This means that the swimming performance of an individual has no predictive value for jumping performance and vice versa. We therefore found no direct evidence for a trade-off between jumping and swimming performance or for a coupled optimisation. This could be due to the importance of overall quality (Van Damme et al., 2002), as expressed by the fact that some frogs possess greater overall muscularity than others, irrespective of their body size. Another explanation can be found in the fact that some morphological characteristics have a positive effect on both locomotor modes and others do show a trade-off effect. The net effect of these characteristics could result in an overall absence of correlation between the two locomotor performances. Another suggestion for a lack of correlation between the two performance measurements is the difficulty in quantifying the motivation of an animal to perform a certain task. However, this is solved by repeating the measurements and by using an adequate sample size.

In conclusion, swimming and jumping in frogs seem to be two independently evolving behaviours. This is not a novel statement. Abourachid and Green (1999) came to the same conclusion using a completely different approach. They observed out-of-phase movements during swimming in a primitive frog and used this as evidence to support the idea of two separate evolutionary derivations of the two locomotor modes, under the assumption that this out-of-phase swimming was a unique behavioural characteristic of primitive frogs. However, we were able to show that more derived frogs use this gait pattern during swimming and during terrestrial locomotion, but only at slow speeds (Nauwelaerts and Aerts, 2002). The use of this gait pattern at low speeds was explained by a difference in energetic (mechanical) costs.

### *Morphology*

Morphological variation is believed to have fitness consequences through its effect on locomotor performance (Braná, 2003). Semi-aquatic animals are assumed to be under selection for effective locomotion in both media. Arnold (1983) provided a conceptual framework to study the adaptation process at the intraspecific level by splitting up this process into a performance gradient and a fitness gradient. We concentrated on the link between morphology and performance. Therefore, we looked at intraspecific variation in morphology and tried to link this to performance

variation. This correlative study showed that it is primarily size that determines jumping ability, but that swimming performance is mainly independent of size. The fact that jumping performance was influenced by body size is, however, a consequence of the choice of performance measure. Performance was expressed as the maximal ground reaction force that a frog can exert. Weight is a component of this force. Expressed in maximal velocity attained during push-off, the effect of size on jumping performance disappears. Hill (1950) provided a scaling model that predicted that maximum speed should be independent of body size in geometrically similar animals. His argument is based on physiological evidence that the intrinsic rate of shortening of muscles is faster in smaller animals. Within the size range studied, frog shape was found to be highly conservative and most morphological characteristics scaled isometrically with size, suggesting that Hill's predictions (1950) seem to hold true for locomotion of frogs.

Apart from size, no distinctive morphometric characteristics significantly enhanced locomotor ability. Data on the muscle masses reveal that it is beneficial in both locomotor modes to have a larger *m. iliacus externus*/*m. iliofemoralis*, both hip flexors. During jumping, there is an additional positive effect of a larger *m. gracilis major*, a hip extensor, but this actually amounts to a size effect.

