

A functional analysis of how frogs jump out of water

SANDRA NAUWELAERTS*, JAN SCHOLLIERS and PETER AERTS

Department of Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Wilrijk (Antwerpen), Belgium

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Euphlyctis cyanophlyctis and *E. hexadactylus* are two common frog species from south-east Asia. Both species have the remarkable ability to leap from a floating position out of the water. *Rana esculenta* is a European species from the same family that barely manages to do so. The species' morphology, however, looks roughly the same. We studied the unique abilities of the *Euphlyctis* species by videotaping the three species mentioned above whilst they jumped out of the water. These recordings enabled us to study the hind leg movements and to test several hypotheses. Differences between the species only became apparent when details of the behaviour were analysed. The three species mainly differed in their slip factor at the start of the propulsive phase, resulting in a difference in slip distance. This difference could be traced back to the difference in web shape by means of a physical model. The *Euphlyctis* species can prevent their feet from slipping because of their rounded and convex webbing, resulting in a larger take-off velocity and thereby a successful emergence out of the water. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 83, 413–420.

ADDITIONAL KEYWORDS: Anura – locomotion – movement analysis – physical model.

INTRODUCTION

Euphlyctis cyanophlyctis and *Euphlyctis hexadactylus* are two aquatic frog species commonly seen in south-east Asia that are well known for their unusual ability to skitter across the water (Gans, 1976). Equally remarkable is the ability of the *Euphlyctis* species to jump, starting from a floating position at the water surface, up to 50 cm high (Fig. 1). Holding a flying insect above the water surface can easily trigger this behaviour. Jumping out of the water in this way was described by Altevogt, Holtmann & Kaschek (1986), but that study focused on the ecology of prey catching, rather than on the mechanism(s) of how *Euphlyctis* emerge from the water.

Rana esculenta is a common, semi-aquatic frog species in Europe with a very similar general body morphology compared to the *Euphlyctis* species. The three species belong to the same family, the Ranidae. However, individuals of *R. esculenta* are not capable of

jumping out of water. When presented with a flying insect above the water surface, individuals only succeed in emerging from the water up to a height of 7 cm (see below), despite making attempts when presented with a flying insect at various heights above the water.

The reason(s) why *Euphlyctis* can and *Rana* species cannot jump out of water are not known. As the performance of the species differs so drastically, in terms of the height they gain after take-off, they must use differing techniques in order to reach their take-off velocity. Once the frog has emerged from the water, the effects of friction and air resistance are limited, and the only significant force is gravity. We can therefore assume that kinetic energy [i.e. the energy a body possesses by virtue of its motion ($\frac{1}{2} \times m \times v^2$)] will change into potential energy [i.e. the energy a body possesses by virtue of its position ($m \times g \times h$)] in such a way that the total mechanical energy remains constant. This means that the height of the jump only depends on velocity. The frog must therefore maximize its take-off velocity in order to gain more height. This

*Corresponding author: E-mail: sandran@uia.ua.ac.be

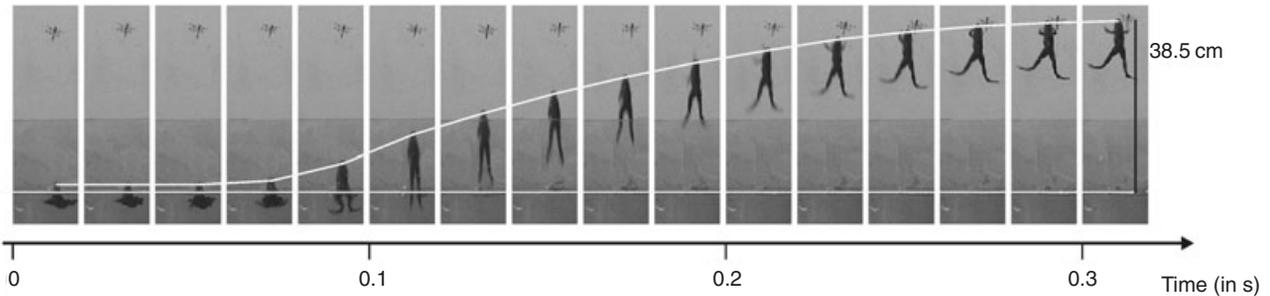


Figure 1. A typical 'performance' sequence of *Euphlyctis hexadactylus*, recorded at 50 Hz, in which the remarkable capacity of this species to jump out of the water is shown. The water surface is indicated with a horizontal white line.

