Pelvic Function in Anuran Jumping: Interspecific Differences in the Kinematics and Motor Control of the Iliosacral Articulation During Take-Off and Landing

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ABSTRACT Although the anuran pelvis is thought to be adapted for jumping, the function of the iliosacral joint has seen little direct study. Previous work has contrasted the basal “lateral-bender” pelvis from the “rod-like” pelvis of crown taxa hypothesized to function as a sagittal hinge to align the trunk with take-off forces. We compared iliosacral movements and pelvic motor patterns during jumping in the two pelvic types. Pelvic muscle activity patterns, iliosacral anteroposterior (AP) movements and sagittal bending of the pelvis during the take-off and landing phases were quantified in lateral bender taxa Ascaphus (Leiopelmatidae) and Rhinella (Bufonidae) and the rod-like Lithobates (Ranidae). All three species exhibit sagittal extension during take-off, therefore, both pelvic types employ a sagittal hinge. However, trunk elevation occurs significantly earlier in the anuran rod-like pelvis. Motor patterns confirm that the piriformis muscles depress the urostyle while the longissimus dorsi muscles elevate the trunk during take-off. However, the coccygeoiliacus muscles also produce anterior translation of the sacrum on the ilia. A new model illustrates how AP translation facilitates trunk extension in the lateral-bender anurans that have long been thought to have limited sagittal bending. During landing, AP translation patterns are similar because impact forces slide the sacrum from its posterior to anterior limits. Sagittal flexion during landing differs among the three taxa depending on the way the species land. AP translation during landing may dampen impact forces especially in Rhinella in which pelvic function is tuned to forelimb-landing dynamics. The flexibility of the lateral-bender pelvis to function in sagittal bending and AP translation helps to explain the retention of this basal configuration in many anurans. The novel function of the rod-like pelvis may be to increase the rate of trunk elevation relative to faster rates of energy release from the hindlimbs enabling them to jump farther. J. Morphol. 277:1539–1558, 2016.

KEY WORDS: anurans; Ascaphus; Lithobates; Rhinella; locomotion

INTRODUCTION

The origin of the Anura and their specialization for jumping with bilateral limb-extension seems to be related to the set of traits distinguishing the anuran morphotype from those other tetrapods. This includes longer hindlimbs, a shortened vertebral column and extremely long ilia that position the acetabula and posterior pelvis behind the end of the fused tail vertebrae (urostyle). The longer ilia and shorter vertebral column result in a body

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: Faculty Research Funds from Southern Illinois University at Edwardsville (to R.L.E.); Contract grant sponsor: National Science Foundation; Grant number: MRI DBI-0922988; Contract grant sponsor: Ohio Board of Regents, the Ohio University Office of the Vice President for Research; Contract grant sponsor: Postdoctoral support from the Ohio University Heritage College of Osteopathic Medicine; Grant number: NSF IOS-1456810.

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Author Contributions: SMR, SJM, RLE performed all of the research and data analysis and the majority of writing and study design. AS, CK, and EN assisted in experimental analyses and EN assisted in data extraction and analysis. MEJ aided in muscle descriptions and prepared the CT imagery. All authors provided comments on the manuscript.

Received 26 May 2016; Revised 10 August 2016; Accepted 15 August 2016.

Published online 31 August 2016 in Wiley Online Library (wileyonlinelibrary.com). DOI 10.1002/jmor.20594
in which leaping forces generated by the legs and hips are transmitted through the long pelvis to the movable iliosacral joint near the mid-body. This peculiar configuration of an iliosacral joint in the middle of the body creates unique biomechanical consequences for controlling the posture of the trunk and head relative to the pelvis and legs during jumping locomotion.

Hypothetical functions of the anuran iliosacral joint during terrestrial jumping are based on the work of Green (1931), Whiting (1961), Emerson (1979, 1982), and Emerson and de Jongh (1980) all of who contrasted two primary iliosacral configurations. In one, rod-like sacra project posterodorsally and attach to the dorsal tips of the ilia via small ligaments. Hypothetically this pelvic configuration functions primarily as a sagittal-hinge, in which extension at the iliosacral and sacro-urostylic joints aligns the trunk and head with take-off forces (sagittal bending is illustrated for *Lithobates* in Fig. 1). This rod-like pelvis is associated with the ability to jump longer distances (Emerson, 1979). In the second configuration, laterally expanded bow tie-like sacral diapophyses articulate with the ilia via long sliding ligaments. Emerson (1982) proposed that this pelvic configuration facilitates unilateral anteroposterior (AP) translation in opposite directions, thereby allowing lateral rotation of the pelvis during walking and burrowing (bilateral AP translation is illustrated for *Rhinella* in Fig. 1). Anteroposterior translation has also been shown during swimming (Videler and Jorna, 1985; Robovska-Havelkova et al., 2014), however, the focus of this study is to investigate the pelvic function during terrestrial jumping locomotion. Recent phylogenetic reviews of a suite of pelvic traits across Anura have shown that the “lateral-bender” configuration is both basal and generalized for walker/hoppers.
whereas the rod-like “sagittal hinge” configuration has appeared independently multiple times within several crown group neobatrachian anurans (Reilly and Jorgensen, 2011; Jorgensen and Reilly, 2013).

Only three studies have quantified pelvic movements during jumping. Jenkins and Shubin (1998) verified dorsal rotation in a rod-like frog (Lithobates pipiens) in which there was 18–20° of sagittal extension during take-off. However, in the other two studies (Emerson and de Jongh, 1980), both pelvic types were reported to exhibit sagittal extension during take-off (rod-like: Lithobates pipiens and lateral-bender forms: Kaloula pulchra, Anaxyrus americanus and Bufo boreas). In the only electromyographical study of anuran pelvic muscles, Emerson and de Jongh (1980) found that both types of pelvic have similar motor patterns consistent with the hypothesis that during take-off, the urostyle is fixed between the ilia while the anterior trunk is elevated relative to the pelvis. However, none of these studies quantified or discussed AP translation of the pelvic girdle during jumping. Furthermore, these studies focused on take-off; the function of the pelvis during landing has not been investigated. Therefore, it is not clear how AP translation and sagittal bending contribute to jumping mechanics. More data are needed to test Emerson’s hypotheses that the lateral-bender and sagittal-bend configurations function along different primary axes of bending (i.e., lateral or sagittal).

We completed a comparative study of kinematics and forces during jumping (take-off through landing) in several species of anurans (Reilly et al., 2016). Quantitative comparisons revealed that the take-off phase is similar across anurans but landing in the most basal frogs (Ascaphus) differs significantly from landing in the crown group anurans Lithobates and Rhinella (Fig. 2). The most basal anurans land on their body and do not recycle the arms or legs forward until well after ground-reaction forces have abated (Essner et al., 2010; Reilly et al., 2016). In Lithobates, the hands hit first, followed by the belly, pubis and thighs slapping down in sequence such that the body absorbs most of the landing forces. The legs bounce and finish folding up before the feet are placed down by the time that landing forces abate. The more basal Bombina orientalis has the same landing behavior. Rhinella is different; most of the landing forces are absorbed by the arms, followed by the coordinated landing of the fully folded legs with the rest of the body.

A second component of our comparative study was to record pelvic muscle activity and movements at the iliosacral joint during jumping, which we present here. Muscle activity patterns, AP translation and sagittal bending of the pelvis during the take-off and landing phases were analyzed in Ascaphus, Lithobates, and Rhinella. Patterns of pelvic function were compared to the take-off and landing behaviors and force patterns described in Reilly et al. (2016). This is the first comprehensive comparative analysis of the function of the unique anuran pelvic system and provides a new model for the function of the lateral-bender configuration during jumping. In addition, we investigate how pelvic function during landing varies in relation to the major differences found in landing behavior in these species (Fig. 2; Reilly et al., 2016).

**MATERIAL AND METHODS**

Three model anuran species were selected to represent key terrestrial taxa spanning the anuran phylogeny. The Rocky Mountain Tailed Frog, *Ascaphus montanus* (Mittleman and Myers, 1949), represents the ancestral belly-flopping form of landing (Essner et al., 2010). The Bullfrog, *Lithobates catesbeianus* (Shaw, 1802) and the Marine Toad, *Rhinella marina* (Linnaeus, 1758), represent the two major groups of the Neobatrachia (Ranoidea and Hylidea, respectively) that typically use the pectoral girdle (Griep et al., 2013) and forelimbs to control landing (Nauwelaerts and Aerts, 2003; Gillis et al., 2014; Gillis and Gillis, 2015; Reilly et al., 2016). Henceforth the study species are referred to by their generic names. *Ascaphus* and *Rhinella* have expanded sacral diaphyses of the lateral-bender morphotype, whereas, *Lithobates* has the sagittal-hinge morphology (Reilly and Jorgensen, 2011).