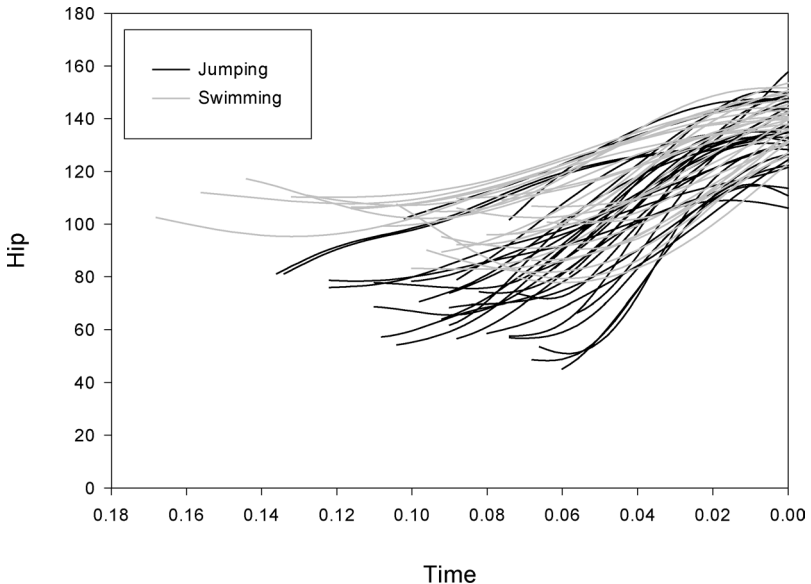
### Kinematics

During both locomotor modes, a forceful extension of the legs results in an acceleration of the centre of mass. Since this is essentially the same task, the kinematics of the leg segments are expected to be identical. When comparing the kinematics of jumping and swimming, the addition of a suitable covariable, a measure of the effort it takes to realise the examined kinematics, became necessary. From terrestrial studies, it is known that velocity has a major effect on the movement patterns of an animal. Since movements are comparatively more strenuous when performed in water, overall locomotor speed is not a reliable covariable when comparing movements in air and water. Instead, we used a derived covariable, impulse, that not only accounts for differences in velocity but also considers the balance of external forces throughout the entire propulsion phase (Nauwelaerts and Aerts, 2003). The remarkable result was that although a full behavioural range was attained for both locomotor modes, the impulse ranges of swimming and jumping did not fully overlap. The impulses reached during jumping were significantly larger. We have four hypotheses that can explain the differences in impulse. For the swimming impulses, we used a mathematical approximation of the impulse based on the path of the centre of mass (CM) through time according the following formula:

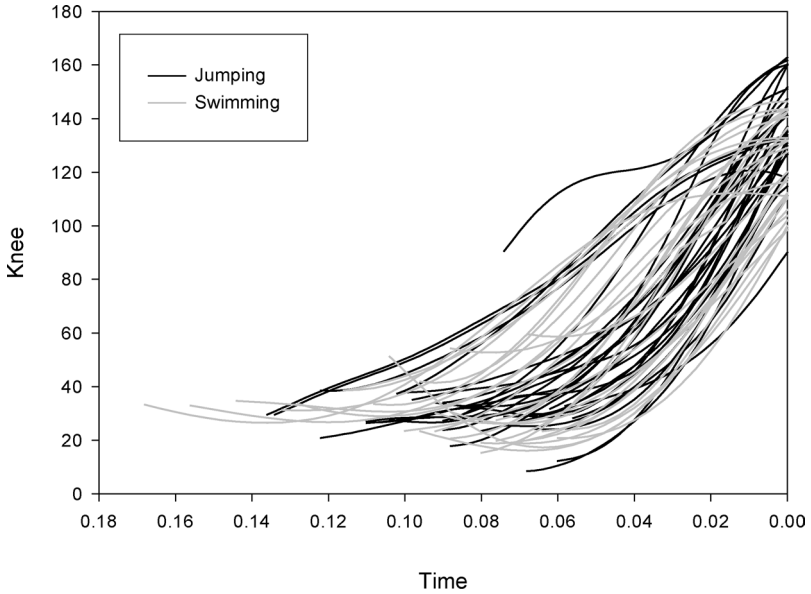
$$\int_{t_1}^{t_2} F_{\text{prop}} dt = m * (1 + \text{AMC}) * (v_{\text{max}} - v_{\text{min}}) + \frac{1}{2} C_d * \rho * A * \frac{v_{\text{min}}^2 + v_{\text{max}}^2}{2} * \Delta t$$

with  $C_d$  = drag coefficient = 0.14;  $\rho$  = density medium = 1000 kg/m<sup>3</sup>;  $A$  = area = snout-vent length<sup>2</sup>;  $(v_{\min}^2 + v_{\max}^2)/2$  = average squared velocity;  $\Delta t$  = duration of propulsion;  $AMC$  = added-mass coefficient = 0.2; and  $v_{\min}$  and  $v_{\max}$ , respectively, maximal and minimal velocity. It is possible that we underestimated the impulse by underestimating either the drag coefficient or the added-mass coefficient in these equations. In the impulse calculations, we only considered movements in the direction of movement. If lateral forces are larger during swimming, it is possible that the resultant force delivered by the hind limb muscles is similar in size in the two locomotor modes, and the difference in impulse that we found originates from a lower mechanical efficiency during swimming rather than a difference in muscle output. A third explanation was postulated as a difference in coordination between the two locomotor modes, while a final hypothesis was formulated as a reduced force transmission due to a lower external load (Nauwelaerts and Aerts, 2003).