can be achieved by attaining greater acceleration during the propulsive phase (either by shortening their propulsion time over a similar distance or by lengthening the extension distance for a similar time) or by maintaining the same acceleration over a longer period of time. Both means of maximizing take-off velocity are conditional upon the drag on the feet being sufficiently high, so as to minimize backwards slipping of the feet. Because the kick is most probably a drag-based system, performance will also have a direct correlation with the level of drag on the feet. Drag, in turn, is a function of area, velocity and a drag coefficient (Vogel, 1994). The dramatic difference in height between the three species can therefore be explained in four different ways, none of which are mutually exclusive:

1. the *morphometrics* of the segment lengths are disparate. If the same angle kinematics are used to rotate longer segments of the hind legs, then the legs extend faster and this will result in a higher maximal velocity of the centre of gravity. However, if the mass distribution remains approximately the same, the rotation of longer segments will require higher torques (or higher forces) because of their larger moments of inertia
2. *Rana* differs from *Euphlyctis* in the manner in which the legs are extended, i.e. the kinematics. Either the amplitude differs, or a temporal aspect of the kinematics is involved in the different kinematics
3. the species differ in the area of their webbed feet. The more drag that can be realized between the web and the water, the more propulsion force can be generated and backwards slipping of the feet will be minimized
4. a difference in the shape of the webs can also influence the drag, by changing the drag coefficient of the web.

We investigated the aforementioned hypotheses by comparing the three species in all of these aspects of their complex locomotory behaviour.

MATERIAL AND METHODS

ANIMALS

Ten individuals of *Euphlyctis hexadactylus* were collected in Wakwella and 20 individuals of *Euphlyctis cyanophlyctis* in Magedara, both in the Galle district of Sri Lanka, during October 2001. Animals were transported to the University of Matara's Department of Zoology, where the experiments were performed. Frogs were held in 10-L plastic aquaria (three specimens to each aquarium) with access to aged tap water and were fed live dragonflies. Four individuals of each species who were willing to jump at dragonflies while illuminated with two strong lights (150 W) were selected for filming.

Four individuals of *Rana esculenta* were captured in Kalmthout, Belgium, and brought into the lab at the University of Antwerp, Belgium. Animals were kept in similar conditions to the *Euphlyctis* species.

EXPERIMENTS

The selected individuals of the three species were put in an aquarium, of which the water level was adjusted to the individual's size, to prevent them touching the bottom of the aquarium during take-off. In a first series of experiments, a Sony handycam was used to videotape the performance of the jumping frogs. Maximal height of the snout tip was thereby taken as a performance measure (Fig. 1). In a second series of experiments, detailed video recordings were made to examine the kinematics involved in the jumping behaviour. In this case, a mirror was placed beneath the aquarium at an angle of approximately 45°. A JVC GR-DVL 9800 camera was placed at a distance of approximately 2 m, level with the bottom of the tank. This setup enabled us to videotape both the lateral/frontal and ventral views simultaneously. The jumping behaviour was triggered by holding a live dragonfly or cricket on a string above the water surface.

MEASUREMENTS

The segment lengths of trunk, upper leg, lower leg, mid foot and longest toe of each individual were measured to the nearest mm using Mitutoyo CD-15DC calipers [Mitutoyo (UK) Ltd, Telford, UK].

For the second series of recordings, the snout tip, shoulder, hand, cloaca, hip, knee, ankle, mid foot and the five toe tips of 43 sequences were digitized using the Kwon 3D 3.0 analysing system (Visol Inc., Seoul, Korea). Five sequences for each of the four frogs were selected for *R. esculenta*. Only one frog of *E. cyanophlyctis* was large enough to obtain good 3D sequences, of which we used five sequences. Four individuals of *E. hexadactylus* were selected because of their eagerness to cooperate in the experiments and we used either four or five sequences from each individual. The coordinates were filtered using a fourth order Butterworth filter with a cut-off frequency of 10 Hz (Winter, 1990). The trunk, hip, knee, ankle and foot angles were calculated and derived once to obtain the angular velocities.

From the digitized data, four distances were calculated (Fig. 2):

A. the potential functional propulsion distance, defined as the difference between the maximal and

minimal distance between the z-coordinates of the cloaca and the ankle

B. the extended leg distance, defined as the maximal 3D distance between the cloaca and the ankle

C. the distance between the two ankles at the end of the propulsion phase, defined as twice the horizontal distance between ankle and cloaca. If this distance is large, a part of the propulsive potential is lost in lateral movement

D. the functional propulsion distance, defined as distance A minus the distance travelled by the cloaca during the propulsion phase. This distance is a measure of slip.