The pelvic kinematics and motor patterns of *Rhinella* and *Lithobates* were recorded from the same animals and with the same trials used in our previous study of jumping behavior in relation to ground reaction forces (Reilly et al., 2016). These species were obtained commercially and included two *Lithobates catesbeianus* (13.70 ± 0.23 cm; 317.0 ± 13.7 g) and three *Rhinella marina* (13.61 ± 0.12 cm; 255.0 ± 17.9 g). Our sample study also included three *Ascaphus montanus* (Snout-vent length [SVL] = 4.37 ± 0.04 cm; Mass = 6.2 ± 0.1 g) collected from Beauty Creek, Coeur d’Alene National Forest, Idaho (47°36′39″ N; 116°40′13″ W) under permits from the U.S. National Forest Service and Idaho Fish and Game (Permit # 130502). In *Ascaphus*, different individuals were used to record pelvic kinematics and motor patterns than in Reilly et al. (2016).

**Experimental Data Collection**

Individuals were induced to take-off and land on force plates while being recorded with high-speed video and fine-wire electromyography. Details of force-recording methods and variables are available in Reilly et al. (2016). A synchronized Oqus 3+ high-speed camera recording at 200 frames-per-second (fps) in lateral view (Qualisys Motion Capture Systems, Sweden) was used to record the timing of behavioral kinematic events. In addition, an array of four additional synchronized Oqus cameras was calibrated to record the 3D-positions of infra-red reflective landmarks at 500 fps. Landmarks (3 mm diameter on Ascaphus, 6 mm on the other species) were glued (cyanoacrylate) to gauge patches and then glued to the occiput of the skull, the left and right sacral diaphyses and on the posterior aspects of the left and right ilia. One caveat of this study is the use of external markers to quantify movements of internal structures. However, the occiput and sacral skin is attached to the underlying bones and thus landmarks here confidently represent the positions of the skull and sacral diaphyses. For the third landmark (posterior bases of the ilia), the gauge foundations secured the landmark sphere to a wider area of skin to minimize skin movements relative to the underlying fascia. Videos and landmark positions were recorded using Qualisys Track Manager (Qualisys Motion Capture Systems, Sweden). The 3D-landmark tracking field was calibrated with Qualisys calibration tools providing less than 0.5° error in angle measurements and a maximum of 0.3 mm error in the linear measurements. Prior to any
analyses, the 3D-position traces of the infra-red reflective landmarks were filtered using a moving average over five frames. During a recording session, individuals were placed on the force plate in starting position with their snouts pointing down the longitudinal axis of the experimental setup. They either jumped spontaneously after several seconds or were induced to jump by an approaching hand or by gently tapping the posterior of the body. Because of differences in thermal preferences (Essner et al., 2010), recording sessions were carried out at 15°C for *Ascaphus* and at 20–22°C for the other two species. We selected five or six jump sequences per individual from numerous recordings reviewed that were 1) parallel with the long axis of the force plate and 2) where the hindlimbs were used in synchrony (Table 1). All analyses include the selected take-offs and their subsequent landings.

**Take-Off and Landing Events and Force Variables**

Key behavioral and force events from the analysis of these species by Reilly et al. (2016: Fig. 2) are applied to this study.
The jump begins with the onset of hindlimb extension (Start hindlimb extension, Time 0). This was recorded as the frame before any noticeable movement occurred between the knee and the body and was coordinated with the time that vertical and fore-aft forces began to change from body weight and zero, respectively. \textit{Take-off time} was the time at which the last toe left the ground; this corresponded with both the vertical and fore-aft forces reaching zero. Landing started with substrate contact (Body-hit in \textit{Ascaphus}, Hands-hit in the other species) and ended with a stereotypical behavior of putting the longest toe down (\textit{Toe-down}) which signaled the behavioral end of the jump.

\textit{Take-off duration} is defined as the difference in time between the onset and offset of accelerative fore-aft forces. Start hindlimb extension to \textit{Take-off time} was used for \textit{Ascaphus} pelvic and EMG records. The \textit{maximum vertical} and \textit{maximum fore-aft} (accelerative) \textit{forces} and the times at which they occurred (which were statistically coincident; Reilly et al., 2016) were quantified for both take-off and landing. Ground reaction forces during landing started at impact, increased to exhibit patterns of landing forces and then returned to static levels; that is, vertical forces returned to body weight and fore-aft forces returned to zero, indicating the end of forward movement. This period, from the time of substrate contact to the time that the fore-aft forces return to 0 is termed \textit{TFAO} and is the \textit{landing duration}. The visual time to stop moving was used as a proxy for TFAO in the EMG/kine- matic \textit{Ascaphus} sample. Note that much of the landing behavior (i.e., leg recycling in particular) in \textit{Ascaphus} occurs after TFAO, but the end of the behavioral landing (\textit{Toe-down}) was coincident with the end of landing forces (TFAO) in the other two species (Reilly et al., 2016). The timing of kinetic events was standardized over take-off or landing duration.

\textbf{Pelvic Kinematics}

\textit{AP translation}. Fore-aft movements at the iliosacral joint were measured as the distance between the midpoint between the two ilia landmarks and the midpoint of the sacral landmarks (Fig. 3). To remove any body-size effects, we converted this distance to percentage of trunk length (the distance from the occiput to sacral midpoint). For statistical comparisons of \textit{AP translation} across species, we calculated the \textit{AP excursion} at the onset of the \textit{Ap} super-compression in the other two species (Reilly et al., 2016). The \textit{Take-off duration} (TFAO) was coincident with the end of landing forces (TFAO) in the other two species (Reilly et al., 2016). The timing of kinetic events was standardized over take-off or landing duration.

Statistical differences among species are indicated in the MANOVA column.

Abbreviations: SVL, snout-vent length; TL, trunk length; TOD, take-off duration; TFAO, the time that the fore-aft force returns to zero.

\*Time to return to the starting angle in \textit{Ascaphus}.

\begin{table}[h!]
\centering
\caption{Mean (± SEM) jump characteristics and pelvic kinematics for three species of anurans}
\begin{tabular}{|l|ccc|}
\hline
 & \textit{Ascaphus} & \textit{Lithobates} & \textit{Rhinella} & MANOVA \\
\hline
Number of individuals & 3 & 2 & 3 & \\
Number of jumps & 15 (5,5,5) & 10 (5,5) & 16 (5,5,6) & \\
SVL (cm) & 4.37 ± 0.04 & 14.70 ± 0.23 & 13.61 ± 0.12 & \\
Trunk length TL (cm) & 1.73 ± 0.02 & 5.10 ± 0.20 & 6.90 ± 0.20 & \\
Jump distance (cm) & 23.69 ± 1.83 & 38.13 ± 0.35 & 31.88 ± 2.82 & \\
Take-off duration (TOD) (ms) & 121 ± 27 & 182 ± 18 & 176 ± 6 & \\
Landing duration (TFA0) (ms) & 157 ± 11 & 147 ± 9 & 225 ± 13 & \\
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jump (start of leg extension), at the instant of take-off, at the onset of landing (body hit or hands hit) and at any maxima and minima observed in each profile. In addition, we measured AP excursion at the time of peak take-off forces (averaging time to peak vertical force and time to peak fore-aft force; from Reilly et al., 2016). This is the time when maximum take-off forces have been imparted to pelvic movements.