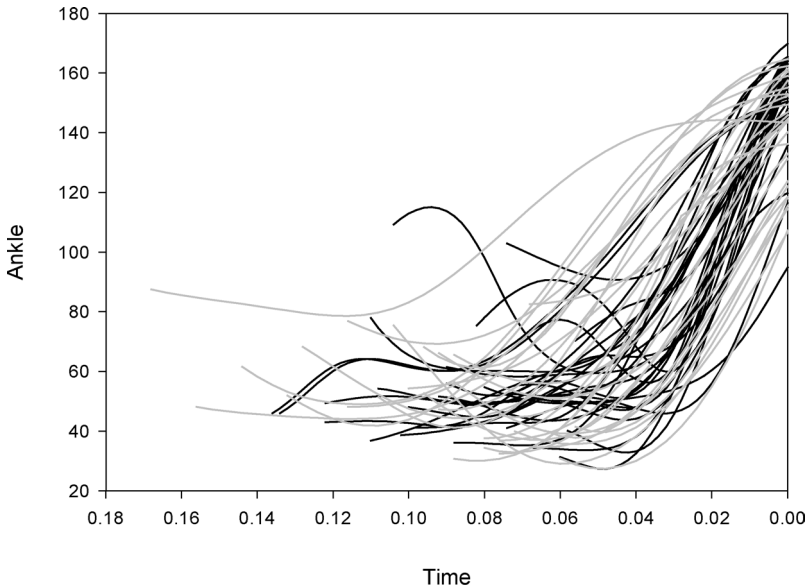
The comparison of the joint angle profiles of the hip, knee and ankle between swimming and jumping was restricted to the propulsive phase and yielded a difference in hip joint angle at the start of propulsion (see figs. 1-3). The 3D hip angle, defined as the 3D angle between the midsagittal axis of the trunk and the length axis of the upper leg, was smaller, and thus more flexed, at the start of propulsion during jumping than during swimming (Nauwelaerts and Aerts, 2003). This is probably a passive effect of the weight of the body on the hind limbs at initial posture during terrestrial locomotion. Other differences in kinematic profiles were small.



**Figure 1.** 3D hip angle profile for both swimming and jumping. Each sequence is a line, blue for swimming, and red for jumping. Data are restricted to the period during which the snout tip accelerates. Zero on the time scale is the end of propulsion.



**Figure 2.** 3D knee angle profile for both swimming and jumping. Each sequence is a line, blue for swimming and red for jumping. Data are restricted to the period during which the snout tip accelerates. Zero on the time scale is the end of propulsion.



**Figure 3.** 3D ankle angle profile for both swimming and jumping. Each sequence is a line, blue for swimming, and red for jumping. Data are restricted to the period during which the snout tip accelerates. Zero on the time scale is the end of propulsion.

The kinematic study also revealed a difference in coordination pattern between jumping and swimming. Coordination patterns are hereby defined as the sequence of joint motions, which can be easily deduced from the first derivatives of the angle profiles. During aquatic locomotion, all joints extend simultaneously, while on land the joints are extended in a proximo-distal sequence; first hip, then knee and ankle. We will discuss this observation more thoroughly in the following section.