To obtain information on a possible difference in pelvic function, we measured the relative length change of the trunk during propulsion. Movement of the pelvic girdle has been shown to be of importance in amphibian locomotion (Whiting, 1961; Emerson, 1979; Videler & Jorna, 1985).

Another way of measuring slip is by calculating the slip factor, which is obtained by dividing the vertical velocity of the snout by the vertical velocity of the ankle (by analogy with Webb, 1975). If the slip factor is one, the ankle does not move, hence there is no slip. If the slip factor is zero, the ankles move downwards, but this

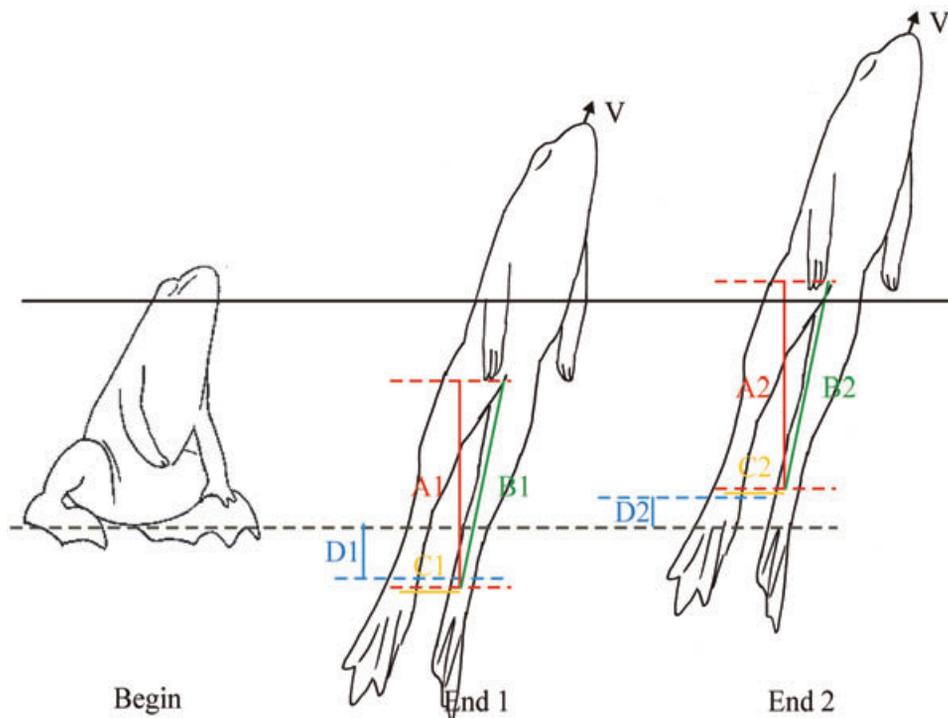


Figure 2. This figure illustrates how the different propulsive distances were measured. At the beginning of the propulsion, the ankles are held at a certain height. At the end of the propulsion phase, several distances can be measured: the potential functional propulsion A, the 3D length of the extended leg B, the distance between the legs C and the functional propulsion distance D. The second case (End 2: a drawing from a real sequence) shows how the distance D can become negative if the ankles end up higher at the end of the propulsion phase, compared to the height at the start.

does not result in a displacement of the snout, so slip is maximal.

Functional web areas were measured on the ventral views of the recordings, and real maximal web areas were measured on photographs of the feet. Both sets of measurements were taken using the Optimas 6.5 system.

To investigate whether web kinematics could explain the difference in performance, the expansion of the web was calculated by summing the 3D distances between the five toes. All distances in time were expressed as fractions of the maximal 3D distance.