**Angular excursion.** Sagittal bending at the iliosacral joint was quantified by computing the pelvic angle. First, we calculated the angle between the midpoint between the two posterior ilial landmarks, the midpoint between the two sacral landmarks and the occiput landmark (Fig. 3). This provided an angle in the mid-sagittal plane reflecting the angle of the long axis of the ilia relative to the trunk. For comparisons across species, we converted the raw pelvic angle values to net angular excursion by subtracting the value at the starting position from each value. Increases in pelvic excursion indicate sagittal extension at the iliosacral joint and decreases reflect sagittal flexion. If sagittal flexion surpasses the starting value (0) this angle is negative, indicating super-flexion. From the pelvic angle profiles recorded for each trial we extracted the angle at the onset of the jump (start of leg extension), at the instant of take-off, at the onset of landing (body hit or hands hit) and at any maxima and minima observed in each profile. We also measured angular excursion at the mean time of peak take-off forces (averaging time to peak vertical force and time to peak fore-aft force; from Reilly et al., 2016).

**Pelvic Configurations**

Pelvic configurations and traits are from Reilly and Jorgensen (2011). In most lateral bender-forms, the ilia and urostyle are smooth and provide a shallow zone of attachment space for the pelvic muscles extending from the ilia to the urostyle (Fig. 4), although some species (e.g., Rhinella) develop a dorsal ridge on the anterior half of the urostyle to increase the muscle attachment.

![Fig. 3. Kinematic landmarks and AP translation variables illustrated on Lithobates catesbeianus. IR reflective beads are glued to gauze patches which are glued to the landmark locations.](image)

![Fig. 4. Axial muscles and features associated with the pelvis. Ascaphus and Rhinella are proposed to have primarily lateral-bender configurations with smooth ilia and expanded sacra, whereas Lithobates is proposed to have a sagittal-hinge configuration with rod-like sacral diaphyses and massive ridges on the ilia and urostyle. LD, the longissimus dorsi (orange) runs along the vertebral column to the urostyle. CI, the coccygeoliliacus (blue), extends from the urostyle in an anterolateral direction to the medial surface of the ilia. PF, the piriformis (red) extends from the tip of the urostyle to the proximal femur. IL, the iliolumbaris (green) lies lateral to the LD along the lateral tips of the ribs of some vertebrae to the anterior aspect of the ilium. CS, the coccygeosacralis (blue) extends from the urostyle in an anterolateral direction to the posterior surface of the sacrum, and was not studied.](image)
area for the *longissimus dorsi* muscles (Fig. 4, middle). In contrast, the sagittal-hinge forms (Fig. 4, right) have massive dorsal ridges all along the urostyle and posterior 90% of the ilia (no ridges at area of iliosacral articulation) resulting in longer and deeper muscle attachment surfaces on these bones and, therefore, larger muscles between the pelvic elements.

### Muscles and Their Proposed Functions

The myology of the anuran pelvis has been reviewed (Noble, 1931; Ritland, 1955; Dunlap, 1960; Whiting, 1961; Emerson and de Jongh, 1980; Pugener and Maglia, 2009; Prikryl et al., 2009); here, we provide descriptions based on the literature and observations from dissections of our study species. The four major muscle pairs of the pelvis are remnants of the tetrapod epaxial masses that run down the trunk over the sacrum and onto the tail (Fig. 4). The literature provides some discussion of their proposed functions during the take-off, but their use in landing has not been considered.

The greatest muscles are the *longissimus dorsi* (LD, orange in Fig. 4) running along the vertebral column to the urostyle. As in other tetrapods, the LD muscles stabilize and extend the axial column. In anurans, it is thought that contraction of these muscles is the primary force straightening the body at the tail-sacral joint during the take-off (Emerson and de Jongh, 1980).

The LD has a deep portion just dorsal to the transverse processes and ribs that extends to the anterior edge of the sacrum, and a superficial portion running to the urostyle. Dissection revealed that the superficial portion in all three species was free from the sacral diapophyses providing a muscle belly that can slide over the sacrum to the urostyle. In *Ascasphus* and most lateral-bender morphs, the superficial portion inserts all along the tube-shaped urostyle to its posterior tip. In *Rhinella*, the LD inserts on a small vertical ridge along the anterior half of the urostyle. In *Lithobates*, the superficial portion of the LD attaches to a large vertical ridge running about two-thirds the length of the urostyle. In addition, the superficial muscle belly in *Lithobates* could be easily separated from the ventral portion above the last three presacral vertebrae. Thus, the *Lithobates* superficial belly is independent from the rest of LD from the level of the fifth vertebra over the sacrum to its insertion on the urostyle. Henceforth, we use LD to refer to the superficial belly of the muscle extending posterior to the sacrum.

In anurans, the *piriformis* muscle (PF, red in Fig. 4) extends from the posterior tip of the urostyle to the proximal femur. The muscle is similar in all three species, but was too small to study in *Ascasphus*. It is positioned to depress the urostyle. The general hypothesis (Englman and Shubin, 1998) is that during the take-off, the PF holds the urostyle down while the large LD muscles contract to produce sagittal extension to raise the trunk in line with take-off forces. In our species, the PF and overlying fascia and skin limit the dorso-medial movement of the tip of the urostyle relative to the ischium to about 2–4 mm.

Deep to the LD are the *coecygeosacralis* and *coecygeoilialicus* (CS and CI, respectively, blue in Fig. 4), which extend from the urostyle in an anterolateral direction to attach on the posterior margin of the sacrum (CS) and medial surfaces of the ilia (CI), respectively. The CS is thought to stabilize the urostyle on the sacrum in the horizontal plane (Emerson and de Jongh, 1980). It was not studied because it is small and it is not in a position to move the pelvis. In *Ascasphus*, the CI attaches along the posterior half of the urostyle and inserts on the anterior third of the ilium medially. In *Rhinella*, the CI attaches posterior to the second thirds of the urostyle and the anterior half of the ilium. In these species the orientation is oblique and forward; this suggests the CI protracts the sacrum relative to the ilia via AP translation, thereby extending the trunk on the pelvis. Emerson and de Jongh (1980) showed that during walking in *Kaloula pulchra*, the CI muscles fire alternately and retract the ilia under the sacrum to rotate the pelvis from side to side on the sacrum during trotting steps. Thus, we know that each CI can produce AP translation unilaterally during walking. However, the bilateral use of the CI muscles in AP translation during jumping is little understood, except that Emerson and de Jongh (1980) reported that they fire tonically during take-off. In *Lithobates*, the CI fibers are oriented more laterally and span the entire area between the large dorsal ridges on the urostyle and ilia that are not taken up by the reduced CS anteriorly.

The *Hiliomuslaris* (IL, green in Fig. 4) lies lateral to the LD and extend from the tips of some of the vertebral transverse processes to the anterior aspect of the ilium. In *Ascasphus* and *Rhinella*, the anterior attachments of the IL are on the transverse processes (mostly on their cartilaginous tips) of presacral vertebrae 4–6, with just a few fibers to 7. In *Lithobates*, the IL takes on a more narrow shape extending as individual slips between consecutive transverse processes and it extends more anteriorly to the exoccipitals of the skull. Posteriorly in *Lithobates*, the IL is narrow and extended as individual slips between consecutive transverse processes and anteriorly, to the exoccipitals of the skull. Posteriorly in *Lithobates*, the IL has some fibers that extend to the anterior edge of the sacrum. The position of the IL suggests it might be involved in AP translation of the ilia; however, it is thought to function primarily in body stabilization (Emerson and de Jongh, 1980).

### Electromyography

Muscle activity was recorded using standard fine-wire electromyography (EMG, as in Reilly et al., 2010). Electromyographical recordings were made from 0.002 mm diameter bipolar stainless steel electrodes, which were implanted through the skin directly into each muscle (bilaterally) while the animals were anesthetized. The bared metallic tips of each electrode were 0.25 mm long. The bundle of electrodes on the pelvis (LD, PF, CI) were glued together, passing anteromedially between the sacral landmarks, joined with the IL electrodes and sutured to the skin anterior to the sacrum on the midline. Electrodes were implanted at the locations muscle labels illustrated in Figure 4. Animals completely recovered from anesthesia within 2 h and synchronized EMG data were recorded as they jumped and landed on the force plates. Animals were restrained about 5–10 min between jumps. EMG signals were amplified 10,000 times using AM Systems model 1700 differential AC amplifiers with a bandpass of 100–3,000 Hz (and a 60 Hz notch filter), and then recorded on Cambridge Electronics MICRO 1401 analog-to-digital converter that generated a synchronization pulse simultaneously recorded by the Qualysis system.