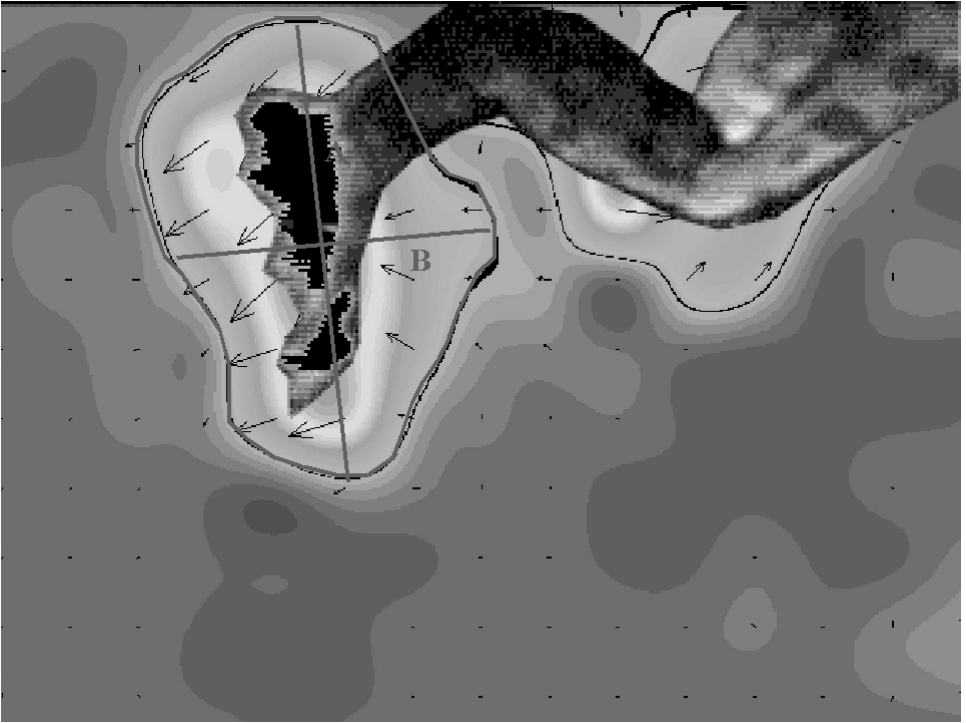
### *Forces*

The first two hypotheses that were formulated in order to explain the difference in impulse between jumping and swimming (see Performance), could be tested by targeting the external forces on the hind feet during swimming and jumping. In a terrestrial environment, the external forces consist of the gravitational forces and the ground reaction forces. The forces of gravity act downwards through the centres of mass of each segment and are equal to the magnitude of the mass times acceleration due to gravity ( $-9.8 \text{ m/s}^2$ ). The ground reaction forces can be measured directly with a force plate.

Determining the external forces in an aquatic system is far more complex and requires a special set-up. In order to propel itself, a frog must interact with the surrounding water. The physical properties of the water, the laws of fluid mechanics and the swimming movements of the frog determine this interaction. The amount of thrust generated by the frog depends on the rate and the direction in which it changes the momentum of the surrounding water. One method of estimating the external forces is to study the flow induced by the animal's movements (Muller, 1997).

We used a DPIV set-up to quantify the external forces on the hind feet during swimming. Using an impulse-momentum approach, we obtained force profiles through time (Nauwelaerts et al., in press). With this approach we estimated, by tracing an iso-velocity line that marked the boundary between affected and unaffected water using Optimas 6.51 (Media Cybernetics, L.P., Silver Spring, MD, USA) (fig. 4), at any instant during the kick, the volume of water affected by the movements of the feet through the water. Since the velocity of the centroid of this water volume could also be measured, we obtained the change in momentum through time. Force is then calculated as the difference in momentum during a chosen time interval, the impulse, divided by the duration of this time interval. We could compare the profiles we obtained in this manner with the profiles resulted from the CM (the impulse method of the kinematics study, see Kinematics), and with the force profiles of jumping. The first comparison yielded an overestimation of about 15% of the forces calculated using the CM method, probably due to an overestimation of the drag coefficient. This means that the difference in overall impulse between jumping and swimming is even larger than previously stated. The force profiles for jumping and swimming differ in the maximal force and in the shape of the profiles. The average maximal force for jumping is  $0.38 \text{ N}$  ( $\pm 0.09 \text{ N}$ , variance = 0.008) and is significantly larger than that measured for swimming





**Figure 4.** A magnitude plot resulting from a DPIV analysis on a sequence of a swimming frog, showing the velocity distribution of the water surrounding the frog's foot. The picture of the frog was cut from the original recordings and pasted onto the magnitude plot. An iso-velocity line was traced to show how the area of the affected water volume was determined. A and B are the major and minor axis of an ellipse that was used to model the volume. A and B were determined on recordings using a horizontal sheet, while B and C were obtained from experiments using a vertical sheet. Combining the data resulted in the calculation of the change in water mass. The movements of the centroid of the area were used as measures for the kinematic patterns shown by this water mass.