PHYSICAL MODEL

Physical models are useful tools in biomechanical research (Koehl, 2002) and can provide insights when flow patterns are complex and unpredictable. To investigate whether differences in web shape could explain the difference in performance of the three frog species, a special setup was built. Physical models of the webs were constructed out of orthoplast splints (Johnson & Johnson), based on the six times enlarged ventral images of the webs of the jumping frogs (the projection areas). Care was taken to ensure that the three different models (*Euphlyctis* flat vs. *Rana* vs. *Euphlyctis* camber) had equal surface areas. Due to the thermal properties of the orthoplast, heating them slightly allowed the models to be moulded into a 3D cambered shape. A screw was fastened in the centre of each web, and connected via a 125-g aluminium rod to a cable-extension position transducer (CELESCO, type PT1DC-30-up-z10-MC4-5G), enabling direct measurements of displacements. The physical models were submerged 3 cm under the water surface and then released. Gravitational force, serving as a constant input force, was the same for all models. Differences in the sinking distance, i.e. the displacement during the first 250 ms, were taken as a measure for differences in drag of the three models during the acceleration phase. After a certain displacement a constant, terminal velocity was reached, and this velocity was taken as a measure for drag in steady state conditions. During these experiments, care was taken to keep Reynolds numbers of the simulations in the same order of magnitude as the real jump data by holding the velocities approximately six times reduced.

STATISTICAL ANALYSIS

Morphometrics of the three species, the relative trunk lengthening and the functional web area were compared by performing a MANOVA in STATISTICA for Windows v. 5.1.

To compare the kinematics of leg extension and the slip factor profiles, a linear mixed model (ANCOVA) was built in SAS for Windows v. 10.0, using the velocity of the snout at the end of the propulsion phase as a covariate. This model compared the profiles after adjustments (1) for individual differences, and (2) for correlations within a sequence (a first order autoregressive covariance-structure). A general Satterthwaite method was used for correcting the degrees of freedom (Littell *et al.*, 1996). A similar model was used to test whether web kinematics differed between the three species.

The terminal velocity and the displacement during the first 250 ms of the physical models were compared by performing a MANOVA in STATISTICA for Windows v. 5.1.

RESULTS

The height measurements taken from the first series of experiments showed that the *Euphlyctis* species jumped maximally 50 cm out of the water, while *Rana* never succeeded in catching a cricket that was held higher than 7 cm above the water surface.

The maximal performances obtained in our high-speed sequences matched the expected values based upon the law of conservation of mechanical energy (see Introduction) reasonably well: *R. esculenta* attained a maximal velocity between 0.3 and 2.1 m s⁻¹ (expected maximum 1.17 m s⁻¹), while the *Euphlyctis* species had a maximal velocity of 2.9 m s⁻¹ (expected maximum: 3.1 m s⁻¹).

A typical sequence consists of a retractive and a propulsive phase (Fig. 3). In the retractive phase, the legs are flexed under the body. If the body lies horizontal at the start of this phase, the flexion of the legs coincides with the tilting of the body. While flexing the legs, the webs are closed and curled inwards. At the start of the propulsive phase, the toes are spread, resulting in a flat surface (*R. esculenta*) or a camber (*Euphlyctis*). Due to this convexity, the physical web areas probably differ slightly, but in terms of drag, it is the projection of this area on the plane perpendicular to the motion that is of importance. Furthermore, the webs are held horizontally during the propulsion phase until just before the full extension of the legs, at which point the toes are closed quickly and the feet are extended. During the first part of the flight, the legs and feet are kept extended in order to facilitate emergence from the water.

The morphometrics of the three species did not differ (Table 1), except for the length of the foot if we compare the species two by two: *R. esculenta* had longer feet than *E. hexadactylus* ($P = 0.03$). The functional web areas, i.e. the projection areas on the plane perpendicular to the direction of motion, also did not dif-

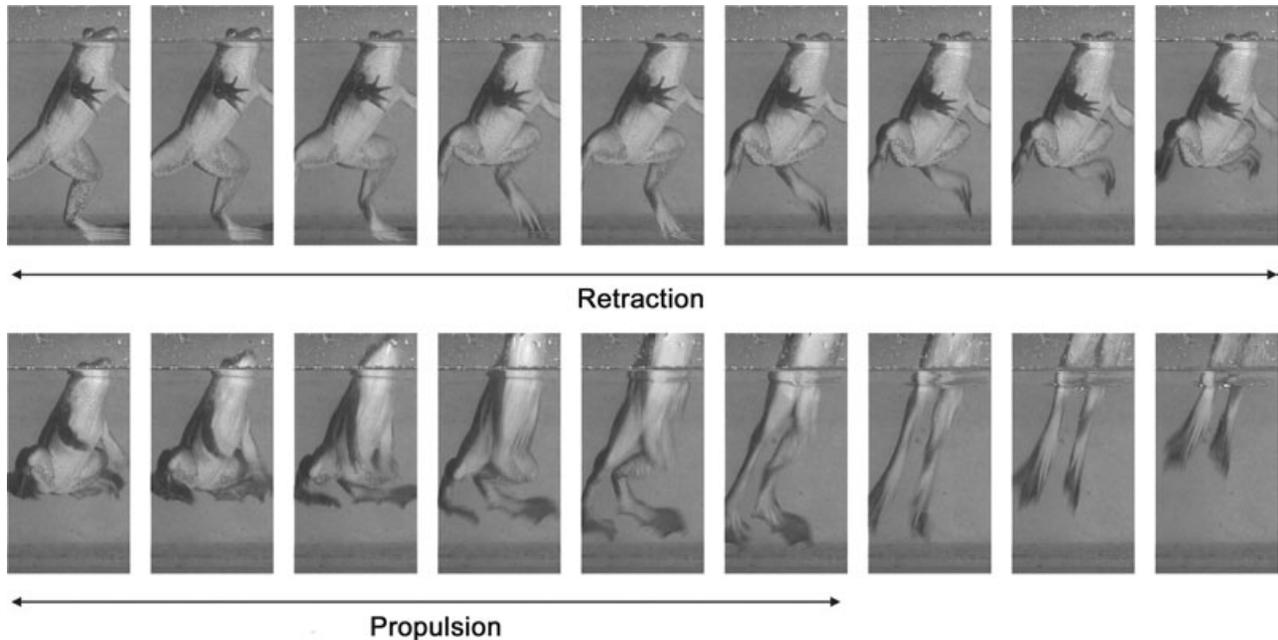


Figure 3. A typical 'kinematics' sequence, a lateral view on the leg extension kinematics of an individual of *Euphlyctis cyanophlyctis*, recorded at 100 Hz, in which the two major phases of the jumping sequence are shown.

fer. Web areas, measured directly on the feet, differed ($P = 0.045$) and were slightly larger for *Euphlyctis* if we took the difference in size into account.

The angle kinematics of the extension of the legs did not differ significantly, except for the maximal velocity of the hip ($P = 0.012$, Table 1).

Slip did not differ significantly between *E. hexadactylus* and *R. esculenta*, if it was expressed as the slip factor at the moment of the highest downward velocity of the ankle, but differed significantly when expressed as a distance (distance D, $P < 0.01$) and when the slip factor profiles were compared ($P = 0.014$, Fig. 4). The slip distance was larger for *R. esculenta* and the slip factor profiles differed due to more slip (smaller slip factor) at the beginning of the propulsion for *R. esculenta*. *E. cyanophlyctis* did not differ from *R. esculenta*, but their performance ranges did not overlap and performance was significantly higher for *E. cyanophlyctis*, meaning that they had similar slip at different velocities. The other distances, the potential functional propulsion distance A, the 3D length of the extended leg B and the distance between the legs at the end of propulsion C did not differ between the three species.

The web kinematics, expressed as the change in 3D distance between the toes in time, differed between the three species, both linearly ($P < 0.01$) and parabolically ($P < 0.01$) (Fig. 4). *E. hexadactylus* differed from *E. cyanophlyctis*, which had similar web kinematics to *R. esculenta*, but this resulted in better per-

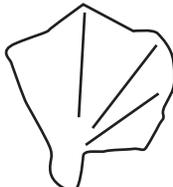
formance in the *E. cyanophlyctis*. Contrary to expectations, *R. esculenta* succeeded in spreading its toes faster and holding the maximal surface area for longer.

The influence of web shape, as measured by the physical model, was small but significant in both measures, the terminal velocity and the displacement during the first 250 ms. The distance travelled during the first 250 ms was 38.7 mm for the *Rana* model, and 33.0 mm for the *Euphlyctis* flat model. The two *Euphlyctis* models did not differ (*Euphlyctis* cambered, on average, travelled 31.6 mm). However, terminal velocities differed only slightly between the two flat models (0.263 m s^{-1} for *Rana* and 0.256 m s^{-1} for *Euphlyctis*), but camber caused the terminal velocity of the web to drop to 0.223 m s^{-1} .

DISCUSSION

When height of the jump is taken as a measure of performance, *Euphlyctis* species' performance is seven times that of which the *R. esculenta* species is capable. When we use the differences in height to calculate the required take-off velocity [$v = (2 \times g \times h)^{0.5}$], the effect is less striking, but the performance of the *Euphlyctis* species is still 2.6 times greater than that of *R. esculenta*. The small underestimation of the maximal velocity of *Euphlyctis* may be due to the fact that we only used sequences in which the snout was visible during the entire take-off phase. Because we zoomed

Table 1. Summary of all ANOVA and ANCOVA statistics. Mean and standard deviation are given of all morphometric data, all four distances and the significant kinematic variables for each species. Sample sizes are added for each experiment, exceptions are shown within parentheses. Drawings of the web shape are added to the table

	<i>E. hexadactylus</i>	<i>E. cyanophlyctis</i>	<i>R. esculenta</i>	P-value
Max performance (cm)	50	45	7	< 0.001
Performance vs <i>N</i>	18	5	20	
Mean \pm SD (m s ⁻¹)	1.99 \pm 0.60	2.34 \pm 0.18	1.30 \pm 0.47	< 0.001
Minimum (m s ⁻¹)	0.85	2.06	0.331	
Maximum (m s ⁻¹)	2.87	2.68	2.07	
Morphometrics				
<i>N</i>	7	4	4	
Snout-vent (mm)	55 \pm 19	42 \pm 7	50 \pm 3	0.36
Upper leg (mm)	28 \pm 9	23 \pm 3	25 \pm 3	0.40
Lower leg (mm)	27 \pm 8	22 \pm 3	24 \pm 2	0.45
Mid foot (mm)	15 \pm 5	13 \pm 3	15 \pm 1	0.70
Longest toe (mm)	29 \pm 9	22 \pm 1	29 \pm 1	0.17
Funct. web area (mm ²)	508 \pm 485 (5)	278 (1)	373 \pm 47	0.79
Real web area (mm ²)	650 \pm 620 (5)	310 \pm 73	380 \pm 60	0.04 (ANCOVA)
Trunk length change in % (mm ²)	11 \pm 7 (12)	9 \pm 5 (5)	11 \pm 4 (18)	0.70
Distances				
<i>N</i>	18	5	20	
A (mm)	40 \pm 15	47 \pm 3	41 \pm 7	0.39
B (mm)	39 \pm 15	36 \pm 2	39 \pm 7	0.86
C (mm)	34 \pm 18	15 \pm 13	35 \pm 16	0.17
D (mm)	-4 \pm 15	14 \pm 3	12 \pm 9	< 0.001
Slip factor at v_{\max} ankle	0.76 \pm 0.15	0.55 \pm 0.19	0.71 \pm 0.18	0.052
Kinematics				
<i>N</i>	18	5	20	
v_{\max} hip ($^{\circ}$ s ⁻¹)	3744 \pm 1658	4676 \pm 804	2532 \pm 804	0.012
Web form				

in quite heavily to ensure a good view of the jumping phase, we had to eliminate a considerable portion of the sequences during the screening process. The slight underestimation of the maximal velocity of *R. esculenta* could be due to the fact that we calculated the take-off velocity from the height, and the take-off velocity does not necessarily coincide with the maximal velocity.

In spite of the large difference in performance, no large differences in terms of morphology or behaviour were found between the three species. Only counterintuitive differences in morphometrics were found and of all the kinematic variables only the maximal hip velocity differed. This finding means that the three species are not only morphologically very similar, but that they also display similar behaviour.

We did, however, observe a difference in the slip factors at the beginning of the propulsion phase between the three species. *Euphlyctis* species displayed severe slip (small slip factor) only in the high performance sequences and were able to maintain the small slip (slip factor close to 1) in the low performance sequences. In contrast, *R. esculenta* showed considerable slip earlier in the propulsion phase and already in the low performance sequences. This means that *Euphlyctis* frogs are capable of preventing their feet from moving backwards at higher velocities. The most obvious reason for this is the larger area of the webs of *Euphlyctis*. The area measured directly on the web is indeed slightly bigger, but the maximal functional areas, measured *in vivo* on the ventral views, are the same for all species. Moreover, the web kinematics show that *Rana* is capable of spreading its toes to the

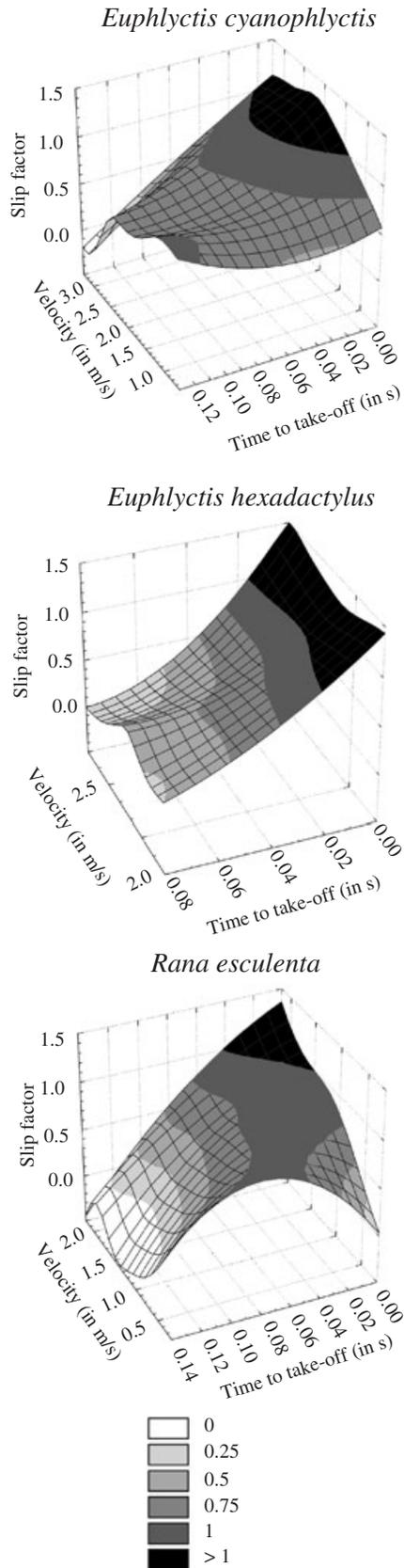


Figure 4. The slip factor throughout the propulsion phase is shown for the three species. A slip factor of one means that the slip is small, the snout tip gains height, but this does not result in a loss of height of the ankles. In contrast, a slip of zero means that the feet move downwards, but this does not result in the snout tip moving upwards. In these graphs, the resulting performance velocity is taken into account. Overall, more slip (lower slip factor) is found in the higher region of the performance range. This figure also shows that the slip is higher for *Rana esculenta* at the beginning of the propulsion phase and that slip is already high at low performance.

maximal area faster and for a longer period of time than *Euphlyctis*. Because the difference in slip is most conspicuous at the beginning of the propulsive phase, we divided the web kinematics profiles in two parts and compared the spreading of the toes at the beginning of the propulsion phase. At this crucial phase with regards to the slip factor, there were no differences in web kinematics, and therefore a different expansion of the webs cannot explain the difference in slip. However, the shape of the webs differs: a *R. esculenta* web tends to be longer but narrower. It is known that the shape of an object is a crucial factor affecting the level of drag, but if we regard both webs as flat planes, the difference in the aspect ratio (0.8 vs. 0.5) can not explain the difference in slip, as the drag coefficient (C_d) tends to be a constant of approximately 1.18 for aspect ratios between 1 and 0.2 (Hoerner, 1965). However, Hoerner (1965) measured these C_d values under steady flow circumstances. It is likely that the shape of the web influences both the manner of the flow around the edges of the web, and the time it takes for the flow to build up. As a more circular object has a smaller circumference, we expect the drag to be larger for *Euphlyctis*. Another possible effect may be the irregularity of the web edge of *R. esculenta*. In addition to this, the web of *Euphlyctis* is curved, resulting in a camber, which is known to increase drag on the concave side (Stamhuis & Videler, 1998). When the fluid flow is expected to be complex and unpredictable, a physical model can be used to unravel overall differences in flow patterns. Our model shows that the difference in 2D shape results in a small difference in drag during the accelerating phase of the drop experiment. It is unlikely that during the propulsive phase the webs encounter a steady-state environment, especially as the difference in slip seems to be made during the initial phase of the propulsion. Camber seems to affect the drag in such a way that steady-state is attained faster and at a lower velocity, which means that the cambered model slowed down faster and thus experienced more drag. More drag would then result in more effective propulsion.

In conclusion, the *Euphlyctis* species can jump out of the water more spectacularly because they can prevent slip at the beginning of the propulsive phase. Small variations in 2D and 3D shape seem to cause differences in drag on the webs. This strongly suggests that subtle differences in web morphology can have strong effects on behaviour, which results in a better suited *Euphlyctis* than *Rana esculenta* for jumping in a viscous medium.

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