EMG data were recorded and analyzed using the Cambridge Electronics SPIKE 5.0 software with the sample rate for each channel set at 10,000 Hz to obtain reliable recordings of EMG patterns (Jayne et al., 1990). EMG profiles were inspected for possible patterns revealing crosstalk. Immediately after data collection, each animal was euthanized by overdose of anesthetic and preserved in 10% formalin. Electrode position was confirmed by dissection and only individual preparations in which the electrode lay completely within the muscle were used. Onsets and offsets of each burst of muscle activity were digitized for each of the take-off and landing bursts observed. The rectified integrated area was measured for each burst and this was divided by burst duration to calculate the mean amplitude of each burst. Take-off bursts always had greater mean amplitude than landing bursts so the relative amplitude (% of jump burst) was calculated by dividing the mean amplitude of each subsequent burst by the mean amplitude of the take-off burst. This is a measure of the relative intensity of muscle contraction in jump and landing bursts within each jump. All procedures were completed under approved University animal research protocols.

### Data Normalization

Several studies have already reported significant effects of body size and jump distance in anurans, both intra and
Take-off bursts are scaled to take-off duration (TOD) and landing bursts are scaled to the force landing duration (TFA0). Statistical differences among species are indicated in the MANOVA column. Abbreviations: TOD, take-off duration; TFA0, the time that the fore-aft force returns to zero.

<table>
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<tr>
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<th>Aesopus</th>
<th>Lithobates</th>
<th>Rhinella</th>
<th>MANOVA</th>
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<tr>
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<td>176 ± 6</td>
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<td>Landing duration (TFA0) (ms)</td>
<td>157 ± 11</td>
<td>147 ± 9</td>
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<td><strong>Piriformis (PF)</strong></td>
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<td><em>Take-off burst</em></td>
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<td><strong>Landing burst 1</strong></td>
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<td>Onset (% TFA0)</td>
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<td>Offset (% TFA0)</td>
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<td>Relative amplitude (% of TO burst)</td>
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<td>na</td>
<td>39.6%</td>
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<td><strong>Landing burst 2 (only in Rhinella)</strong></td>
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<td>71.4 ± 1.0</td>
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<tr>
<td>Offset (% TFA0)</td>
<td>na</td>
<td>na</td>
<td>98.8 ± 0.7</td>
<td></td>
</tr>
<tr>
<td>Relative amplitude (% of TO burst)</td>
<td>na</td>
<td>na</td>
<td>39.6%</td>
<td></td>
</tr>
<tr>
<td><strong>Coccygeoiliacus (CI)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Take-off burst</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset (% TOD)</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td>Offset (% TOD)</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td><strong>Landing burst 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset (% TFA0)</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td>Offset (% TFA0)</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td>Relative amplitude (% of TO burst)</td>
<td>na</td>
<td>na</td>
<td>39.6%</td>
<td></td>
</tr>
<tr>
<td><strong>Landing burst 2 (only in Rhinella)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset (% TFA0)</td>
<td>na</td>
<td>na</td>
<td>74.1 ± 0.9</td>
<td></td>
</tr>
<tr>
<td>Offset (% TFA0)</td>
<td>na</td>
<td>na</td>
<td>98.6 ± 0.8</td>
<td></td>
</tr>
<tr>
<td>Relative amplitude (% of TO burst)</td>
<td>na</td>
<td>na</td>
<td>21.7 ± 2.8</td>
<td></td>
</tr>
</tbody>
</table>

Take-off bursts are scaled to take-off duration (TOD) and landing bursts are scaled to the force landing duration (TFA0). Statistical differences among species are indicated in the MANOVA column. Abbreviations: TOD, take-off duration; TFA0, the time that the fore-aft force returns to zero.
these variables are compared to mean force data and mean timings of kinematic events from Reilly et al. (2016).

**AP Translation**

All of the AP excursion means at kinematic events were significantly different from starting position zero), indicating that there is significant AP translation during jumping in all three species (within species t-tests, \( P's < 0.001 \). *Ascaphus* had significantly greater AP excursion (except for the minimum; Table 1) than the other species and had greater variability in AP excursion at each event during jumping (SEM’s; Table 1). The three species had similar patterns of AP translation at the
pelvis during jumping, with three basic phases (Fig. 5, bottom traces).

**Take-off AP extension.** AP excursion increases during take-off indicating that there is AP extension of the trunk on the ilia during the launch. AP excursion increases soon after the start of leg extension and then increases slightly through the time of peak forces, with the maximum extension occurring by the beginning (in *Ascaphus*) or the middle of the aerial phase (in *Lithobates* and *Rhinella*). Therefore, most of the AP excursion occurs by the time of peak forces but continued into the aerial phase. After the aerial peak, AP excursion decreases but not significantly in *Ascaphus* and *Lithobates* (i.e., the means at landing impact were not significantly lower; non-significant paired \( t \)-tests). This indicates that in these species, AP extension plateaus in the late aerial phase until landing impact. In *Rhinella*, AP excursion at hands hit is significantly lower than the aerial peak, indicating AP compression begins during the aerial phase. The earlier onset of AP compression in *Rhinella* may be related to the earlier and more ventral protraction of the hindlimbs.

**Landing AP compression.** In all three species, AP excursion decreases rapidly during landing, passes through the starting position and continued to a minimum significantly below zero. This shows that the early stages of the landing phase are characterized by AP compression and then super-compression as the pelvis translates forward on the sacrum beyond its starting position. The time of minimum AP excursion (i.e., maximum super-compression) coincides with the end of landing forces in *Ascaphus* (86% of TFA0). In *Lithobates*, minimum AP excursion coincides with the time of feet slap (58.8% vs. 53% TFA0, respectively) and peak body-landing forces (58.8% vs. 52–54% TFA0; nonsignificant paired \( t \)-tests). In *Rhinella*, minimum AP excursion occurred at the time of peak forelimb landing forces (29.5 vs. 26–27% TFA0, nonsignificant paired \( t \)-tests). Therefore, as landing forces are absorbed by the forelimbs and trunk, the momentum of the pelvis and legs causes the ilia to slide forward on the sacrum past the resting position to maximum AP super-compression as they reach peak landing forces.

**Landing AP extension.** After maximum AP compression, AP excursion increases back to the starting position (0) as the ilia recycle forward on the sacrum in the latter part of the landing. In *Lithobates* and *Rhinella*, the ilia return to the pre-jump position by the end of the foot placement phase and TFA0. In *Ascaphus*, in which limb protraction and foot placement phases occur well after TFA0, the pelvis returned to its starting position much later than in the other species.

**Pelvic Angle**

All pelvic angular excursion means at key events are significantly different than the starting position (zero), indicating that there are significant amounts of angular excursion in all three species (within species \( t \)-tests, \( P < 0.001 \)). Each species starts with a pelvic angle of about 141–144° and has angular excursions between 15 and 20° during the take-off phase (Table 1). Therefore, both pelvic configurations (rod-like and lateral benders) are characterized by equal magnitudes of sagittal extension. Surprisingly, *Ascaphus* has the greatest angular excursion (19.5°) but it is not significantly different than that of *Lithobates* (18.5°); *Rhinella* has the least angular extension (14.5°). Patterns of the timing of sagittal extension during take-off and landing differ among the three species.

**Ascaphus (Lateral-bender morphotype).** Angular excursion increases through the take-off phase (~9°) and early in the aerial phase (for another ~10°), levels off, and then peaks just before landing. The aerial increase corresponds to the “early flight head extension” behavior that is consistently observed in *Ascaphus* videos, in which they continue to extend the trunk and elevate the head after take-off. Maximum angular excursion does not differ from the value at body hit (nonsignificant paired \( t \)-test). In some trials with slightly more head-first landings, the impact would increase sagittal excursion such that the maximum occurs just after body hit. Subsequently, pelvic angular excursion decreases about 10° during the body-landing phase and slowly returns to the starting pelvic angle near the end of the foot placement phase (501% of TFA0), which coincides with toe down (494% of TFA0). The extra trunk extension in the aerial phase and the maintenance of a straight body early in landing seem to be related to the elevation of the limbs and head out of the way during their belly-flopping landings.

**Rhinella (Lateral-bender morphotype).** Like *Ascaphus*, toads increase the pelvic angle through the take-off phase (~11°) to reach a maximum in the aerial phase. Statistically, the angle at peak forces is smaller than at take-off (\( t \)-test = −5.71, \( P < 0.001 \)); however, the excursion at take-off, the aerial maximum excursion, as well as that at the instant of hands-hit do not differ (nonsignificant \( t \)-tests). This indicates that sagittal extension plateaus during the entire aerial phase. In contrast to *Ascaphus*, angular excursion decreases rapidly starting at hands hit and passing through the resting angle to a minimum of 3.5° past the starting position during the hand-landing phase. The time of minimum angular excursion (i.e., maximum super-flexion, 58.9% TFA0), coincides with the time the feet and body hit (55.7% TFA0), signaling the end of the hand-landing phase. Therefore, the hand-landing phase is characterized by rapid sagittal flexion followed by super-flexion up
to the point of peak landing forces. Starting at hands-
hit, the trunk becomes the stationary component of
the body and the pelvis and legs are the moving com-
ponents. Thus, landing forces of the hand-hit phase
seem to produce sagittal flexion back toward the start-
ing angle and may contribute to super-flexion. Subse-
quently, pelvic angular excursion increases as the
pelvic angle returns to the starting position by the end
of the body + feet landing period (Fig. 5).

**Lithobates (Sagittal-hinge morphotype).**
Lithobates differs in having sagittal extension peak
and then wane by the end of the aerial phase. Maximum angular excursion (18.5°) occurs at 70% of
take-off duration, which corresponds to peak
take-off forces (~73% TOD). It then decreases to 6°
at the instant of take-off and returns to the starting
position by the time the hands hit. During landing,
the pelvic angle remains at the starting position except for a variable small spike in pelvic angle at
the time that leg-slap (and peak landing forces) occur(Fig. 5).

**Variability in Motor Patterns**

Figure 6 presents sample electromyograms in
relation to jumping phases and events. Muscle
activity patterns in the IL muscles are highly vari-
able. In contrast to the other three muscles, we
could not discern repeatable patterns in the IL
across our sample. Reviewing 20 IL recordings in
each species revealed that the presence of continu-
ous small bursts of activity throughout the take-
off and landing periods is the most common pat-
tern (50% occurrence in each of the three species;
Fig. 6, see *Ascaphus*). In the rest of our sample,
all three species have a mix of a landing burst only
(Fig. 6, see *Lithobates*), a jump burst only
(Fig. 6, see *Rhinella*) or a jump and a landing
burst. The single-jump burst pattern is similar to
the EMG sample reported for *Rana esculenta* by
Emerson and de Jongh (1980), who found that the
IL motor amplitude is not related to jump height
and concluded that the IL muscle acts to stabilize
the presacral vertebrae relative to the pelvic gir-
dle. Our data support this function, but the varia-
tions in burst patterns suggest that the IL can
stabilize the trunk continuously, during take-off or
landing, or both. Although the IL is a small mus-
cle, it is positioned to pull the ilia forward in AP
extension. However, the IL is intermittently active
during AP extension during take-off and/or during
AP compression during landing. This indicates
that the muscle cannot be associated directly with
controlling AP translation of the ilia on the sacrum in jumping. The variable activation pat-
terns provide evidence that the IL functions in
trunk stabilization *as needed* during the take-off,
the landing or both phases of jumping. Because of
the variable IL motor patterns and the evidence
that it is not consistently correlated with pelvic
movements in jumping, we did not undertake fur-
ther analysis of this muscle.

The remaining three muscles exhibit stereotypi-
cal patterns of activity during take-off and landing
behaviors that reflect differences among the spe-
cies. Table 2 presents mean motor patterns and
statistical comparisons of species and the resulting
mean motor patterns are illustrated as bar dia-
grams in Figure 5. In all of the muscles studied,
take-off activity starts significantly earlier than
does leg extension (*t*-tests, *P* < 0.001) and ends in
the latter half of the take-off; this pattern is simi-
lar to the leg extensor muscles in other studies
(Kamel et al., 1996; Gillis and Biewener, 2000).

**Motor Patterns in Relation to Sagittal
Bending of the Pelvis (LD and PF)**

The onset of LD activity occurs at the same rela-
tive time in all three species (about −47% of TOD)
and the PF (not studied in *Ascaphus*) becomes
active later at about −24% of TOD. Both muscles
ramp up activity to maximal levels in this pre-
take-off period that begins at or just after the
onset of take-off (Fig. 6). Thus, the LD and PF
have high levels of EMG activity by the time that
angular extension starts. At this point, the PF sta-
bilizes the urostyle and the LD extends the anteri-
or body relative to the pelvis. Note that extension
of the trunk on the ilia would stretch the PF and
improve its ability to depress the urostyle. These
muscles maintain high levels of activity (Fig. 6)
throughout the take-off period when sagittal
excursion goes from 0 to near maximum levels
(Fig. 5). Thus, the proposed functions of the LD/ PF
in extending the trunk on the pelvis and
depressing the urostyle during take-off (Emerson
and de Jong 1980; Jenkins and Shubin, 1998) are
confirmed in all three species. After take-off, each
species is characterized by its own pattern of mus-
cle activity.

**Ascaphus (Lateral-bender morphotype).**
Sagittal extension increases about 9° by the end of
the LD take-off burst (50% TOD). The LD then
relaxes before contracting again shortly before
take-off (86% of TOD); this differs from the aerial
onset times of the other two species. The early
onset of the landing burst seems to be related to
the “early flight head extension” behavior
observed. Activity in the LD continues through the
landing phase until 274% of TFA0, which occurs
just before the end of the limb flexion phase (352% TFA0; Fig. 6). Therefore, the landing LD burst in
*Ascaphus* seems to increase sagittal extension dur-
ing the aerial phase to extend the body prior to
and during landing. The highest amplitudes of LD
activity occur during this time (Fig. 6) and then
lower levels are maintained to stiffen the trunk
during the limb recovery phase. We would expect
the PF to exhibit the same pattern.

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**Rhinella** (Lateral-bender morphotype). In toads, sagittal extension continues to increase after the offset of LD and PF activity; it then statistically plateaus during the aerial phase. It is unclear why sagittal extension continues after the muscles have gone silent, but it could be maintained by the action produced by the LD/PF burst. *Rhinella* has two landing bursts that involve staggered bursts in the LD and PF similar to those seen during take-off.

The first set of landing bursts starts early in the aerial phase and ends in the hand-landing phase. The LD muscles seem to maintain sagittal extension, preload the axial column for landing, and stop firing at about the time that peak landing forces occurred during hand landing. The intensity of LD and PF landing bursts are about 30% or less than that of take-off bursts when angular excursion increases. Thus, the hand-landing bursts of

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Fig. 6. Representative electromyograms during jumping for three species of anurans in relation to kinematic events during the jump. Traces are scaled to take-off duration and the percent TFA0 (the period from hit to when fore-aft forces return to zero) is indicated on landing images. *Iliolumbaris* (IL) activity patterns are highly variable across jumps and include patterns of continuous activity, activity in landing only, activity in take-off only (illustrated in *Ascaphus*, *Lithobates*, and *Rhinella*, respectively), or separate take-off and landing bursts (not illustrated). The PF muscle was not studied in *Ascaphus*. 

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the LD and PF muscles seem to act in lower-intensity eccentric contraction to control trunk flexion on the pelvis. This is likely correlated with the dynamic motor control of the forelimb landing and rotation of the body on the forelimbs and pectoral girdle in *Rhinella* (Gillis et al., 2010; Griepp et al., 2013; Gillis et al., 2014).

In the middle of the landing phase, both LD and PF muscles become inactive just before the angular excursion passes through the resting position, indicating there may be a period of passive flexion and super-flexion just prior to the time the body and feet hit the ground. The second landing burst occurs in the last quarter of the landing phase when muscles seem to return to concentric contraction as the pelvic angle returns to its starting position and the toes are put down.

**Lithobates (Sagittal-hinge morphotype).** In bullfrogs, the LD and PF take-off bursts occur during the rapid increase in sagittal extension. The offset times of both muscles do not differ significantly from the times to maximum sagittal extension and of maximum take-off forces (nonsignificant t-tests). Emerson and de Jongh (1980) reported a similar pattern for the LD take-off burst in *Rana esculenta*. Thus, as was expected, the activity of the sagittal extensors corresponds to the increase to maximum pelvic angle during take-off in *Lithobates*. However, in contrast to the other species, as soon as LD and PF activity stops, the pelvis quickly flexes back to the prejump pelvic angle by the end of the aerial phase. In the last third of the aerial phase, LD and PF activity resume at a lower level (~30% of take-off burst amplitude) until the end of the landing (TFA0). Because there is no change in angular excursion during this time, the LD and PF seem to preload the axial column to prepare for the landing impact. Subsequently, the lower level of activity in both muscles seems to indicate that isometric contraction maintains the pelvic angle at the starting angle throughout the hand-landing and body-landing phases. However, there is evidence that peak landing forces that occur during the feet-slap phase may cause a small rise in angular extension at the pelvis at the time maximal landing forces occur (Fig. 5).

**Motor Patterns in Relation to AP Translation of the Pelvis (CI)**

**Take-off.** As described above, the three species have similar patterns of AP extension during take-off. In each species, the take-off bursts of the CI start before the beginning of jump movements and end at the same time as the LD and PF take-off burst (60–68% of TOD). Emerson and de Jongh (1980) found similar patterns of activity in *Rana esculenta*. This indicates that the CI may preload the system prior to the onset of AP extension. After the initial preloading period, the CI bursts are coincident with the period of increasing AP extension. The CI seems to protract the urostyle; as a consequence, the sacrum slides on the ilia which extends the trunk relative to the pelvis. *Ascaphus* differs in having a long preloading period in the CI (~68% of TOD) compared to the other species (~12 to ~22% of TOD for *Lithobates* and *Rhinella*, respectively). The longer preloading phase may explain why *Ascaphus* had a faster rate of increase to a significantly higher AP extension (about double that of the other species).

In all three species, AP extension continues to increase after the CI (and the other muscles) have gone silent, until reaching its maximum in the aerial phase. Thus, AP extension seems to continue passively to its highest point without any contribution of the CI muscles. The question then arises as to how the trunk continues to pull away from the pelvis. This may be related to differences in momentum between the pelvic girdle and the center of mass situated in the trunk. Inertia is conveyed to the trunk by a combination of 1) forces imparted to the pelvis by the legs and hips and 2) the extension of the urostyle and trunk on the ilia by the contracting CI muscles. Maximum inertia is conveyed to the trunk by the time that peak forces occur (about 70% of TOD). As take-off forces wane and the feet come off the ground, the take-off function of the posterior body ends and the pelvis and legs drag behind the trunk. Therefore, we propose that the passive increase in AP extension late in the take-off phase and during the aerial phase may result from the difference between the momentum of the trunk and the inertia of the pelvis and legs. In addition, in all anurans except Leiopelmatids, the legs begin to fold right after take-off peak forces (Reilly et al., 2016). Thus, in these species, the internal inertial effects of the legs being drawn forward may pull the pelvis posteriorly relative to the trunk. This may explain the later aerial phase peaks in AP extension in *Rhinella* and *Lithobates*.

**Landing.** During landing, all three species have a period of AP compression followed by AP extension. In *Ascaphus* and *Lithobates*, the activity in the CI starts in the middle of the aerial phase and continues until TFA0 in *Lithobates*, and well beyond that in *Ascaphus*. Mean landing amplitudes in the CI are smaller than the take-off bursts, but they are relatively greater in *Ascaphus* (51%) than in *Lithobates* (20%). Thus, in these species, the CI preloads before impact and then, acting in lower intensity eccentric contraction, controls AP compression into super-compression as landing forces rise. After peak AP compression, CI activity continues and seems to shift back to concentric contraction that then re-extends the trunk back to its starting position by the end of TFA0 (or much later in *Ascaphus*).
During landing in *Rhinella*, the CI motor pattern is characterized by two bursts (as are the LD and PF). This is likely related to their two-phase landing behavior – i.e., hand landing first followed by the body-feet landing (Reilly et al., 2016). However, the first CI landing burst is noticeable in only about half of the trials recorded for two individuals, and totally absent in the third individual. Note that the largest burst observed is the one shown in Figure 6. Therefore, the first landing burst was not digitized and can be considered inconsequential. The lack of consistent CI activity in the hand-landing phase suggests that the pattern of AP compression and super-compression of the pelvic girdle observed during this phase may be entirely passive. As landing forces increase to their maximum during the hand landing phase, the ilia seem to slide from maximum extension to maximum compression. Thus, the pelvic girdle in *Rhinella* is proposed to function as a passive breaking mechanism that slides the ilia forward to the maximum extent allowed by their large iliosacral ligaments. After this, CI activity again seems to extend the pelvis back to its starting position actively (by the time that the toes are put down).

**DISCUSSION**

**Presence of Sagittal Bending and AP Translation During Take-Off**

Our goal was to understand how AP translation and sagittal bending contribute to jumping mechanics in anurans. Contrary to expectations, all three species extend the trunk at the pelvic girdle during the rise to maximal take-off forces. The range of sagittal extension (13–20°) we observed during take-off matches that (17–20°) reported for freely jumping *Lithobates catesbeianus* (Jenkins and Shubin, 1998). Sagittal extension is controlled by the activity of the LD and PF muscles. This confirms the original hypothesis that pelvic movements align the trunk with take-off forces (Whiting, 1961; Emerson and de Jongh, 1980) and that the PF depresses the urostyle while the LD elevates the trunk (Jenkins and Shubin, 1998). Although this hypothesis was originally proposed only for the rod-like pelvic configuration (*Lithobates*), our data show that anurans with the lateral-bender configuration also align the trunk with take-off forces using the same motor patterns.

In addition, all three species produce measureable amounts of AP extension (~4–11% of trunk length; 3–20 mm) during take-off; the amount of extension seems to be controlled by the contraction of the CI. Previously, it had only been considered in relation to walking. Our data reveal that AP translation is an integral component of both take-off and landing.

**Decoupling of Sagittal Bending and AP Translation in the Rod-Like Pelvis**

In the rod-like pelvis of *Lithobates*, the pelvic angle quickly increases and plummets back to near the starting position by the end of the aerial phase (Fig. 5). This supports Emerson’s (1982) proposal that the rod-like sacral diapophyses do not interfere with sagittal rotation of the ilia. Our data show that *Lithobates* reaches its peak sagittal extension in significantly less time than do the other species. Therefore, a key feature of the rod-like pelvis seems to be the ability to extend the trunk faster than the lateral-bender configuration.

Based on the short iliosacral ligament of the rod-like configuration, Emerson (1982) concluded that movement in the horizontal plane was not possible; thus, she did not consider AP translation to be a component of pelvic function. In contrast, our data show that the pelvic girdle of *Lithobates* extends 4% of trunk length during take-off. This can be explained by the contraction of the CI muscles that extend the urostyle and trunk on the ilia to the extent possible with its short iliosacral ligaments. After take-off, AP translation in *Lithobates* seems to be related to the different inertial relationships of the trunk and pelvic. AP extension continues to increase during the aerial phase as the body drags the pelvis and legs. Subsequently, when inertial relationships reverse during landing, AP compression occurs as the anterior body slows down first, while the legs and pelvis continue moving forward relative to the body. The kinematics suggest that AP compression may contribute to a breaking function during landing, both passively, as the iliosacral ligaments are stretched to their posterior limits, and actively, via the eccentric contraction of the CI muscles.

In summary, AP translation does not seem to be functionally linked to sagittal movements in *Lithobates*. It increases through the pulse of sagittal extension and flexion during take-off, and then, rapidly drops back to the starting angle prior to the AP compression movements during landing. Therefore, we propose that another key feature of the rod-like pelvis is a decoupling of AP translation and sagittal bending during jumping. In other words, sagittal bending functions in take-off to rapidly align the trunk with take-off forces, whereas AP translation functions later to absorb landing forces.

**Dynamic Coupling of AP Translation and Sagittal Bending in the Lateral-Bender Pelvis**

The parallel patterns of angular and AP excursion profiles in *Ascaphus* and *Rhinella* reveal a correlation between AP translation and sagittal bending in the lateral-bender configuration. During take-off, both *Ascaphus* and *Rhinella* are
characterized by an early increase in AP extension and sagittal extension until reaching their maximum in the aerial phase. During landing, the pelvis responds to impact forces, and transitions to AP compression and sagittal flexion to return to the starting position, albeit much later in Ascaphus. Clearly, sagittal extension occurs when the sacrum slides backward on the ilia, whereas sagittal flexion occurs when the sacrum slides forward on the ilia. Thus, AP translation and sagittal bending are coupled in the lateral-bender pelvis.