( $0.26 \text{ N} \pm 0.12 \text{ N}$ , variance = 0.015) when tested with a t-test assuming unequal variances ( $p_1\text{-tail} = 0.028$ ;  $p_2\text{-tail} = 0.055$ ), and this maximum is reached later in the kicking phase. This postponement of the peak force results in a larger area under the force-time curve, which is the impulse. This means that the difference in impulse between jumping and swimming is real and is mainly a consequence of a difference in timing.

The propulsive forces are only delivered by the kicking legs during the first 70% of the extension phase (Nauwelaerts et al., in press). Surprisingly, however, thrust is already being produced, even before the start of the extension phase. During the recovery phase, the phase during which the legs are retracted behind the body, some adherent water is dragged along in the direction of motion. This water mass is being slowed down by the feet when their webbings are spread and placed perpendicular to this flow. The velocity of the mass is eventually even reversed when the feet start

moving backwards. This slowing down of flow moving towards the frog provides extra propulsion before the legs start to extend (Stamhuis and Nauwelaerts, in press).

The lateral forces on the feet are small during jumping compared to the other force components and neutralise each other, especially when the jump is symmetric. During swimming, the volume of water moves only slightly in the direction perpendicular to the direction of motion: the magnitude of the lateral force is about 20% of the size of the thrust force. This is confirmed by the fact that the vortices travel away from the feet at an angle of  $11^\circ$  to the direction of motion. The lateral forces, therefore, cannot explain a difference in impulse simply by a difference in propulsive efficiency.

The difference in shape of the force profiles of swimming and jumping may result from a difference in coordination. When we look at the first derivatives of the joint angles through time, we can conclude that the timing of the joint extension does differ (Nauwelaerts and Aerts, 2003). When swimming, all joints are extended synchronously, causing the maximal force to be reached early in the extension phase. In contrast, during jumping a proximo-distal sequence in joint extension causes the timing of the maximal force peak to be late in the extension phase, as close as possible to take-off. This can be explained in terms of optimal coordination strategy. Maximal velocities of the centre of mass can be reached when all joints extend simultaneously (Van Ingen Schenau, 1989). This, however, results in a disadvantageous timing of the velocity peak; maximal velocity is reached before full extension of the legs and before take-off. A proximo-distal sequence of joint extension ensures full extension and maximal velocity as close to take-off velocity as possible (Alexander, 1989). The drawback of this proximo-distal sequence is that the maximal velocity will be smaller. During swimming, the timing of maximal velocity is not important because extension can be executed in all possible circumstances. An early hip extension, as in a proximo-distal sequence, would, however, result in a kick upwards instead of backwards and, by simultaneously extending all joints, a higher maximal velocity can be reached.

In conclusion, *Rana esculenta*, a semi-aquatic frog, succeeds in combining aquatic and terrestrial locomotion as expected. No evidence could be found for the existence of a trade-off or a coupling of the two locomotor modes. When performance is expressed as a measure of velocity, the performance and morphology of this frog follow Hill's predictions within the adult size range. However, a difference between jumping and swimming was found when the impulse realised during the kick was taken as a measure of 'effort'. This difference could be traced back to a difference in force profile, which in turn was due to a difference in coordination. The fact that no proof of a trade-off is found and yet the impulses during jumping are much greater, suggests that the adaptation process in this semi-aquatic species is slowed down by an historical constraint, having descended from terrestrial ancestors.

