

Landing in basal frogs: evidence of saltational patterns in the evolution of anuran locomotion

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Received: 22 May 2010 / Revised: 21 June 2010 / Accepted: 22 June 2010
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Abstract All frogs are assumed to jump in a similar manner by rapidly extending hindlimbs during the propulsive phase and rotating the limbs forward during flight in order to land forelimbs first. However, studies of jumping behavior are lacking in the most primitive living frogs of the family Leiopelmatidae. These semi-aquatic or terrestrial anurans retain a suite of plesiomorphic morphological features and are unique in using an asynchronous (trot-like) rather than synchronous “frog-kick” swimming gait of other frogs. We compared jumping behavior in leiopelmatids to more derived frogs and found that leiopelmatids maintain extended hindlimbs throughout flight and landing phases and do not land on adducted forelimbs. These “belly-flop” landings limit the ability for repeated jumps and are consistent with a riparian origin of jumping in frogs. The unique behavior of leiopelmatids shows that frogs evolved jumping before they perfected landing. Moreover, an inability to rapidly cycle the limbs may provide a functional explanation for the absence of synchronous swimming in leiopelmatids.

Electronic supplementary material The online version of this article (doi:10.1007/s00114-010-0697-4) contains supplementary material, which is available to authorized users.

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Keywords Ascaphus · Bombina · Lalagobatrachia ·
Leiopelmatidae · Locomotion · Rana

Introduction

Frogs have experienced a remarkable adaptive radiation since diverging from a common ancestor prior to the Triassic (Anderson et al. 2008; Marjanović and Laurin 2007) and saltation appears to be a key element in their evolutionary success. It is generally assumed that all anurans jump in a similar manner, and morphological evidence has been used to argue that terrestrial jumping was the primitive locomotor mode from which all other locomotor modes evolved (Jenkins and Shubin 1998; Shubin and Jenkins 1995; Přikryl et al. 2009). The propulsive phase of jumping involves rapid hindlimb extension accompanied by loss of forelimb contact. The aerial phase is characterized by midair body and limb rotations in preparation for landing (Duellman and Trueb 1994; Nauwelaerts and Aerts 2006; O'Reilly et al. 2000). Limb recovery begins near mid-flight and involves protraction and flexion of the hindlimbs and protraction, adduction, and extension of the forelimbs, placing them in position to absorb impact forces (Duellman and Trueb 1994; Emerson and De Jongh 1980; Peters et al. 1996). The extended forelimbs also serve as a pivot during landing, allowing the flexed hindlimbs to rotate into position beneath the body, enabling the rapid initiation of another takeoff (Duellman and Trueb 1994; Emerson and De Jongh 1980; Peters et al. 1996). These generalizations are based on observations of landing behavior in a few crown group anurans (Bufonidae, Microhylidae, and Ranidae; Emerson and De Jongh 1980; Gillis et al. 2010; Gillis and Biewener 2000; Kamel et al. 1996; Nauwelaerts and Aerts 2006;

Peters et al. 1996). It is unclear if such generalizations are applicable to basal anurans. Indeed, there is reason to suspect that the basal-most anuran family Leiopelmatidae, represents an exception as evidenced by their plesiomorphic swimming behavior. Leiopelmatids use an asynchronous (trotting) swimming gait, in which the hindlimbs move out-of-phase with one another (Abourachid and Green 1999). In contrast, the primary swimming stroke of their sister group, Lalagobatrachia (Frost et al. 2006), is the “frog-kick,” in which the hindlimbs are extended and flexed together (Nauwelaerts and Aerts 2002) with hindlimb flexion beginning near mid-flight as it does when they jump (Peters et al. 1996).

The goal of this study was to test the generality of anuran jumping by comparing a member of the basal-most living frog family Leiopelmatidae, *Ascaphus montanus* with a basal lalagobatrachian, *Bombina orientalis*, and a derived lalagobatrachian, *Lithobates pipiens* (Frost et al. 2006). In addition to quantitative comparisons among these three semi-aquatic species, we examined representative video footage from two other leiopelmatids from New Zealand, the terrestrial *Leiopelma pakeka* and the semi-aquatic *Leiopelma hochstetteri*.

Materials and methods

A. montanus ($n=6$ males), *B. orientalis* ($n=6$ unknown sex), and *L. pipiens* ($n=6$ unknown sex) were filmed jumping in a 155×60 -cm arena with an AOS X-PRI high-speed video camera at 500 fps and a 45° mirror on an anti-slip surface (3 M Safety Walk tape). *B. orientalis* and *L. pipiens* were filmed at ecologically relevant temperatures of $25 \pm 2^\circ\text{C}$ (Blomquist and Hunter 2009; Choi and Park 1996). Because the primary streams ($<15^\circ\text{C}$) and nocturnal temperatures ($\leq 10^\circ\text{C}$) inhabited by adult *A. montanus* are cold (Metter 1964), we kept them at $15 \pm 2^\circ\text{C}$ during trials. Temperature is known to affect jumping performance in frogs (Hirano and Rome 1984; James et al. 2007). In order to ensure that general features of jumping behavior were not attributable to temperature differences, two *A. montanus* were filmed jumping five times each (ten trials) at 25°C ; whereas, two *B. orientalis* and two *L. pipiens* were filmed jumping five times each at 15°C . Qualitative comparisons of all three species at both 15°C and 25°C revealed no general behavioral differences attributable to temperature.

Frogs were enticed to jump by tapping behind the animal. Each frog was filmed ten times and the five longest distance trials for each individual were used for key performance, timing, and angular variables (30 trials/species). Images were captured using AOS Imaging Studio V2.5.4.1 and imported into APAS motion-analysis software (Ariel Dynamics) for kinematic analysis. Landmarks were

digitized and a series of angular variables was taken from each sequence to describe and compare statistically the three-dimensional movements of the body and limbs (see appendix for details). Timing variables were obtained by marking the appearance of key kinematic events while reviewing video. Statistical comparisons were made using repeated measures ANOVA and post hoc tests for species differences (Scheffe’s multiple comparison). Both *Leiopelma* species were filmed at 250 fps with a Fastek Troubleshooter digital video camera under similar conditions.

Results

A comparison of representative sequences (Fig. 1a–c) and mean jump kinematics for *A. montanus*, *B. orientalis*, and *L. pipiens* (Fig. 2a–c) illustrate key features of jumping behavior (Online Resources 1, 2, 3, 4, and 5). Although launch movements were similar in the three species, *A. montanus* demonstrated limited pitch control resulting in highly variable body attack angles and landing postures. At positive body attack angles (as in Fig. 1a, Online Resource 1), the toes hit first and the body flops down and skids to a stop. At neutral angles, the extended limbs and body hit the substrate simultaneously (Online Resource 2). At negative angles the frog lands nose first and then the body and extended limbs collapse onto the substrate (Online Resource 3). In each case, after a hard landing there is a consistent pattern of forward translation (i.e., skidding) before the animal comes to a stop. Limb recovery on average starts at the end of the landing period. In both *Bombina* and *Lithobates*, the recovery phase begins prior to mid-flight and the frogs land forelimbs first, followed by the body and hindfeet, with much of the landing phase involved with final positioning of the hindlimbs into the resting posture (Online Resources 4 and 5).

Mean kinematic variables are reported in Table 1 along with statistical results. Absolute jump distance was highest in *L. pipiens* (Table 1). However, there was no difference among species in relative jump distance (standardized by SVL) after applying a sequential Bonferroni correction (Rice 1989). Among timing variables, launch duration was longer in *L. pipiens* than in *B. orientalis*. However, flight and recovery durations did not differ among species (Table 1). Jump cycle duration was longer in *A. montanus*, due to a delay in the onset of the recovery phase (time to onset of hindlimb flexion; Table 1). The onset of hindlimb flexion in *A. montanus* always occurred after the onset of landing (Fig. 2a). In contrast, *B. orientalis* and *L. pipiens* reflect the general lalagobatrachian condition of early hindlimb flexion, initiated near mid-flight (Fig. 2b, c).

Knee and ankle angles at landing contact were higher in *A. montanus* (Table 1) reflecting delayed hindlimb recovery.

Fig. 1 Patterns of jumping behavior in frogs. **a–c** Representative jumping sequences for **a** *Ascaphus montanus* (23.3 cm), **b** *Bombina orientalis* (28.6 cm), and **c** *Lithobates pipiens* (46.1 cm). Videos are provided in online resources

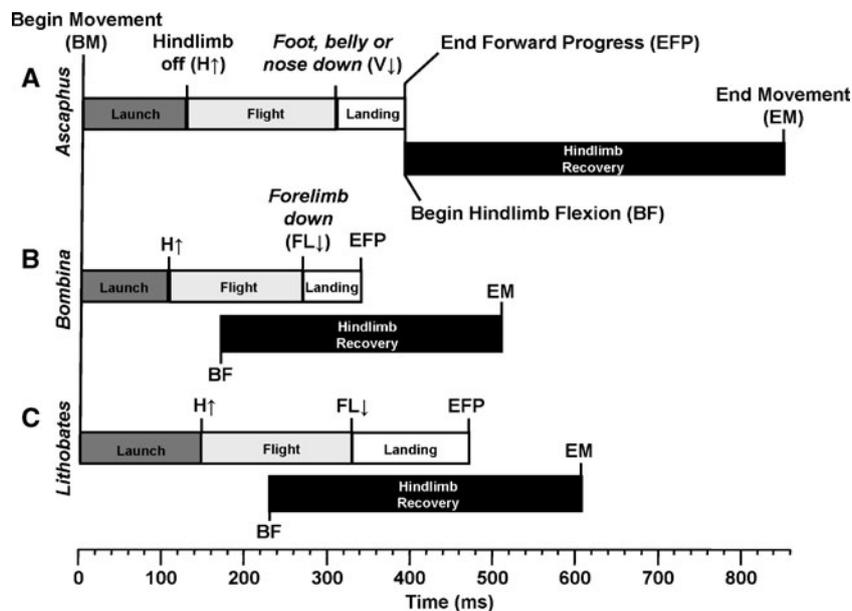
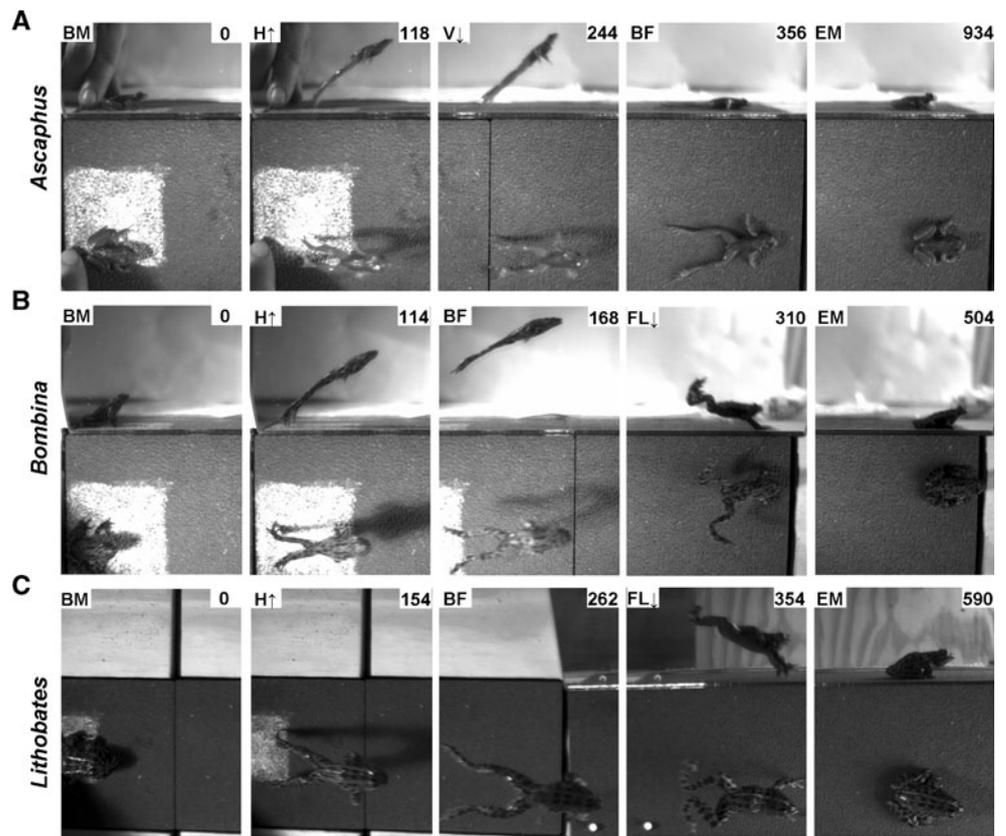


Fig. 2 Jumping kinematics in frogs. **a–c** Mean jump cycle kinematics for **a** *Ascaphus montanus*, **b** *Bombina orientalis*, and **c** *Lithobates pipiens*. Key timing variables are *BM* (beginning of movement), *H \uparrow* (loss of hindlimb contact), *V \downarrow* (landing contact involving variable elements in *A. montanus*), *FL \downarrow* (landing contact involving forelimbs in *Bombina orientalis* and *Lithobates pipiens*), *BF* (beginning of

hindlimb flexion), *EFP* (end of forward progress), and *EM* (end of movement). Mean jump cycle kinematics (from five jumps from each of six individuals per species) were divided into phases based upon the timing of kinematic events: launch (*BM* to *H \uparrow*), flight (*H \uparrow* to *V \downarrow* or *FL \downarrow*), landing (*V \downarrow* or *FL \downarrow* to *EFP*), and hindlimb recovery (*BF* to *EM*)

Table 1 Results of a repeated measures analysis of variance of jumping kinematics in three frog species (Mean \pm SE)

	<i>Ascapus</i>	<i>Bombina</i>	<i>Lithobates</i>	<i>P</i>
Size				
Body Mass (g)	4.7 \pm 0.2	7.5 \pm 0.6	35.7 \pm 0.5	<0.00001
SVL (cm)	3.6 \pm 0.1	4.7 \pm 0.2	7.0 \pm 0.2	<0.00001
Performance				
Absolute jump distance (cm)	28.7 \pm 0.7	28.1 \pm 0.7	48.6 \pm 1.9	<0.0001
Relative jump distance (body lengths)	8.0 \pm 0.2	5.9 \pm 0.1	7.0 \pm 0.3	0.02*
Timing				
Launch duration (ms)	131.9 \pm 7.5	106.4 \pm 4.2	145.4 \pm 7.3	0.008
Flight duration (ms)	177.7 \pm 9.1	165.3 \pm 5.4	182.5 \pm 8.6	0.61
Recovery duration (ms)	429.1 \pm 20.1	343.7 \pm 13.4	377.6 \pm 19.6	0.22
Landing duration (ms)	85.5 \pm 10.5	61.7 \pm 5.3	143.4 \pm 7.7	0.0003
Jump cycle duration (ms)	847.1 \pm 22.9	512.5 \pm 13.2	611.2 \pm 16.1	<0.0001
Time to onset of hindlimb flexion (ms)	418.1 \pm 14.5	168.8 \pm 7.6	233.6 \pm 13.6	<0.00001
Joint and body angles at landing				
Knee angle (degrees)	146.2 \pm 2.5	77.4 \pm 5.5	96.3 \pm 6.8	0.002
Ankle angle (degrees)	155.8 \pm 2.6	86.1 \pm 5.6	99.3 \pm 6.5	0.001
Elbow angle (degrees)	123.6 \pm 4.4	115.1 \pm 4.6	128.9 \pm 2.8	0.14
Forelimb protraction angle (degrees)	55.3 \pm 3.1	95.0 \pm 3.1	122.7 \pm 1.8	<0.0001
Body attack angle (degrees)	-10.8 \pm 6.4	-7.8 \pm 3.1	-24.5 \pm 1.2	0.32

*Indicates lack of significance following sequential Bonferroni correction.

On average, landing body attack angle did not differ among species. However, as shown above, attack angles (and landing postures) in *A. montanus* were highly variable (ranging from $+62^\circ$ to -71°) compared to the consistently negative angles (and consistent landing postures) exhibited by *L. pipiens* (mean = $-24.5 \pm 1.2^\circ$; Table 1). Elbow angles did not differ among species; however, forelimb protraction angles were significantly different, with *A. montanus* protracting to a lesser degree than the other species (Table 1). In all cases, *A. montanus* did not use forelimbs first landings, contributing to their greater forward translation (Fig. 1a), while the others consistently landed on their forelimbs (Fig. 1b, c).

Video footage from the terrestrial *L. pakeka* (Online Resource 6) and the semi-aquatic *L. hochstetteri* (Online Resource 7) indicates that delayed hindlimb recovery is a shared feature of leiopelmatids. *Leiopelma* spp. protract their forelimbs to a greater extent than does *A. montanus*. However, unlike the lalagobatrachians in this study, *Leiopelma* spp. abduct their forelimbs such that they do not land on them; although, their protracted position may serve to minimize skidding since there was less forward translation at landing.

Discussion

Leiopelmatid frogs provide insight into the evolution of anuran jumping. It has been hypothesized that jumping evolved in a riparian context as a means of rapidly escaping (diving) into water (Gans and Parsons 1966). Our results are consistent with this hypothesis because late limb recovery and variable landing postures pose few problems

for escape diving into water, but seem less suited to terrestrial environments. Nevertheless, as shown here, leiopelmatids do jump during terrestrial escapes, but not like other frogs. Landing forces are not directed through forelimbs as in lalagobatrachians studied to date, but are distributed across a range of ventral elements.

The unusual landing behavior of leiopelmatids may provide a functional explanation for some enigmatic morphological features. Their small body size limits the risk of exceeding safety factors of skeletal elements during landing. However, soft tissues (e.g., viscera or ova) could be damaged by uncontrolled landings, which may explain the presence (retention) of large, shield-shaped epipubic cartilages in leiopelmatids, as well as the novel inscriptional ribs of *Leiopelma* (Green and Cannatella 1993).

Our finding of a temporal separation of jumping and limb recovery in leiopelmatids suggests that the evolution of jumping in frogs was a two-step process with symmetrical hindlimb extension jumping appearing first and mid-flight hindlimb recovery and landing on adducted forelimbs appearing in the ancestor of lalagobatrachians. Studies of basal frogs have shown that swimming behavior has also evolved in a step-wise fashion at the same place on the phylogeny (Abourachid and Green 1999). We propose that an inability to rapidly cycle the hindlimbs provides a functional explanation for the absence of synchronous swimming in leiopelmatids.

The switch to lalagobatrachian landing and swimming behavior appears to have involved a simple evolutionary change in the timing of limb muscle motor patterns, shifting the onset of hindlimb flexors to an earlier point in the stride cycle. All else being equal, if *A. montanus* shifted the onset of recovery so that flexion began at mid-

flight it would land on its limbs like other frogs. Thus, the simple shift to early hindlimb recovery may have been a key feature in the evolutionary history of frogs, facilitating controlled terrestrial landings and enabling rapid repetition of jumping and swimming cycles. These changes may have offered advantages for longer distance locomotion, better landing postures, and improved predator avoidance and foraging.

Acknowledgments We thank Paul Brunkow, Mike Jorgensen, Sandra Nauwelaerts, Mike Paulin, James Robins, and John Scheibe for their comments and assistance. The Idaho Department of Fish and Game and United States Forest Service provided collecting permits. This work was supported by a Summer Research Fellowship and a Funded University Research grant from Southern Illinois University Edwardsville to RLE and an Ohio University Research Challenge grant to SMR.

Appendix

The following landmarks were digitized: snout, occiput, urosacrum, shoulder, elbow, wrist, hip, knee, ankle, and tarsometatarsus. Jump distance was measured as the difference in position of the snout from the beginning of movement to the end of forward progress. Knee angle was measured as the angle formed by the hip, knee, and ankle. Ankle angle was measured as the angle formed by the knee, ankle, and tarsometatarsus. Landing body attack angle was measured as the angle formed by the snout, urosacrum, and horizontal. Elbow angle was measured as the angle formed by the shoulder, elbow, and wrist. Forelimb protraction angle was measured as the angle formed by the wrist, occiput, and urosacrum.

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