Evolution/Évolution

Morphometric ratio analyses: Locomotor mode in anurans

Tamara G. Petrović a, Tanja D. Vukov b, Nataša Tomašević Kolarov b,c

a Faculty of biology, university of Belgrade, 11000 Belgrade, Serbia
b Institute for biological research, department of evolutionary biology, university of Belgrade, 142, Bulevar despoti Stefan, 11000 Belgrade, Serbia

c Corresponding author.
E-mail addresses: b3045_2014@stud.bio.bg.ac.rs (T.G. Petrović), tvukov@ibiss.bg.ac.rs (T.D. Vukov), natasha@ibiss.bg.ac.rs (N. Tomašević Kolarov).

A R T I C L E   I N F O

Article history:
Received 9 August 2016
Accepted after revision 23 February 2017
Available online xxx

Keywords:
Locomotor groups
Anura
Forelimbs
Hindlimbs
Sacral size

A B S T R A C T

Current studies of anuran morphology use sacral vertebrae, hindlimbs as main predictor for locomotor modes, while forelimbs and their segments were not analysed in this context. Due the fact that the complex interplay of numerous morphological traits determines the locomotion ability of anurans, we used ratios for both fore- and hindlimbs to obtain useful information of the structural and functional properties of locomotor system. We examined patterns of variation in total length of fore-, and hindlimbs as well as sacral vertebrae width and diapophyseal expansion in order to position two locomotor modes (jumpers and walkers) in a morphological shape space. Further, we investigated patterns of variability in limbs proximal, medial and distal elements to highlight differences in intra- and inter-limb relations in two locomotor modes. Our results showed that the ratios between total hindlimb length and sacral width/diapophyseal expansion, as well as ratio between humerus and tibiofibula relate the most to locomotor modes. This implies that functional specialization in different locomotor modes is attained through modifications of ratios, not only within hindlimbs, but also through modifications of the whole integrated system, which consists of forelimb, hindlimb, and girdle elements.

1. Introduction

Locomotion represents a complex mechanism that is determined by combinations of structural and functional properties (morphology, muscle structure, and limb kinematic patterns), and is tightly associated with morphology and different aspects of ecology [1–3]. Anurans pose a unique way of locomotion, which required some changes from basic tetrapod’s bauplan in anatomical traits [4–6]. This involves an elongation of hindlimbs, a shortening of the presacral vertebral column, a reduction in the tail, the presence of elongated ilia, and the urostyle [7]. Although developmental and genetic programs (‘Bau- plan machinery’) constrains the range of morphologies available to anurans, they are flexible enough to allow different body morphologies to evolve in the frame of very diverse lifestyles of anurans (burrowing, swimming, walking, hopping, jumping, climbing and gliding) [5,8,9].

Over the past few decades, studies of anuran locomotion showed that different aspects of postcranial morphology (mainly limb proportions and pelvic traits) correlate to a varying degree with locomotor modes [8–11]. Particularly noteworthy is the role of hindlimb length as a predictor of locomotor mode of anuran species [9]. Anurans with relatively long hindlimbs tend to be relatively good jumpers [4,10,11]. Longer hindlimbs are associated with larger muscle and energy storage [12], and higher jumping
force [13]. Opposite to jumpers, walkers have shorter hindlimbs, which provides them movement in a series of short steps and great capacity of sustained locomotion through the forest floor [14,15]. Sacral traits are also related with locomotion, due to their unique biomechanical consequences for controlling the posture of the trunk and head relative to the pelvis and legs during jumping. Small diaphyseal expansions in jumpers allow them to increase their rate of trunk elevation relative to the rates of energy release from the hindlimbs, enabling them to jump farther. On the other hand, an expanded sacrum in walkers allows lateral rotation of the pelvis during walking and burrowing [16]. In contrast to hindlimbs and sacral shape, forelimbs were thought to be less correlated to locomotor modes [9,17], but this point has been less studied in that context. The main roles of forelimbs are to ensure balance during jump control landing [18] and branch grasping [19]. However, forelimbs have a variety of different roles beside locomotion (such as prey capture and manipulation during feeding [20], amplexus [21] and skin-shedding [22]), so we cannot expect clear correlation patterns with different locomotor modes.

The use of ratios of morphometric traits (i.e. of body proportions) has a long tradition and is integrated into taxonomical, phylegenetic and morphological studies. It provides an efficient way of looking at the shape of organisms, which, expressed by ratios, is invariant for a particular measure of the size [23,24]. Due to the fact that the complex interplay of numerous morphological traits determines the locomotion ability of anurans, the analyses of ratios will reveal useful information about the structural and functional properties of the locomotor system, and, as such, they can show differences among locomotor modes. Previous studies showed clear relations between morphological trait ratios and locomotor performances in anurans. For example, the total limb length to body size ratio proved to be important ratio for describing locomotor modes, with shorter hindlimbs and longer forelimbs in walkers compared to jumpers [9,12]. Within hindlimbs, the tibiofibular-to-femur ratio is marked as the key ratio, with higher values in jumpers (>1), increasing the outlever arm, and therefore, the jumping force. In contrast, lower tibiofibula to femur ratios (<1) enhance the walking and burrowing capacities required by walker species [10,25,26].