The question as to why there is an impulse difference in swimming and jumping remains unresolved. A major difference between the two locomotor modes is a difference in external load (Nauwelaerts and Aerts, 2003). It is possible that

the differences in kinematics (range of motion and timing) are a consequence of this difference in external load, together with a decreased force transmission during swimming. In concordance with this decreased force transmission, a higher extension velocity is expected during swimming because of the inverse relationship between force and velocity of the muscle, yet a drastic difference in extension velocity does not occur (Nauwelaerts and Aerts, 2003). It is also unlikely that the frog is swimming at its extension velocity limit, because this velocity is slightly higher during jumping. One possibility is a deliberate change in control between jumping and swimming. This is indirectly confirmed by EMG experiments on *Bufo marinus*, where the EMG burst duration of m. cruralis, a knee extensor, was halved during swimming (Gillis and Biewener, 2000), and on *Rana pipiens* where the hip and knee extensors were activated relatively longer in hopping and the ankle extensor relatively longer in swimming (Kamel et al., 1996). This change in control could be due to the fact that maximised contraction, which is effective during jumping, would cause less coordinated, ineffective movements during swimming. A different explanation can be found in a power amplification mechanism acting only during jumping. The existence of such a mechanism has been speculated before (Marsh and John-Alder, 1994; Peplowski and Marsh, 1997; Navas et al., 1999; Roberts and Marsh, 2003), because in several studies the power requirements for jumping exceeded the power available from the hind limb muscles. These supra-maximal powers would result from the rapid release of strain energy from elastic elements (Marsh, 1994). Since we only looked at the phase during which the centre of mass accelerates, we do not have any knowledge on what happens before propulsion. It is possible that, during jumping, elastic energy is stored in the muscle-tendon systems and ligaments of the hind limbs and released during propulsion, thereby enhancing the impulse. Since swimming is a cyclic event, this is much more unlikely.

## ACKNOWLEDGEMENTS

The authors would like to thank Joe Carragher for his comments on an earlier version of the manuscript. This work was supported by an IWT grant and an ISB travel grant to Sandra Nauwelaerts, and a GOA-BOF grant to Peter Aerts.

## REFERENCES

- Abourachid, A. & Green, D.M. (1999) Origins of the frog-kick? Alternate-leg swimming in primitive frogs, families Leiopelmatidae and Ascaphidae. *J. Herpetol.*, 33, 657-663.
- Alexander, R. McN. (1989) Sequential joint extension in jumping (Reaction to G.J. van Ingen Schenau, 1989). *Hum. Mov. Sci.*, 8, 339-345.
- Arnold, S.J. (1983) Morphology, performance and fitness. *Am. Zool.*, 23, 347-361.
- Bennet-Clark, H.C. (1977) Scale effects on jumping animals. In: T.J. Pedley (Ed.), *Scale Effects in Animal Locomotion*, pp. 185-201. Academic Press (London) Ltd, UK.

- Brana, F. (2003) Morphological correlates of burst speed and field movement patterns: the behavioural adjustment of locomotion in wall lizards (*Podarcis muralis*). *Biol. J. Linn. Soc.*, 80, 135-146.
- Biewener, A.A. & Corning, W.R. (2001) Dynamics of mallard (*Anas platyrhynchos*) gastrocnemius function during swimming versus terrestrial locomotion. *J. Exp. Biol.*, 204, 1745-1756.
- Biewener, A.A. & Gillis, G.B. (1999) Dynamics of muscle function during locomotion: accommodating variable conditions. *J. Exp. Biol.*, 202, 3387-3396.
- Emerson (1978) Allometry and jumping in frogs: helping the twain to meet. *Evolution*, 32, 551-564.
- Gillis, G.B. & Biewener, A.A. (2000) Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). *J. Exp. Biol.*, 203, 3547-3563.
- Gillis, G.B. & Blob, R.W. (2001) How muscles accommodate movement in different physical environments: aquatic vs. terrestrial locomotion in vertebrates. *Comp. Bioch. Phys. A*, 131, 61-75.
- Hill, A.V. (1950) The dimensions of animals and their muscular dynamics. *Sci. Prog.*, 38, 209-230.
- Irschick, D.J. & Jayne, B.C. (1998) Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Biol.*, 201, 273-287.
- Kamel, L.T., Peters, S.E. & Bashor, D.P. (1996) Hopping and swimming in the leopard frog, *Rana pipiens*. 2. A comparison of muscle activities. *J. Morphol.*, 203, 17-31.
- Nauwelaerts, S. & Aerts, P. (2002) Two distinct gait types in swimming frogs. *J. Zool.*, 258, 183-188.
- Nauwelaerts, S. & Aerts, P. (2003) Propulsive impulse as a covarying performance measure in the comparison of the kinematics of jumping and swimming in frogs. *J. Exp. Biol.*, 206, 4341-4251.
- Nauwelaerts, S., Stamhuis, E.J. & Aerts, P. (in press) Propulsive forces in swimming frogs. I. A momentum impulse approach. *J. Exp. Biol.*
- Marsh, R.L. (1994) Jumping ability of anuran amphibians. In: J.H. Jones (Ed.), *Advances in Veterinary Science and Comparative Medicine*, vol. 38B, pp. 51-111. New York, USA, Academic Press.
- Marsh, R.L. & John-Alder, J.B. (1994) Jumping performance of hyloid frogs measured with high-speed cine film. *J. Exp. Biol.*, 188, 131-141.
- Muller, U.K., van den Heuvel, B.L.E., Stamhuis, E.J. & Videler, J.J. (1997) Fish foot prints: morphology and energetics of the wake behind a continuously swimming mullet (*Chelon labrosus risso*). *J. Exp. Biol.*, 200, 2893-2906.
- Navas, C.A., James, R.S., Wakeling, J.M., Kemp, K.M. & Johnston, I.A. (1999) An integrative study of the temperature dependence of whole animal and muscle performance during jumping and swimming in the frog *Rana temporaria*. *J. Comp. Physiol. B*, 169, 588-596.
- O'Reilly, J.C., Summers, A.P. & Ritter, D.A. (2000) The evolution of the functional role of trunk muscles during locomotion in adult amphibians. *Am. Zool.*, 40, 123-135.
- Peplowski, M.M. & Marsh, R.L. (1997) Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.*, 200, 2861-2870.
- Pilarski, J.Q., Nishikawa, K.C. & Pierotti, D.J. (2003) Power amplification by pre-activation of hind limb muscles in *Rana pipiens* and *Osteopilus septentrionalis*. *FASEB*, 17, A1287.
- Pierotti, D.J., Nishikawa, K.C., Lappin, K. & Pilarski, J.Q. (2003) Power amplification during the fast phase of frog semimembranosus muscle shortening is load dependent. *FASEB*, 17, A1287.
- Roberts, T.J. & Marsh, R.L. (2003) Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.*, 206, 2567-2580.
- Seebacher, F., Elsworth, P.G. & Franklin, C.E. (2003) Ontogenetic changes of swimming kinematics in a semi-aquatic reptile (*Crocodylus porosus*). *Aust. J. Zool.*, 51, 15-24.
- Shine, R., Cogger, H.G., Reed, R.R., Shetty, S. & Bonnet, X. (2003) Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). *J. Zool.*, 259, 261-268.
- Stamhuis, E.J. & Nauwelaerts, S. (in press) Propulsive forces in swimming frogs. II. A vortex ring approach. *J. Exp. Biol.*

- Van Damme, R., Wilson, R.S., Vanhooydonck, B. & Aerts, P. (2002) Evolutionary biology — Performance constraints in decathletes. *Nature*, 415, 755-756.
- van Ingen Schenau, G.J. (1989) From rotation to translation: Constraints on multi-joint movements and the unique action of bi-articular muscles. *Hum. Mov. Sci.*, 8, 301-337.
- Videler, J.J. & Jorna, J.T. (1985) Functions of the sliding pelvis in *Xenopus laevis*. *Copeia*, 1, 254-257.
- Wake, M.H. (1998) Amphibian locomotion in evolutionary time. *Zoology*, 100, 141-151.
- Williams, T.M., Ben-David, M., Noren, S., Rutishauser, M., McDonald, K. & Heyward, W. (2002) Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? *Comp. Biochem. Phys., A*, 133, 203-212.