Emerson (1982) proposed the long overlapping articulation of the ilia under the expanded arcs of the sacral diaphyses forms a fore-aft sliding joint used unilaterally during walking. She found that the ilia were able to slide fore and aft in opposite directions on the sacral diaphyses as the pelvis rotated laterally about 9–14°. Emerson (1982) and many previous workers (Gadow, 1901; Green, 1931; Gregory, 1935; Noble, 1931; Parker, 1932) hypothesized that the ilia were "fixed"—that is, unable to bend sagittally because of the tight connections of the iliosacral ligament. However, Emerson reported sagittal extension occurring during jumping in lateral-bender forms, but did not discuss how sagittal bending occurred or how it related to AP translation, which was not measured for jumping. To understand the function of the lateral-bender pelvic configuration during jumping, we examined the relationship between AP translation and sagittal bending by manipulating clear-and-stained and fresh specimens. AP translation of the ilia outside the overlapping "fixed" zone on the sacrum reveals how the lateral-bender pelvis bends sagittally during take-off and landing.

A Model for Pelvic Function in the Lateral-Bender Configuration in Jumping

When specimens are manipulated in the range of positions shown in Figure 1, sagittal bending does not occur as long as the entire iliosacral ligament stays dorsal to the sacral arc. This is because, as posed in the literature, the full AP length of the ligament maintains a sufficiently long longitudinal overlap of the ilia and ventral sacral surface to prevent sagittal bending (Fig. 7c,d). However, if the trunk is extended farther, the ligaments slide off the rear of the sacrum and the sacrum/trunk extends dorsally (Fig. 7e,f). This is because the iliosacral ligaments and their sesamoid bones slide off the rear of the sacral arc and begin to pull linearly between the ilia and their dorsal attachments on the dorsomedial surface of the sacrum. In contrast, when the ilia slide anteriorly, the ligaments slide back over the sacral arc and engage the sesamoids laterally on the sacra to lock the joint into its sagittally immovable position (Fig. 7c,d). When the ilia slide farther anteriorly, the ligaments and sesamoids slide off the front of the sacral arcs and the anterior tips of the ilia immediately rotate up in front of the sacrum to project into the dorsum of the trunk, whereas the posterior tips of the ilia easily flex ventrally (Fig. 7a,b). Therefore, AP compression and super-compression phases of the trunk result in sagittal flexion of the pelvic girdle relative to the trunk.

Based on specimen manipulations, pelvic kinematics, motor patterns and force recordings, we propose the following model for the function of the lateral-bender configuration of the anuran pelvis during jumping.

Starting position. Prior to the jump, the iliosacral ligaments are positioned in front of the overlap zone with the sacral diaphyses, with the tips of the ilia rotated in front of the sacrum; thus, the trunk is angled at a low angle relative to the ground. This posture produces the noticeable sagittal bend usually observed in anurans when they are sitting at rest.

Take-off. During take-off, extension of leg muscles aligns the pelvis to the take-off angle and the ilia become the static component from which the trunk is free to translate on the iliosacral joint. High amplitude activity of the pelvic muscles depresses the urostyle (PF), elevates the trunk (LD), and extends the urostyle, sacrum and trunk on the ilia (CI). The initial forward motion of the sacrum causes the iliosacral ligaments to slide over the sacral arcs, engage the sesamoids on the lateral arcs of the sacrum and set the iliosacral joint into the overlap zone that elevates the trunk in line with the ilia early in the take-off. Therefore, we hypothesize that AP extension and the action of LD muscles elevates the trunk and locks the ilia and sacrum in a linear configuration as take-off forces begin to mount.

As sacral extension continues, the sacrum slides through the overlap zone with the ilia during the middle of take-off. For more than a century, overlap of the sacrum and the ilia in the lateral-bender pelvic configuration has been thought to create a rigid articulation between the ilia and the trunk. Our work shows that the pelvis only works in this rigid manner to maintain the trunk-pelvis alignment during the power phase of take-off.

As take-off progresses, the sacrum extends farther on the ilia owing to the contraction of the CI, which moves the ligaments off the back of the sacral arcs, thereby tightening the ligaments and extending the trunk even farther dorsally—as observed in the aerial phase (Fig. 5). As proposed above, the difference between the momentum of the trunk and the inertia of the pelvis and legs also may contribute to AP and sagittal extension after the LD and PF stop contracting. Therefore, it seems that AP super-extension also may create additional sagittal extension when the ligaments slide off of the back of the sacrum.

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Landing. During landing, the dynamics change as the trunk becomes the static component and the pelvis and legs move in from behind and articulate through the moveable iliosacral joint. During impact, the ilia rapidly slide anteriorly through the “fixed” overlap zone until the iliosacral ligaments slide off of the front of the sacrum and stretch to their anterior limit (i.e., supercompression). In *Rhinella*, rapid angular flexion follows, passing through the resting angle and beyond as the rear of the body super-flexes on the trunk as peak forces occur. Subsequently, AP and angular extension returns the toad to its rest position.

Braking During Landing

In all three species, the impacts of landing produce the same effect on the iliosacral joint in the horizontal plane. The pelvis goes from its maximum point of AP extension through the starting position into super-compression by the time peak forces occur. Ligaments and other tissues are known to store and return energy in other hopping animals (Farley et al., 1993; Roberts and Marsh, 2003; Astley and Roberts, 2012; Schnyer et al., 2014) and the anuran pelvis may act as a braking mechanism in which the ligaments are stretched to their anterior limits during AP compression. In addition, in *Ascaphus* and *Lithobates*, braking during AP compression seems to be mediated by eccentric contractions in the CI, an observation that supports an earlier proposal that the CI seems to function as a shock-absorber during landing (Whiting, 1961). Leg muscles in anurans have much greater passive elastic properties than do mammalian muscles (Azizi, 2014; Roberts and Marsh, 2003) and eccentric contractions may facilitate the passive elastic properties of the pelvic muscles as well. *Lithobates* returns to starting body angle before it hits and the LD seems to maintain this angle throughout landing, thus, potential spring-like braking seems to be acting only in the AP direction in this species.

In *Rhinella*, there is little to no activity in the CI during hand landing and the pelvis seems to act as a completely passive mechanism; the toads seem to rely on their large iliosacral ligaments (Fig. 1). In addition, the ilia in *Rhinella* swing forward and rotate into maximal sagittal flexion with AP super-compression; thus, their passive braking system may act in two dimensions. This seems to facilitate the complete pre-folding of the legs during the hand-landing phase which is unique to toads (Gillis et al., 2014). It is interesting to note that lateral-bender forms tend to have shorter transverse processes in the posterior region of the vertebral column allowing the ilia to project anterior to the sacrum without hitting them.
Aerial Rotation and Controlled Landing

As Emerson (1985) discussed, jumpers must control clockwise axial rotation during take-off (when viewed from the right) to keep the body from falling over and to maximize jump distance. In anurans, sagittal pelvic extension is used to raise the trunk in line with hindlimb forces during take-off. With the advent of forelimb landing, forelimb extension, and folding of the hindlimbs in the aerial phase moves the center of mass forward. This rotates and aligns the body axis to control torque during landing. Based on the leioptematids, the basal anurans also employed sagittal body extension to raise the trunk during the launch. They take-off with a ski-jumper posture (all four limbs extended posteriorly); they do not use the limbs to control body rotation in the aerial phase and they crash into the substrate in this ski-jumper posture. However, they do seem to employ several actions to control axial rotation. First, keeping the limbs back would keep the center of mass in a more posterior location to prevent rotation as seen in jumping mammals with long heavy tails. Second, *Ascaphus* has a longer CI preloading phase, a faster rate of increase in AP extension and significantly great AP extension than *Rhinella*. This indicates that their pelvis proceeds through the rigid “overlap zone” faster to straighten the body earlier and prior to take-off. This is combined with the pre take-off return of LD activity to elevate the trunk even farther before and during the aerial phase. Thus, their early flight, extra extension behavior may be a way to increase counter-clockwise rotation to counteract body rotation, increase jump distance and to keep the head and limbs out of the way in anurans that have not evolved controlled landings.

Implications for the Evolution of Anuran Jumping

Although we only have data for two lateral-bender taxa and one rod-like species, our quantitative data provide new insights and raise further questions about the evolution of pelvic function in anurans. First, the presence of the sagittal extension and flexion reveals that the lateral-bender pelvis can act as a lateral bender and a sagittal hinge. Extreme bilateral and bidirectional antero-posterior translation is key to the sagittal-bending function of the lateral-bender pelvis and the sacroiliac articulation may act as a passive braking system in landing. Bilateral AP translation facilitates sagittal bending during jumping without compromising the ability to use AP translation unilaterally in opposite directions during other locomotor modes. This functional flexibility seems to be the key to its widespread retention across the Anura because it permits a range of locomotor behaviors. Indeed, the lateral-bender pelvis is both basal and general to anurans that are walkers, hoppers, jumpers, burrowers, and climbers (Reilly and Jorgensen, 2011). The basal-most anurans (leioptematids) which rarely jump in nature (Reilly et al., 2015a) are characterized by extreme body extension prior to the belly-flop landing (Reilly et al., 2016). In contrast, toads exemplify tight coordination of pelvic movements with controlled hand-landing in the hopping and bounding locomotion that has allowed them to become one of the most cosmopolitan assemblages of anurans (Reilly et al., 2015b). In hylids frogs, the lateral-bender pelvis supports for vertical walking (climbing) and long-distance jumping (Marsh and John-Alder, 1994); this doubtless has contributed to their exploitation of many terrestrial niches and speciation.

Second, why has the rod-like pelvis and its large dorsal flanges appeared convergently in so many anuran taxa (Reilly and Jorgensen, 2011)? Taxa with the rod-like configuration usually have longer jump distances (Zug, 1978); thus, this pelvic configuration is thought to be an adaptation for better jumping performance (Emerson, 1979). However, jumping performance has been studied primarily from the perspective of the hindlimbs, in which take-off capacity has been related to longer legs, more musculature and higher contractile rates that generate faster and more powerful take-offs (Zug, 1972, Emerson, 1978; Choi and Park, 1996; Choi et al., 2000, 2003). Interestingly, the burst type of locomotion in anurans that jump greater distances has been shown to depend more on the rate of energy release than the total amount of energy released by jumping muscles (Choi et al., 2000). Therefore, if the legs are propelling the ilia more rapidly during the take-off to jump farther, then the iliosacral joint must also work faster to align the trunk and center of mass with the take-off trajectory. In fact, we found that in the rod-like pelvis of *Lithobates*, the frog extended the trunk to its maximum angle significantly faster than the lateral-bender taxa. Thus, in terms of pelvic behavior, the rate of trunk extension seems to have increased to match the faster rate of energy release predicted to be coming from their larger muscles and longer legs.

Morphologically, several of the features of the rod-like pelvis seem to be related to bringing pelvic function into line with faster energy release in the legs. First, the urostyle and longer ilia with their large dorsal crests provide deep and wide attachment sites to accommodate larger muscles. Emerson and de Jongh (1980) reported that taxa with the rod-like pelvis had two to three time greater cross-sectional area in the CI and LD muscles; this would increase forces extending the trunk. Second, the more lateral orientation and shorter fiber lengths of the CI muscles may be related to a faster stabilization of the urostyle and more forceful connection of the ilia with the
uropyle to provide a fixed joint from which the trunk extends sagittally. Last, the postero dorsal orientation and narrowing of the sacral rods provides several advantages. The dorsal elevation of the diaphyses provide a large trough through which the larger LD muscles can contract and slide over the sacrum. The posterior shift of the tips of the rods adds to pelvic length and moves the fulcrum of the iliolsacral articulation point posteriorly, directly over and farther from the bicondylar articulation point of the urostyle on the sacrum. The postero-dorsally directed rods also position the LD muscles closer to the midline, which would increase their resultant force vector and its effects on elevating the trunk on the urostyle. A similar argument has been made for the narrower interiliac width of the rod-like pelvis creating a greater resultant take-off vector for the legs by moving the hindlimb force vectors closer to the midline (Gabriel, 1984; Hildebrand, 1988; Choi and Park, 1996). Functionally, the shift to the rod-like pelvis for a more powerful jump makes sense. Interestingly, there seems to be strong canalization in pelvic development to account for at least five Neobatrachian taxa to have evolved convergently nearly identical sets of anatomical traits characteristic of the rod-like pelvic configuration (Reilly and Jorgensen, 2011; Jorgensen and Reilly, 2013). Comparisons of the anatomy, development and function of the pelvic girdle in these taxa is an area in need of additional research. Finally, despite our new appreciation of the functional flexibility of sagittal bending in the two terrestrial anuran pelvic configurations, the functional reason for the evolution of the anuran Bauplan remains to be explained. Traditionally, the anuran Bauplan has been widely regarded as an adaptation to increase jumping distance to escape predators (Inger, 1962; Gans and Parson, 1966; Jenkins and Shubin, 1998; Handrigan and Wassersug, 2007). Thus, one would expect the earliest anurans to escape by jumping significant distances. However, a recent study has shown that the basal-most living anurans (Leiopelmatidae; Reilly et al., 2015a) 1) prefer to walk rather than jump, 2) riparian species jump on land more frequently into the water, and 3) the terrestrial species were rarely (Leiopelma pakeka) or never (L. archeyi) observed to jump. There is ample additional evidence that the leiopelmatids rarely escape by jumping (Bell, 1982, 1995; Daugherty and Sheldon, 1982; Green, 1988; Melzer et al., 2011, 2012; Metter, 1964). If ancestral anurans resembled leiopelmatids, they likely were not jumping to escape, but rather, employed short jumps as a way of moving around the environment.

If the basal anuran Bauplan promoted jumping, one might expect anurans to be more accomplished jumpers than other tetrapods. This is not borne out in published measures of jump distances in anurans compared to those of other tetrapods. Jump distances (in snout-vent lengths) for four leiopelmatids recorded in the lab (4.3–6.4: Reilly et al., 2015a), six toad species (1.5–5.1: Wermel, 1934; Rand, 1952; Zug, 1972, 1985), two Bombina (3.4–3.8: Reilly et al., 2016; Wermel, 1934), two hylids (6.3–7.8: Zug, 1978, 1985), and five species of ranids (5.6–7.7; Zug, 1978) are the same as or lower than those recorded in other small tetrapods (10 species of Anolis lizards (5.9–9.2; Bels et al., 1992; Toro et al., 2004), four species of Niveoscincus skinks (4.5–6.1: Melville and Swain, 2003), the salamanders Eurycea bislineatus and Desmognathus ocoee (1.6–2.4: Ryerson, 2013; Dowdew and Brodie, 1989) and three species of terrestrial jumping fishes (5.0–6.5: Gibb et al., 2013). Therefore, based on an array of living anurans, including the most basal taxon, the advent of the anuran pelvis capable of sagittal extension is not related to an increase in jumping ability. Jumping ability does increase in some crown-group taxa including most of the rod-like species and a few taxa of both pelvic configurations with extremely well developed legs (Jorgensen and Reilly, 2013; James and Wilson, 2008). Furthermore, a broad-scale analysis has shown that shifts in jumping ability are more related to niche diversification in crown group radiations than differences in pelvic type (Gomes, et al., 2009). These patterns call into question the relationship between jumping ability and the ancestral anuran Bauplan and support the hypothesis of Gans and Parsons (1966) that jumping as an escape strategy evolved not in the Proanura, but in the Lalagobatrachians or Neobatrachians. Recent inferences based on ancestral reconstructions of anuran morphology and jumping performance came to the same conclusion (Herrel et al., 2015).

In sum, the more we learn about anuran locomotion the less we know about the enigmatic emergence of the anuran Bauplan. Although, the anuran pelvis probably was not a key innovation for long-distance jumping, it does function to align the trunk with take-off forces and it is widely adaptable for different patterns of landing and different locomotor modes. However, as Emerson (1985) and Choi et al. (2000, 2003) have posed, the quickness of movement rather than jump distance may be the more biologically important critical parameter in anurans that may have driven the shift to having the iliolsacral joint in the middle of the body.

ACKNOWLEDGMENTS

We thank three reviewers that provided helpful comments and suggestions on a previous version of the manuscript. We also thank Susan Williams for discussions about patterns of anuran jumping behavior. All procedures were approved by the Ohio University Institutional Animal Care and Use Committee.