In the present study, we investigated how patterns of variation in morphological traits and their ratios (fore-, hindlimbs, and sacral vertebrae) are related to two different types of locomotion, jumpers and walkers. First, we described patterns of variation of basic structural parts relevant to locomotion: total length of forelimbs, total length of hindlimbs, sacral vertebrae traits (sacral width and diaphyseal expansion). In this way, we will be able to compare our results with literature data. Second, as was noted by Enriquez-Urzela et al. [25], studies about anuran morphology associated with locomotion, usually considers fore-, and hindlimbs as a single functional unit. But, biomechanically, every part (proximal, medial, and distal) has specific functional output, so relationships between them may differ between jumpers and walkers. For that reason, as a novel approach, we analyzed patterns of variability in fore- and hindlimb proximal (humerus/femur), medial (radioulna/tibiofibula) and distal elements (carpals, metacarpals/tarsals, metatarsals, and phalanges) to highlight how within- and between-limb relations are linked to two locomotor modes (jumpers and walkers).

2. Materials and methods

The study sample consisted of 217 adult individuals (125 males and 92 females) belonging to nine anuran species (Table 1), originating from the Balkan Peninsula, in order to minimize the influence of local environmental conditions on life-history traits, which can influence phenotypic change [25]. The sex of the frogs was determined based on gonads. Although the most anuran species are characterized by marked sexual dimorphism, a preliminary analysis (two-way ANOVA, factors: species, sex) showed that the differences between species were more pronounced than between sexes (structure: species: \( F_{12,278} = 183.75, P < 0.001 \), sex: \( F_{4,197} = 15.97, P < 0.001 \); limb parts: species: \( F_{40,949} = 115.76, P < 0.001 \), sex: \( F_{2,213} = 19.11, P < 0.001 \)). Therefore, we pooled sexes to increase the number of individuals and to maximize differences between locomotor modes as the main question of this paper. All individuals were deposited at the osteological collection of the Institute for Biological Research “Siniša Stanković”, Belgrade, Serbia.

The analysed anuran species were associated with two locomotor groups based on the published literature [8,9,12,25]: walkers and jumpers (Table 1). Out of nine analysed species, five of them (P. fuscus, P. syriacus, B. variegata, R. graeca, P. esculentus complex) were studied for the first time in a framework of limb morphology and locomotor modes [8,9,25].

2.1. Data

The samples were preserved in 75% ethanol and prepared as cleared whole mounts that were differentially stained, according to Dingerkus and Uhler [27], using alizarin red for bone, and alcian blue for cartilage. All skeleton measurements were taken on the right-hand side of the frog with a digital calliper (precision: 0.01 mm). The lengths of forelimb elements: humerus (H), radioulna (R),

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Species</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hyla arborea</em></td>
<td>30</td>
<td><em>Bombina variegata</em></td>
<td>30</td>
</tr>
<tr>
<td>loc: Vir Pazar</td>
<td></td>
<td>loc: Prohor Pčinjski</td>
<td></td>
</tr>
<tr>
<td><em>Pelophylax esculentus</em></td>
<td>25</td>
<td><em>Bufo viridis</em></td>
<td>18</td>
</tr>
<tr>
<td>complex</td>
<td></td>
<td>loc: Fruška Gora</td>
<td></td>
</tr>
<tr>
<td><em>Rana graeca</em></td>
<td>18</td>
<td><em>Pelobates fuscus</em></td>
<td>28</td>
</tr>
<tr>
<td>loc: River Gornja Tršnica</td>
<td></td>
<td>loc: Deliblatska peščara, Hrastovača</td>
<td></td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>21</td>
<td><em>Pelobates syriacus</em></td>
<td>22</td>
</tr>
<tr>
<td>loc: Šar planina</td>
<td></td>
<td>loc: Deliblatska peščara, Durica</td>
<td></td>
</tr>
<tr>
<td><em>Rana dalmatina</em></td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc: Vražja bara</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1 Sample size of species and locomotor modes. N, sample size; loc, locality.

Please cite this article in press as: T.G. Petrović, et al., Morphometric ratio analyses: Locomotor mode in anurans, C. R. Biologies (2017), http://dx.doi.org/10.1016/j.crvi.2017.02.004
دریافت فوری متن کامل مقاله

امکان دانلود نسخه تمام متن مقالات انگلیسی
امکان دانلود نسخه ترجمه شده مقالات
پذیرش سفارش ترجمه تخصصی
امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
امکان دانلود رایگان ۲ صفحه اول هر مقاله
امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
دانلود فوری مقاله پس از پرداخت آنلاین
پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات